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Diet, feeding behaviour and habitat-use patterns of bowhead whales in the Eastern Canadian Arctic

submitted by Sarah Fortune in partial fulfillment of the requirements for

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Abstract

Climate induced changes in prey quality and quantity may affect the foraging success of bowhead whales (*Balaena mysticetus*) in coming years. However, little is known about the diet and feeding behaviour of bowhead whales under present environmental conditions. I studied the eastern Canada-West Greenland population (ECWG) of bowhead whales to determine 1) where their important feeding areas occurred, 2) what their primary prey was, and 3) how they foraged. Through analysing long-term movement and dive data to assess behaviour (satellite-telemetry time-depth recorders), I concluded that ECWG bowhead whales feed year-round, with peak feeding occurring between July and September. Of all their feeding habitats, Cumberland Sound, Nunavut, appears to be the most important because of the dominance of large-bodied, energy rich Arctic copepods (e.g., *Calanus glacialis*). I found that the depth where the whales fed varied temporally over seasonal and diel time-scales, and matched the ontogenetic vertical movement of zooplankton (assessed using an optical plankton counter and mesh nets). Collecting fine-scale information about dive behaviour and prey distribution, I found that bowheads in Cumberland Sound used two alternate feeding strategies. They either 1) exploited shallowly aggregated prey that occasionally occurred in high concentrations, or 2) dove to a deeper layer of lower but more consistent abundance comprising larger and more energy rich organisms. Using drones to record whale behaviour, I observed bowhead whales moulting during summer and actively rubbing against large rocks. Thus, Cumberland Sound is a multi-use habitat that supports skin exfoliation and year-round feeding—and is of greatest importance during summer and fall. Overall, my findings provide new insight into the diet, seasonal movements, habitat-use and year-round foraging behaviour of bowhead whales in the eastern Canadian Arctic.

Lay Summary

Bowhead whales live in a rapidly changing environment and are likely to experience further changes in the quality and quantity of their prey. To understand how bowheads use their Arctic habitat under current environmental conditions, I determined when and where whales fed, and what they ate. Using aerial video of animals to observe behaviour, and satellite-linked transmitting tags to determine locations and diving depths, I found that bowhead whales feed year-round—especially during summer and fall. Cumberland Sound, Nunavut is a particularly important habitat for bowhead whales that contains energy rich zooplankton, as well as large boulders to rub off loose skin during the annual moult. My findings provide new insight into the diet, movements, seasonal moult, habitat-use, and year-round foraging behaviour of bowhead whales in the eastern Canadian Arctic.

Preface

I was responsible for the initial identification and design of the research program and further developed it with the help of my supervisors, committee members and collaborators. The long-term satellite telemetry and time-depth recorder data used in this study (Chapters 3 and 4) were collected before I began my PhD and were graciously provided by Dr. Steven Ferguson and Bernard LeBlanc (Fisheries and Oceans Canada). I conducted the fine-scale tagging (Chapter 2) and prey sampling data collection (Chapter 2, 3, 5) with the help of field assistants (who helped collect zooplankton and oceanographic data) and a drone operator (who collected aerial still images and video of whales). I analyzed all of data and was given information on bowhead whale sex (genetics) and length (boat-based and aerial) by project collaborators.

A version of Chapter 5 has been published. [Sarah Fortune], Koski, W., Higdon, J., Trites, A., Baumgartner, M., and Ferguson, S. (2017) Evidence of moulting and the function of “rock-nosing” behaviour in bowhead whales in the eastern Canadian Arctic. PLoS ONE 12:1-15.

My collaborators helped with visual assessments of individual animal’s skin condition, measuring the body length from aerial images, generating a location map and contributing ideas to the interpretation of my results and editing of the manuscript. I wrote the manuscript and conducted all analysis with the exception of the photogrammetry measurements.

The unmanned aerial systems data were collected under Special Flight Operation Certificate File Number 5812-11-682, ATS 16-17-00014027, RDIMS 12044419 and approved by the University of British Columbia Animal Care Committee (Animal Care Amendment A14-0064-A002). Bowhead whale behavioural data were collected under Department of Fisheries and Oceans License to Fish for Scientific Purposes S-12/13-1014-NU, S-13/14-1009-NU and S-16/17 1005-NU and Animal Use Protocol FWI-ACC-2012-034, FWI-ACC-2013-018 and FWI-ACC-2016-09. All fieldwork was similarly approved by the Pangnirtung Hunter and Trappers Organization prior to data collection.

My thesis abstract and lay summary were translated by Fisheries and Oceans Canada into Inuktitut, which is a principle Inuit language in Canada and commonly spoken in the region of my study—the Eastern Canadian Arctic.

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Chapter 1: General introduction

Bowhead whales (*Balaena mysticetus*) are an ice-associated baleen whale species (George et al. 1999, 2011) belonging to the Balaenidae family. They are the longest-lived mammal (living to ~150 years) and are the only species of large whales that lives year round in the Arctic and sub-Arctic (e.g., George et al. 2011, Ferguson et al. 2010, Citta et al. 2012, Heide-Jorgensen et al. 2012, Nielsen et al. 2015). As such, they have thick blubber that keeps them warm and provides energy during periods of reduced prey availability (e.g., Haldiman & Tarpley 1993, Rosa 2006, George et al. 2007). They are noteworthy for their relatively large heads and lack of a dorsal fin (Fig. 1.1), and are capable of breaking through ice (up to ~18 cm thick) to breath (e.g., George et al. 1989, George 2009, Armfield et al. 2011, George et al. 2016, Greene et al. 2003). It has also been suggested that they may have a hypometabolic rate (i.e., lower metabolic rate than what would be predicted for a homeotherm of their size) and that this may provide the whales greater energetic flexibility during periods of environmental fluctuation (George 2009). All of these adaptations have allowed the bowhead to live in one of the most challenging places in the world due to extreme seasonal variation in environmental conditions.

There are two distinct populations of bowheads in Canadian waters—the Bering-Chukchi-Beaufort and the eastern Canada-West Greenland population (Rugh et al. 2002). Both populations were heavily impacted by commercial whaling and are slowly recovering to pre-exploitation stock sizes (Frasier et al. 2015). Bowhead whales are a culturally important species to Inuit communities in the Eastern Canadian Arctic who conduct subsistence hunts for nutritional, artistic and traditional purposes (NWMB 2000). As zooplanktivorous filter feeders, bowheads are also considered by some to be an ecologically important species because their distribution and abundance likely mirror the conditions of low trophic levels.

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has designated the bowhead whale as a species of Special Concern. The known threats to this species include predation from killer whales (*Orcinus orca*), oil and gas exploration and climatic factors that impact ice conditions and the quality and quantity of prey (Ferguson et al. 2010, Reinhart et al. 2013; Robertson et al. 2013; Mitchell & Reeves 1982). Collectively, these



Figure 1.1: Aerial image of two eastern Canada-West Greenland bowhead whales (*Balaena mysticetus*) collected from an unmanned aerial system in Cumberland Sound, Nunavut in August 2016 as part of the fine-scale diet and feeding behaviour study in Chapter 2 and the rock-rubbing and moulting study in Chapter 5.

threats may impact the species' spatial distribution, habitat use patterns and foraging success, which may ultimately affect the survival of the species.

1.1 Rationale

As the largest marine mammal feeding on the smallest prey in the Arctic Ocean, bowhead whales are certain to face changes in habitat quality over time. Currently, bowheads are believed to be moderately vulnerable to future climate shifts that will likely alter the availability, abundance and composition of their prey (Moore & Huntington 2008). Zooplankton species may experience range expansions and contractions due to the continuous warming trend in the Arctic (Lalande et al. 2013). Furthermore, long-term trends in decreasing zooplankton body size have also been observed in the North Sea (Beaugrand 2009). Consequently, changes are expected to occur in the abundance, distribution, and diversity of zooplankton species available to bowhead whales in the future. Such potential changes to the

feeding regime of bowhead whales in the eastern Canadian Arctic make understanding how they forage under current environmental conditions essential to evaluating the sensitivity of the species to future changes in prey quality and quantity.

1.2 Habitat-use

Satellite tagging of individuals belonging to the eastern Canada-West Greenland (ECWG) population show that bowhead whales are widely distributed throughout their range, and that they make long, seasonal migrations (Fig.1.2; Reeves et al. 1983, Cosens & Innes 2000, Ferguson et al. 2010, Citta et al. 2012, Heide-Jorgensen et al. 2012, Nielsen et al. 2015). The ECWG bowheads typically migrate to areas in the high Arctic as sea ice cover decreases, and return south to Hudson Strait when ice forms (Ferguson et al. 2010). During winter, bowheads are found in Hudson Strait, northern Hudson Bay, east Baffin Island and along the ice edge of West Greenland (Reeves & Heide-Jørgensen 1996, Koski et al. 2006), while in spring, individuals reside along the west coast of Greenland, and are scattered along the eastern and southern coasts of Baffin Island in Cumberland Sound, Foxe Basin and Lancaster Sound (Ferguson et al. 2010, Pomerleau, Patterson, et al. 2011). During the summer months, bowheads are observed further north in fiords and bays in the Canadian High Arctic such as the Gulf of Boothia (Pomerleau, Patterson, et al. 2011), and are as far south as Hudson Bay and Foxe Basin (Cosens et al. 1997, Cosens & Innes 2000, Ferguson et al. 2010, Higdon & Ferguson 2010).

Until recently, it was presumed that bowhead whales foraged almost exclusively during the open water season in summer and fall (Finley 2001, Pomerleau et al. 2011, Pomerleau et al. 2011, Pomerleau et al. 2012). It was also believed that bowheads fasted during the winter (Finley et al. 1993, Lowry 1993) while residing in the unconsolidated pack ice in Hudson Strait and Davis Strait (Reeves et al. 1983, Finley 1990, Reeves & Mitchell 1990, Nielsen et al. 2015). However, stable isotope analysis of bowhead baleen indicate that animals feed year-round with lower feeding rates during winter (Matthews & Ferguson 2015, Pomerleau et al. 2018). One of the winter feeding areas appears to be in Hudson Strait based on the recorded diving rate of tagged animals (n=7) (Nielsen et al. 2015). Consequently, the foraging strategy of ECWG bowhead whales is more plastic than previously thought.

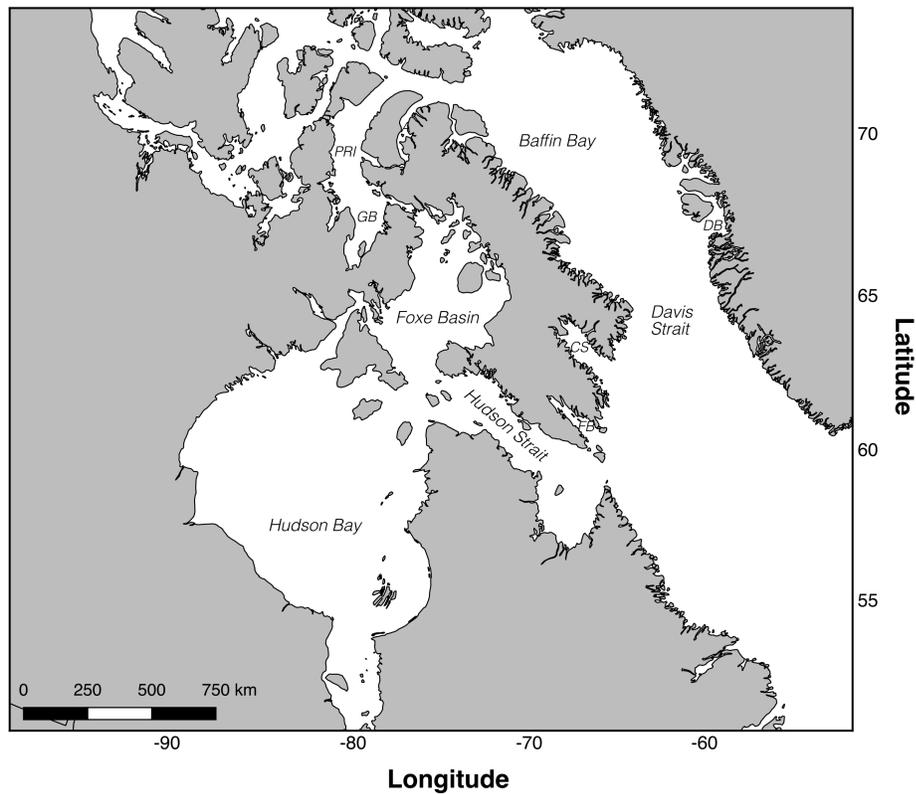


Figure 1.2: Map of the known range of eastern Canada-West Greenland bowhead whales. Habitat names were abbreviated for the Gulf of Boothia (GB), Prince Regent Inlet (PRI), Admiralty Inlet (A), Frobisher Bay (FB), Cumberland Sound (CS) and Disko Bay (DB).

1.3 Diet

Balaenid whales need to routinely locate energy-rich prey patches (e.g., North Atlantic right whales; Kenney et al. 1986, Baumgartner et al. 2017, Fortune et al. 2013). However, the distribution and abundance of zooplankton is highly spatially and temporally variable due to the influence on patch formation of currents, temperature, salinity, ice-formation and recession, phytoplankton availability, and mixing (Hays et al. 2005, Beaugrand et al. 2013). In addition, fluctuations in sea surface temperature and ice conditions (e.g., Stroeve et al. 2007, Kwok et al. 2009, Notz & Stroeve 2016) can influence the abundance, distribution and species composition of important prey such as Calanidae family copepods for zooplanktivorous species such as bowhead whales (Beaugrand et al. 2002, Beaugrand 2009, Chust et al. 2014, Grieve et al. 2017, Feng et al. 2016, 2018). As a consequence, the feeding success of bowhead whales is likely to differ throughout their range and across seasons.

The effect of climate change on the foraging success of bowhead whales is uncertain. It is possible that the continuous warming trend in the Arctic may cause large, lipid rich calanoid copepods such as *Calanus glacialis* and *hyperboreus* to be replaced with smaller species such as *C. finmarchicus* that are lower in lipid content. Changes in zooplankton assemblages may affect the foraging success of large marine predators such as bowhead whales. However, the manner in which these species will respond to environmental changes is unknown.

The species composition of zooplankton likely differs across the range of ECWG bowhead whales under current environmental conditions. In Cumberland Sound, Nunavut zooplankton assemblages are likely to be dominated by large-bodied, energy rich Arctic taxa such as *Calanus hyperboreus* and *C. glacialis* (Dunbar 1958, Aitken & Gilbert 1989, McMeans et al. 2012) due to the strong influence of the Baffin Island Current, which is predominately of Arctic Ocean origin (Tang et al. 2004, Curry et al. 2014, Bedard et al. 2015). However, in Disko Bay, the West Greenland Current is likely to result in a comparatively higher abundance of temperate taxa due to the mixture of Atlantic and Arctic water masses (Tang et al. 2004, Curry et al. 2014, Bedard et al. 2015). Interestingly, both areas are likely to contain a mixture of Arctic and temperate/subarctic taxa because the Baffin Island Current and West Greenland Current are known to mix in both regions (McMeans et al. 2012, Heide-Jørgensen et al. 2013). Thus, the quality and quantity of bowhead whale prey and their feeding ecology is likely to differ seasonally across their range due to the importance of physical oceanographic processes.

1.4 Gaps in knowledge

Diet information for the ECWG bowhead population is limited. Bowhead whale diet in the eastern Canadian Arctic has been directly studied from stomach contents and inferred from fatty acid and stable isotope analysis (Pomerleau, Ferguson, et al. 2011, Pomerleau et al. 2012, 2014, 2018, Matthews & Ferguson 2015). Stomach content analysis on a small number of individuals in the eastern Canadian Arctic found that bowheads fed on epibenthic and benthic prey (e.g., *Mysis oculata*) (Pomerleau, Ferguson, et al. 2011). Further comparisons of carbon and nitrogen isotope ratios of bowhead skin with those of potential zooplankton prey species collected across the eastern Canadian Arctic found that Lancaster Sound, the Gulf of

Boothia and Baffin Bay might be spring and early summer feeding grounds (Pomerleau et al. (2012)). Prey were predominately large Arctic copepods such as *Calanus hyperboreus*, *C. glacialis*, *Metridia longa*, and *Paraeuchaeta* spp., mysids and euphausiids (Pomerleau et al. 2012). However, prey samples were not included from Hudson Strait or Foxe Basin, which means that the species composition and importance of these feeding areas are unknown. Nor has diet information been collected outside of the spring and early-summer feeding period. Consequently, there is relatively little known about seasonal foraging habitats and prey composition in the eastern Canadian Arctic.

The most comprehensive diet and feeding behaviour studies have been done in western Greenland in Disko Bay. This portion of ECWG habitat predominately draws adult females during late winter and early spring to forage (Laidre, Heide-Jørgensen, & Nielsen 2007, Heide-Jørgensen et al. 2010, Heide-Jørgensen, Laidre, Nielsen, Hansen, & Rostad 2013). The whales appear to target predominately *Calanus finmarchicus*—a temperate/subarctic calanoid copepod—at depth in Disko Bay (Laidre et al. 2007, Heide-Jørgensen et al. 2010). Adult females tend to segregate from males and other age classes (Cosens & Blouw 2003, Heide-Jørgensen et al. 2010). Thus, the primary prey of other demographic groups of bowhead whales such as juveniles and adult males that do not come to Disko Bay is largely unknown. Similarly, what adult females consume during other times of year when they are elsewhere within their range is also poorly understood—even during summer when peak feeding is expected to occur (Pomerleau et al. 2018).

1.5 Objectives

The primary goal of my PhD research was to determine how bowhead whales forage under present environmental conditions in the eastern Canadian Arctic. The specific objectives of my research were to: 1) determine what is the primary prey of the adult males and juveniles (i.e., the portion of the ECWG bowhead whale population that seldom go to Western Greenland); 2) determine the feeding range of ECWG bowheads; and 3) how their feeding behaviour varies spatially (i.e., between habitats) and temporally (i.e., over seasonal and diel timescales). Answers to these research questions will facilitate future assessments of how climate driven fluctuations in the quality and quantity of prey affect the feeding success of bowhead whale populations.

1.6 Approach

To gain an understanding of the dietary needs of bowhead whales in the eastern Canadian Arctic, I conducted a fine-scale study of diet and foraging behaviour in Cumberland Sound, Nunavut (located on southeastern Baffin Island) (Chapter 2). This is an area where the sex ratio is near parity (Frasier et al. 2015) compared with Disko Bay, where it is heavily skewed towards non-lactating females (Laidre et al. 2007, Heide-Jørgensen et al. 2010) and not representative of the entire population. Furthermore, this is an area where the species composition of prey likely differs from Disko Bay because of regional differences in ocean currents and water temperature (Tang et al. 2004, Curry et al. 2014, Bedard et al. 2015). I expected feeding conditions to be better in Cumberland Sound because of the potentially greater availability of higher energy Arctic taxa (e.g., *Calanus hyperboreus* and *C. glacialis*; Falk-Petersen et al. 2009, Davies et al. 2012). I also speculated that higher prey quality in Cumberland Sound would better support bowhead whales with higher energy needs—such as juveniles and lactating females (Fortune et al. 2013) more readily than if they fed in Disko Bay.

I equipped whales with fine-scale archival tags to record their feeding behaviour and collected information about the zooplankton species composition and vertical abundance of encountered prey. I also used time-depth telemetry tags to examine spatiotemporal trends in bowhead whale horizontal and vertical movement, and to determine how feeding behaviour varied seasonally in Cumberland Sound (Chapter 3). I then fit hierarchical switching-state-space models to the horizontal movement data to predict when the animals were engaging in transiting vs. area restricted movement behaviour (locations associated with low swimming speeds and high turning angles that are likely to reflect predators searching for and/or consuming prey). Next, I examined how feeding behaviour (i.e., dive depth, shape and duration) changed by day, month, year, and throughout the day and night. I also collected zooplankton samples near bowhead whales during summer to determine the species composition and biomass available to feeding animals. This research helps improve understanding of the overall feeding characteristics of the species and the seasonal importance of Cumberland Sound to bowhead whales.

To determine what areas bowhead whales occupied for feeding purposes and how foraging activities varied seasonally, I examined long-term movement data (horizontal and

vertical) collected using time-depth telemetry tags (Chapter 4). I fit hierarchical switching-state-space models to the horizontal movement data and compared the percentage of locations associated with transiting vs area-restricted movement behaviour to identify probable foraging habitats. I also quantified the proportion of time individuals allocated to feeding type dives per habitat across seasons to: 1) evaluate the relative importance of each area to the feeding regime of the population; 2) determine when peak foraging occurs temporally; and 3) test a previous hypothesis that bowhead whale feeding occurs year-round.

Over the course of my fieldwork in Cumberland Sound, I observed some bowhead whales displaying unusual behaviours in shallow, coastal waters that were inconsistent with foraging. It suggested that bowhead whales were doing more in Cumberland Sound than just feeding as initially thought. To determine the biological significance of these unusual behaviours and better understand the utility of this area to ECWG bowhead whales, I undertook an unmanned aerial systems study to test whether bowheads were undergoing a seasonal moult and engaging in rock-rubbing behaviours to expedite the process while in the warm, coastal waters of Cumberland Sound (Chapter 5). I also collected prey samples in the shallow waters to confirm that these animals were not engaging in feeding activities while occupying the shallow bays.

My thesis is comprised of four data chapters that examine the diet, feeding behaviour and habitat-use patterns of bowhead whales over various spatio-temporal scales in the eastern Canadian Arctic. I begin by determining the quality and quantity of bowhead whale food and their feeding behaviour in Cumberland Sound during summer (Chapter 2). I then use diving behaviour data collected from time-depth satellite telemetry tags to identify and relate seasonal and diel feeding patterns with what is known about the ontogenetic vertical distribution of zooplankton (Chapter 3). Next, I identify key foraging habitats throughout the range of the eastern Canada-West Greenland bowhead whale population using long-term time-depth telemetry data and state-space movement models (Chapter 4). Finally, I present the findings of an unmanned aerial system (UAS) study to evaluate unusual bowhead whale behaviours in Cumberland Sound that were inconsistent with feeding activities (Chapter 5). Collectively, my thesis research contributes to identifying the current environmental and behavioural mechanisms that support the population recovery of ECWG bowhead whales.

Chapter 2: Bowhead whales maximize their feeding opportunities by employing a flexible foraging strategy in Cumberland Sound, Nunavut

2.1 Summary

As zooplanktivorous predators, bowhead whales (*Balaena mysticetus*) must routinely locate prey patches of sufficient energetic densities to meet their metabolic needs. However, little is known about eastern Canada-West Greenland bowhead whale foraging behaviour and the quality and quantity of their prey in Canadian waters. I used a new approach to study bowhead feeding ecology that included: 1) multi-scale biologging, 2) an unmanned aerial system (i.e., drone), and 3) vertical prey collection at discrete depths using an optical plankton counter (OPC) and net collections for species identification and enumeration. Tag attachments for 17 whales ranged from 0.8 to 15.6 hours for fine-scale time depth recorders (TDRs), and for several days to weeks for long-term SPLASH tags. Analysis of drone-shot video showed that the whales did not feed at the surface during daytime (0-20 m), while the TDR data indicated that they made two types of probable foraging dives: long deep Square-shaped dives (80% of dives; $260.42 \text{ m} \pm 35.83 \text{ SD}$) and short shallow Square-shaped dives (16%; $22.48 \text{ m} \pm 4.51 \text{ SD}$). Vertical OPC prey samples from 72 casts consistently revealed two layers of prey and the particle size observations suggested that they were comprised almost exclusively of calanoid copepods (dominated by lipid-rich Arctic species—*Calanus glacialis* and *C. hyperboreus*) at depths that corresponded to bowhead whale dive depths. The deep layer consistently contained fewer, but larger, particles (10% greater biomass) than the shallow layer. Higher and more predictable zooplankton biomass at depth may explain why the whales conducted proportionally more deep feeding dives. Bowheads may offset the increased energy costs of prolonged deep foraging dives by opportunistically exploiting shallow prey layers when they occur in high-abundances. Combining drones with TDRs and prey sampling showed a more complex feeding ecology than previously understood, and provides a means to evaluate the energetic balance of individuals under current environmental conditions.

2.2 Introduction

Bowhead whales (*Balaena mysticetus*) feed on patchily distributed prey such as amphipods, copepods, cirripedes, gastropods, euphausiids and mysids in the eastern Arctic

(Laidre et al. 2007, Pomerleau, Ferguson, et al. 2011, Pomerleau et al. 2012). Like other large, zooplanktivorous predators, they must consistently locate energy-rich prey patches (e.g., North Atlantic right whales; Kenney et al. 1986, Baumgartner et al. 2017, Fortune et al. 2013), which are in turn controlled by temperature, salinity, ice-formation and recession, phytoplankton availability, and mixing (Hays et al. 2005, Beaugrand et al. 2013). However, the predictability with which important prey such as calanoid copepods occur is likely to change in the North Atlantic and Arctic Ocean (Beaugrand et al. 2002, 2013, Kjellerup et al. 2012, Chust et al. 2014, Feng et al. 2016, 2018, Grieve et al. 2017, Kvile et al. 2018) due to rapid changes in sea surface temperature and ice conditions (e.g., Stroeve et al. 2007, Kwok et al. 2009, Notz & Stroeve 2016).

Understanding the implications of future shifts in zooplankton species composition, abundance and distribution on bowhead whales requires knowing what they eat under present environmental conditions. However, relatively little is known about the primary prey of bowhead whales throughout their range—particularly in Canadian waters. What is known about bowhead diet in the Eastern Canadian Arctic has come qualitatively from stomach content analysis from a few harvested animals (Pomerleau, Ferguson, et al. 2011) or has been inferred from stable-isotope (Pomerleau, Winkler, et al. 2011, Pomerleau et al. 2012) and amino acid (Pomerleau et al. 2014) analysis. Eastern Canada-West Greenland (ECWG) bowhead whale diet has only been well studied in the eastern limit of their range in Disko Bay (western Greenland).

Disko Bay is predominately occupied by adult female ECWG bowhead whales during late winter and early spring for feeding (Laidre, Heide-Jørgensen, & Nielsen 2007, Heide-Jørgensen et al. 2010, Heide-Jørgensen, Laidre, Nielsen, Hansen, & Rostad 2013). While in Disko Bay, bowheads are known to feed at depth primarily on a temperate/subarctic calanoid copepod—*Calanus finmarchicus* (Laidre et al. 2007, Heide-Jørgensen et al. 2010). This is consistent with expectations of zooplankton species composition in Disko Bay based on the prevalence of the Western Greenland Current that contains both North Atlantic and Arctic water masses (Heide-Jørgensen et al. 2013, Curry et al. 2014). However, it is not known what prey juvenile and adult male whales consume because they are seldom seen in Disko Bay. It is also unknown what prey the Disko Bay females consume at other times of year (such as summer when peak feeding is thought to occur (Pomerleau et al. 2018)) when they are elsewhere within their ECWG range.

Cumberland Sound, Nunavut is another important area for ECWG bowhead whales. The abundance of whales in Cumberland Sound was higher than any other region in the eastern Canadian Arctic (~30-40% of total population based on genetic and aerial survey estimates, respectively; Doniol-Valcroze et al. 2015, Frasier et al. 2015) based on analysis of aerial survey data collected in 2013 and skin biopsies obtained between 1995 and 2013. Unlike Disko Bay, roughly equal numbers of male and female whales use Cumberland Sound (Frasier et al. 2015), and both juvenile and adult animals occupy this habitat (Heide-Jørgensen et al. 2010). Zooplankton species composition is also likely different than Disko Bay, whereby zooplankton assemblages are expected to be dominated by large-bodied, energy rich Arctic taxa such as *Calanus hyperboreus* and *C. glacialis* (Dunbar 1958, Aitken & Gilbert 1989, McMeans et al. 2012) due to regional differences in ocean currents and water temperatures (Tang et al. 2004, Curry et al. 2014, Bedard et al. 2015). As a consequence, the feeding conditions may be improved in Cumberland Sound because of the availability of higher energy prey (e.g., *Calanus hyperboreus* and *C. glacialis*; Falk-Petersen et al. 2009, Davies et al. 2012). Such an energy difference between feeding habitats may mean that Cumberland Sound is better able to support the comparatively high energy needs of juvenile and lactating females (Fortune et al. 2013) more readily than if they fed in Disko Bay.

The goal of my study was to determine the diet and feeding behaviour of bowhead whales during summertime and evaluate the importance of Cumberland Sound as a foraging ground by conducting a predator-prey study. I did so by observing 1) fine-scale bowhead whale dive behaviour (time-depth recorders; hours); 2) long-term vertical and horizontal movement (time-depth recorder telemetry tags; days); and 3) surface behaviour (unmanned aerial system). I then correlated bowhead behavioural data with information about the species composition, abundance and vertical distribution of their prey by determining 4) vertical particle size and abundance (optical plankton counter), 5) species composition (integrated water column net tows) and 6) a detailed snapshot of bowhead whale diet (stomach contents). Combined, these data are important for understanding how the ECWG population forages under present oceanographic conditions in the eastern Canadian Arctic.

2.3 Methods

2.3.1 Fine-scale bowhead whale dive data collection

Detailed foraging behaviour was studied using a modified version of the short-term dermal tag (Baumgartner et al. 2015) during August 2016. The dermal tag was equipped with a Lotek LAT1500 time-depth recorder (i.e., pressure sensor). A 36-kHz Vemco acoustic transmitter was used to assist in tracking the tagged whale during focal follows. The dermal tag was adapted to include a SPOT6 satellite tag instead of a radio transmitter as previously used (Baumgartner et al. 2015) to facilitate tag retrieval for whales that were not actively tracked (i.e., ‘released’; see below) after tagging. The tag was deployed using a compressed air launcher and attached using a 7.5 cm long needle (~0.6 cm in diameter) that was steam sterilized in an autoclave prior to use. Previous studies (Baumgartner et al. 2015) examining the foraging behaviour of bowheads in the western US Arctic found dermal tags to be more successful than commonly used suction-cup tags due to the topography of bowhead skin. I similarly opted for a dermal attachment because animals undergo a moult during the summer in Cumberland Sound, precluding the use of suction cup attachments (Fortune et al. 2017).

The tagging fieldwork for this study involved first observing the behaviour of individual animals and then selecting candidate whales for tagging purposes. Candidates were selected if they were not part of a mother-calf pair and were preferably 8 m or greater. Body length was visually estimated in meters using a small unmanned aerial system (UAS DJI Phantom Professional 3). Candidate whales also needed to exhibit behaviours indicative of foraging (e.g., high-fluking and long dives where bottom depth was ≥ 100 m) and this was assessed prior to tagging using boat-based and UAS observations. The position of the whale and flight altitude were automatically recorded while conducting focal follows with the UAS that was equipped with a global positioning system and altimeter. The average altitude of the UAS was 12.92 m (± 5.43 SD) and the maximum distance was 1000 m (line-of-sight). The UAS was hand-deployed and hand-retrieved from the vessel and flight times lasted between 8 and 12 min.

Once a candidate whale was selected, the individual was approached by a 6-m aluminum vessel for tagging. For the majority of tagging events, the UAS was deployed to record video and images for photogrammetry and photo-identification. Close approaches to whales were conducted in a controlled manner at safe speeds to avoid disturbing the whale and

to ensure that the approach could be terminated at any time. Up to 3 attempts were made to tag an individual that exhibited no or mild reaction to close approaches. Mild reactions included alterations in swim direction, speed and increased dive durations. Tagging attempts were discontinued if the whales continuously avoided the vessel during close approaches. Tagging attempts on animals that exhibited moderate to strong reactions to close approaches (e.g., forceful roll, tail slash, tail lob, breach) were also abandoned. Time restrictions were also placed on tagging attempts whereby continuous pursuits were limited to 60 minutes and non-continuous pursuits were limited to 80 minutes (based on previous DFO Animal Care permit applications). Continuous pursuits were defined as instances where the tagging vessel maintained an approach over consecutive or non-consecutive surfacings of ≤ 10 minutes. Conversely, a non-continuous pursuit represented instances where the target animal surfaced twice (≥ 10 minutes) 100 m or more away from the tagging vessel.

Once the dermal tag was successfully deployed using the compressed air launcher, the tagged animal was photographed and/or videoed and subsequently ‘tracked’ or ‘released’. Photographs were taken of the tag site if possible and of the unique marks (e.g., scars, pigmentation, killer whale (*Orcinus orca*) rake marks; Reinhart et al. 2013) on the whale’s body to avoid retagging the animal. ‘Tracked’ animals were followed using visual observations while at the surface (boat-based and UAS observations). While submerged, the bearing and real-time-depth of the tagged whale was monitored by detecting the acoustic pings of the Vemco transmitter using a directional hydrophone and acoustic receiver. The tracking vessel made every effort to stay far enough away (e.g., 500 m) from the tagged whale to avoid altering the animal’s behaviour but remained within range of the acoustic transmitter (1 km) at all times. While tracking the animal, GPS locations were continuously logged using a handheld global positioning system (GPS) receiver. These data were collected to reconstruct the spatial movements of the tagged animal and to coordinate prey sampling with the oceanographic sampling vessel. On several occasions, the tag placement was high enough on the whale’s back to permit satellite transmission and thus providing Argos locations during surfacings. The real-time dive depths of the tagged whale were recorded and relayed to the zooplankton sampling vessel. Vertical profiles with the OPC and CTD were conducted to the whale’s maximum dive depth using the oceanographic cage.

A sub-set of animals were not tracked and instead were immediately released upon tagging to reduce the post-tagging recovery time and mitigate any potential changes in

behaviour caused by the presence of the focal follow vessel. For animals released upon tagging, oceanographic data were collected in adjacent waters and thus the prey data were not spatially co-located with the tagged whale.

2.3.2 Longer-term bowhead horizontal and vertical movement data collection

To record horizontal and vertical movements over longer spatial scales (days to weeks) I equipped 9 whales with long-term satellite telemetry tags outfitted with time-depth recorders (Wildlife Computers SPLASH MK10). The SPLASH tag provided information on date, time, location, and summary dive behaviour (e.g., depth, duration, shape). The platform transmitter terminals (Ptt) were programmed to transmit up to 400 times a day every second hour during summer, and less frequently during winter (e.g., 100 times every second day) to maximize tag longevity.

Three males and 6 females were tagged in Cumberland Sound between 20 and 28 August 2016. However, one tag failed to transmit during August (Ptt 148499). Juvenile, sub-adult and adult animals were selected for tagging (excluding lactating females), which meant excluding animals < 9 m long that were likely calves and those in mother-calf pairs. The SPLASH tag was attached using a ~20 cm stainless steel anchor that penetrated the animals' skin and blubber. The tag was deployed with an 8-m fiberglass pole, allowing for a simultaneous collection of bowhead tissue from a 4-cm biopsy tip incorporated into the end of the pole, which was used to determine the sex of the tagged animal. Prior to attachment, the anchor and biopsy tip were sterilized with a 1:10 bleach/water solution. The tags were deployed from a wooden canoe freighter and attached dorsally (behind the blow holes).

2.3.3 Horizontal movement analysis

The Square Root Unscented Kalman Filter (SRUKF) was used to re-process the raw Argos data by Service Argos. This SRUKF algorithm uses a correlated random walk model to predict future positions based on an animals previous location and estimated error (Silva et al. 2014, Lowther et al. 2015). The Kalman Filter is preferable over the Least-Squares algorithm because it generally increases the number of positions while improving the accuracy of lower quality Argos locations (i.e., 0, A and B) that are common with large whale studies (Silva et al. 2014, Lowther et al. 2015). I then ran the SRUKF filtered data through a speed filter using

the `vmask` function in the `argosfilter` package in R (R Development Core Team 2016). This function identifies improbable positions based on a maximum swimming speed. Argos locations that resulted from an animal swimming above $>2 \text{ m s}^{-1}$ were removed from my analysis.

To estimate individual animal movement, determine the behavioural state associated with the Argos position (i.e., feeding or transiting) and quantify location error, I fit a hierarchical switching-state-space Model (HSSSM) (Jonsen et al. 2005, 2013) using the `bsam` package in R (Jonsen et al. 2013, R Development Core Team 2016). I fitted a correlated random walk model (CRW) that switched between two behavioural states that reflected area restricted movements (ARM) and traveling (Jonsen et al. 2005), whereby the associated behavioural states differ in mean turn angle and swimming speed (Jonsen et al. 2005). For example, ARM (which is thought to reflect predators searching for and consuming prey; Tinbergen et al. 1967, Kareiva & Odell 1987, Haskell 1997, Fauchald & Tveraa 2003, Higdon & Ferguson 2010, Anderwald et al. 2012) reflected low swimming speeds and high turning angles, while traveling consisted of faster, more linear movements (such as those associated with seasonal migrations). I fit the HSSSM to each data set ($n = 9$ animals) containing individual specific location data with 40,000 Monte Carlo Markov Chain (MCMC) iterations. I dropped the first 30,000 (i.e., burn-in) and retained every 10th sample from the remaining 10,000, resulting in a total of 1,000 samples per chain ($n = 2$ chains).

Bowhead whale behavioural states (b) associated with HSSSM predicted locations were classified based on mean estimates from the MCMC samples, whereby $b = 1$ was assumed to represent transiting behaviour and $b = 2$ was thought to reflect ARM. I used the same thresholds as previous studies (Jonsen et al. 2007, Silva et al. 2014) such that predicted locations with mean estimates of $b > 1.75$ were assumed to indicate ARM; $b < 1.25$ reflected transient behaviour; values between $b \geq 1.25$ & $b \leq 1.75$ were unclassified. To exclude inaccurate location data from my analysis, I filtered the predicted locations from the HSSSM by removing locations that resulted from gaps exceeding 4 consecutive days based on the raw SRUKF data.

2.3.4 Vertical movement analysis

To determine where the SPLASH tagged whales were feeding in the water column, I analyzed the summary time-depth-recorder data. For each dive, I obtained measurements of dive duration, shape (V, U, Square or unknown) as well as minimum and maximum dive depth. For comparison with the fine-scale TDR data, I defined dives as vertical excursions to ≥ 10 m. Wildlife Computers classified dive shape based on three broad categories whereby: V-shaped dives represented those where ≤ 20 % of dive duration was spent at maximum depth, U-shaped dives occurred when > 20 % and ≤ 50 % of the dive duration was spent at maximum depth, and Square dives included those where > 50 % of the dive duration was spent at maximum depth. Behaviour may be inferred based on dive shape whereby previous studies for North Atlantic right whale and bowhead whales found that V-shaped dives reflected search behaviour while Square and U-shaped dives where animals increased the time they spent at maximum depth reflected feeding dives (Baumgartner & Mate 2003, Laidre, Heide-Jørgensen, & Nielsen 2007, Heide-Jørgensen, Laidre, Nielsen, Hansen, & Rostad 2013, Baumgartner et al. 2017).

I filtered the bowhead whale dive behaviour data based on the predicted HSSSM location data to differentiate dives that occurred inside Cumberland Sound with those that occurred inside Kingnait Fiord. I then merged the vertical dive data with the HSSSM location data by matching dates between the two data sets (horizontal and vertical). I assumed that animals in Kingnait Fiord did not make daily excursions to Cumberland Sound and vice versa. Consequently, all dives were assumed to occur within the same habitat where HSSSM predicted locations occurred. To compare bowhead whale dive behaviour with the vertical distribution of zooplankton I excluded bowhead whale dives that occurred after dusk because all zooplankton sampling was conducted during daylight hours. I filtered the dive data using the time of sunrise and sunset for Iqaluit based on the median sampling dates of August 26 and September 15 2016.

2.3.5 Optical Plankton Counter particle size, abundance and biomass

I used a Focal Technologies model OPC-1T optical plankton counter (OPC) to obtain a vertical profile of zooplankton abundance by particle size. The OPC consists of a tunnel through which seawater passes, with a collimated light source on one side of the tunnel and a

photodiode sensor that detects the intensity of the collimated light on the other side of the tunnel. Changes in light intensity are used to detect, size and count individual particles that pass through the tunnel (Herman 1992). The area occluded by a particle when it is detected is proportional to its size, which is quantified as the equivalent circular diameter (ECD, i.e., the diameter of a circle that has the same area as the occluded area). I mounted the instrument in the center of an aluminum protective sampling cage and it was lowered vertically through the water column at 0.75 m s^{-1} . The OPC has a lower ECD size detection limit of 0.25 mm which should accurately detect most species and life-stages of copepods (Herman 1992). The OPC was used to determine the depth where maximum zooplankton abundances occurred. I analyzed the OPC downcast data only in 4-m depth bins to calculate descriptive statistics of 1) equivalent circular diameter (mm) and 2) particle abundance (particles m^{-3}). I further excluded all OPC measurements less than 1.0 mm ECD so as to remove detritus and small copepods (e.g., *Pseudocalanus* spp). I used Ocean Data View software to visualize my OPC data and Data-Interpolating Variational Analysis (DIVA) was selected for spatial interpolation of the in situ OPC data to generate contour plots of particle abundance and mean particle size.

The physical oceanographic characteristics of Kingnait Fiord were determined by collecting co-located physical oceanographic data with each OPC deployment using a Seabird SBE19Plus conductivity, temperature, and depth (CTD) profiler. CTD data were corrected using Seabird software, and temperature and salinity plots were generated using the downcast data for each profile. For visualization purposes, I aggregated the temperature and salinity data into 1 m depth bins. To estimate the base depth of the mixed layer (i.e., the layer of uniform density near the surface where phytoplankton and feeding zooplankton may concentrate; Sverdrup 1953, Thomson & Fine 2003, Smith & Jones 2015), I derived the potential density of the mixed layer using salinity (PSU) and temperature ($^{\circ}\text{C}$) measurements from the CTD profiles using Ocean Data View. I then used the threshold difference method to determine the depth where the potential density changed by $\sim 0.01 \text{ kg m}^{-3}$ (using a range of ≥ 0.01 and $\leq 0.02 \text{ kg m}^{-3}$) relative to the ocean surface density.

To gain an understanding of how zooplankton biomass varied throughout the water column, I used the OPC particle measurements and counts to calculate biomass concentration (mg m^{-3}) by: 1) converting ECD (mm) into wet weight (mg) using:

$$W_{wet} = \frac{4}{3}\pi \left(\frac{ECD}{2}\right)^3 \rho$$

where W_{wet} is the wet weight of a particle (mg) and ρ is the particle abundance (mg m^{-3}) (Suthers et al. 2006); 2) summing W_{wet} for each particle with $ECD \geq 1.0$ mm within a specified depth range; and 3) dividing this total weight (mg) by the volume of water sampled (m^3). I assumed for this calculation that a sphere accurately represents particle volume and that each particle has a density of 1 mg mm^{-3} (Suthers et al. 2006).

2.3.6 Zooplankton collection net sampling

I determined species composition from net collected zooplankton samples taken during August 2016 in two fiords in Cumberland Sound, Nunavut—one where bowhead whales are seldom seen (Pangnirtung Fiord; $66^{\circ}09'22.0''\text{N}$ and $65^{\circ}43'25.3''\text{W}$) and another where bowheads are routinely observed (Kingnait Fiord; $65^{\circ}57'07.1''\text{N}$ and $65^{\circ}19'46.5''\text{W}$) (Table 2.1). Zooplankton samples were collected throughout the water column for enumeration and species identification using a standard 333-micrometer (μm) mesh conical net (60 cm in diameter). Oblique samples were collected by towing the weighted 60-cm diameter net up to the surface at an oblique angle from various depths, and vertical samples were obtained using the same net by lowering it to ~ 5 m above the sea floor and then hauling it straight back to the surface using an auto-hauler. The mouth of the nets were instrumented with a Vemco acoustic transmitter (V16Ps 51kHz or 84 kHz) capable of sampling down to 340 m and 680 m respectively. These transmitters were used with an omni-directional hydrophone and Vemco acoustic receiver to determine the net sampling depth in real-time.

Once the zooplankton nets were brought onboard the ship, the volume of filtered water was recorded using a flow meter and all nets were sprayed down with seawater. Sampled organisms were concentrated into the attached cod end bucket and subsequently filtered through a 333- μm mesh sieve and then transferred to a 250 mL sample jar. Quantitative field samples were kept in seawater and fixed with 5% buffered formalin onboard the vessel for preservation.

Zooplankton species identification and enumeration was conducted in the laboratory. Each net-collected sample was filtered through a 333- μm mesh sieve, rinsed and transferred

to a beaker, and diluted with water. The sample volume was recorded and a homogenous aliquot (i.e., sub-sample of known volume) was obtained using a Hensen-stemple pipette. For dense samples, a Folsom plankton splitter was used for sub-sampling purposes. The total number of times each sample was split was dependent upon the total number of sample organisms. Each aliquot contained a minimum of 200 calanoid copepods and each organism was identified to the lowest possible taxon (e.g., species and genus for calanoid copepods) and life-stage for *Calanus* spp. and *Pseudocalanus* spp. using a dissecting microscope.

Due to the morphological similarity between *Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus* (Grainger 1961, Jaschnov 1970), prosome lengths were measured (e.g., Unstad & Tande 1991, Hirche et al. 1994) for all *Calanus* spp. using a dissecting microscope, stage micrometer and ocular micrometer. All organisms were measured from the same orientation (right lateral side down) to reduce measurement variability. *Calanus* species were assigned based on species-specific prosome size ranges reported by Madsen et al. (2001), however, there is likely some overlap in prosome length between species (Parent et al. 2011), which is likely to introduce error into the identification of early life-stages. Prosome measurements were not made for *Pseudocalanus* spp. and instead mean prosome lengths for early and late staged organisms were determined from values reported in the literature.

Zooplankton biomass was calculated as weight (mg C) for *Calanus* spp. and *Pseudocalanus* spp. using a previously established allometric length-weight relationship:

$$W_{dry} = aL^b$$

where W_{dry} is weight (mg C), L is prosome length (μm) and $a=0.0048$ and $b=3.5687$ for *Calanus finmarchicus* and *C. glacialis* (Madsen et al. 2001), $a=0.0014$ and $b=3.3899$ for *C. hyperboreus* (Hirche & Mumm 1992) and $a=6.12\text{E-}11$ and $b=2.7302$ for *Pseudocalanus* spp. (Breteler et al. 1982). I used my measured prosome lengths for all life-stages of *Calanus* spp. to calculate biomass. To estimate *Pseudocalanus* spp. biomass, I used average prosome lengths for early (CI-CIV: 596.8 μm) and late (C5-Adult; 1009.9 μm) (Liu & Hopcroft 2008) from the literature and the number of enumerated *Pseudocalanus* spp. copepods per station in my samples.

2.3.7 Bowhead stomach contents

Bowhead whale diet composition was directly determined from the stomach contents of a sub-adult female bowhead whale harvested in Kingnait Fiord (Cumberland Sound, Nunavut) on 14 September 2016. In collaboration with local hunters, I obtained a 500 mL sub-sample of the stomach contents to qualitatively identify prey species. My sample collection was approved by the Pangnirtung Hunter and Trappers Association, and local subsistence hunters facilitated the collection in collaboration with Fisheries and Oceans Canada. Due to the size of the stomach, potentially large volume of prey and logistical challenges associated with collecting stomach contents from large whales, I was not able to quantitatively determine the volume of consumed prey. All prey samples were preserved in 5% buffered formalin for subsequent species identification using a dissecting microscope. The same methods employed for net collected samples were used for species identification of stomach collected organisms.

2.4 Results

2.4.1 Fine-scale bowhead dive behaviour

The 6 whales equipped with fine-scale TDR tags had attachment times ranging from 0.83 to 15.6 hrs (Table 3.1). I conducted focal follows on three animals for 0.83 to 9.23 hrs and found that the animals remained close to shore for the duration of the focal follows and displayed behaviours that were inconsistent with feeding, such as conducting shallow, non-fluking dives and occasionally engaging in rock-rubbing behaviour (Fortune et al. 2017). In an effort to minimize any potential effect of the vessel on the behaviour of the tagged animal, I increased my distance from the whale from ~500 m to ~800 m and used the UAS to aerially follow the animal and record behaviour in real-time. The aerial footage failed to record any surface feeding activities, which was consistent with my boat-based observations. Occasionally, I observed individuals with slightly agape mouths in shallow rock-rubbing habitat. However, prior prey sampling in these areas showed extremely low zooplankton abundances suggesting that the whales were more likely engaged in thermoregulation activities than feeding (Fortune et al. 2017). I suspected that the behaviour of the focal followed animals was influenced by the presence of my vessel and excluded their dive data from my analysis.

Three animals were ‘released’ after tagging (i.e., not followed immediately following tagging) and I obtained 8.7-15.6 hrs of diving behavioural data including dives that occurred

during day and night (Fig. 2.1). Unlike the dive data for the focal followed animals, I found that the released whales dove to various depths. The deepest and longest dives were between 115.1 and 305.0 m ($220.6 \text{ m} \pm 63.2 \text{ SD}$) and lasted for 7.6 to 27.6 mins ($14.2 \text{ mins} \pm 6.16 \text{ SD}$). Overall, I found that the whales made 170 dives below 10 m and that the majority were Square-shaped (46%) followed by U (27%) and V (27%). The Square-shaped dives were generally shallow but variable, occurring between 10.1 and 249.6 m ($25.7 \text{ m} \pm 28.1 \text{ SD}$). In comparison, U ($70.7 \text{ m} \pm 88.5 \text{ SD}$) and V ($60.1 \text{ m} \pm 65.9 \text{ SD}$) shaped dives were deeper occurring between 10.05-305.0 m and 10.50-284.1 m.

Table 2.1: Summary information for the 6 bowhead whales that were tagged with the fine-scale TDR in Kingnait Fiord during August 2016. Three of these animals were released upon tagging (TDRs 2, 5 and 6) and their dive data was subsequently analyzed to determine where they were likely feeding in the water column. The date is when the animal was tagged in Kingnait Fiord and the hours is the amount of time represented the amount of hours of behavioural data collection.

TDR	Date	Time (GMT)	Hours	Longitude	Latitude
1	2016-08-15	17:28	0.827	-65.614	66.192
2	2016-08-26	16:29	15.62	-65.500	66.124
3	2016-08-27	18:08	3.196	-65.603	66.074
4	2016-08-28	16:02	9.233	-65.492	66.147
5	2016-08-29	17:20	12.654	-65.210	66.181
6	2016-08-29	19:58	6.365	-65.375	66.181

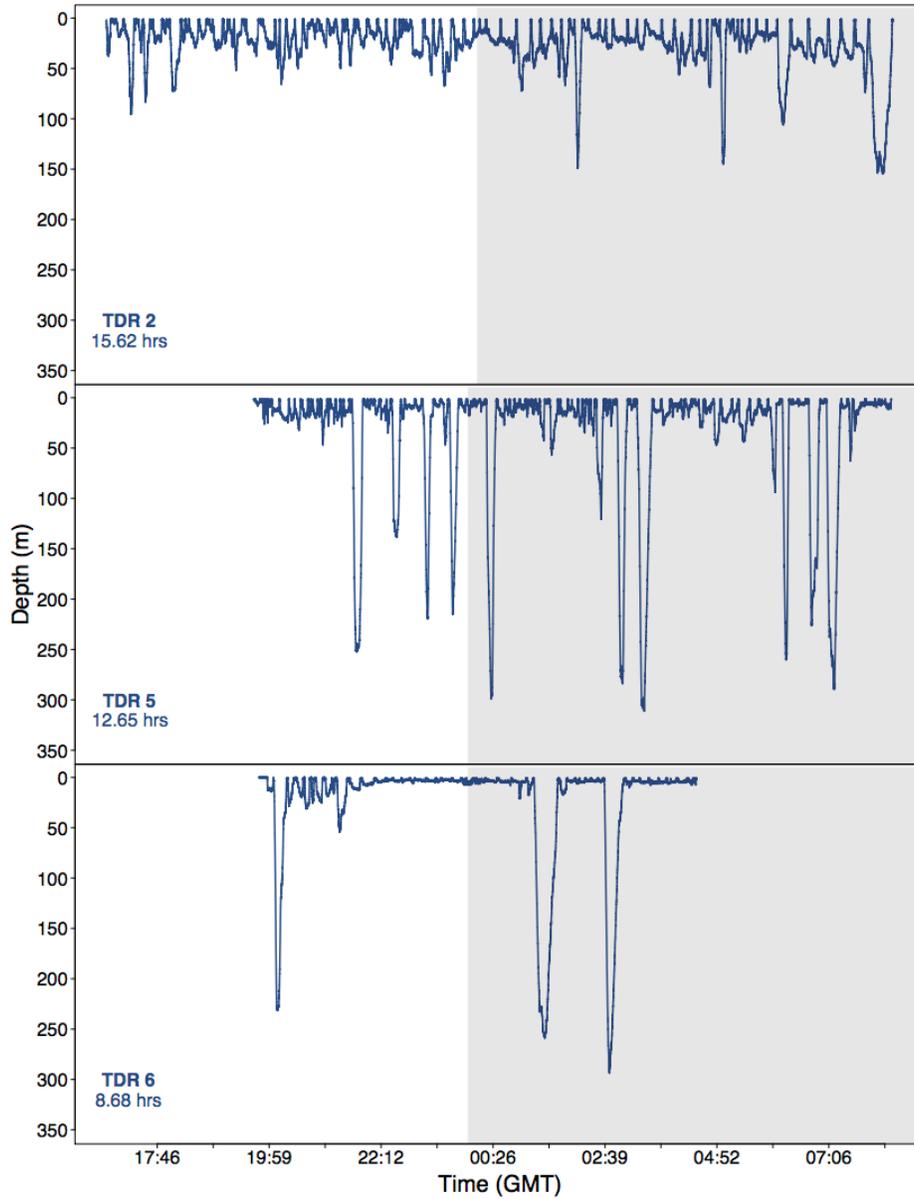


Figure 2.1: Time-depth recorder data (1 Hz sampling frequency) for 3 bowhead whales showing day and night time behaviour (between sunset and sunrise – shaded grey). TDR 2 was tagged on 26 August and TDR 5 and TDR 6 were tagged on 29 August.

Table 2.2: Summary data for bowhead whale equipped with longer-term and coarser scale satellite telemetry time-depth recorder tags (SPLASH tags) during August 2016. Five animals resided exclusively in Kingnait Fiord (Ptt 148499, 148502, 148504, 148505, 126499). The Date is when the individual was tagged and Aug and Sept days is the number of days of telemetry and dive data during each month. Length was estimated based on visual observation of animals from the vessel (e.g., tip of snout to fluke notch). Sex was determined for this animals using genetic analysis of the biopsy samples obtained with each tag deployment. The Longitude and latitude are provided for where the animal was tagged.

Ptt	Date	Time (GMT)	Aug (days)	Sept (days)	Longitude	Latitude	Length (m)	Sex
148499	2016-08-20	16:55	0	3	-65.487	65.771	9	M
148500	2016-08-20	17:19	11	13	-65.497	65.742	9	F
148502	2016-08-23	21:12	8	30	-65.299	65.921	9	M
148503	2016-08-23	22:41	4	22	-65.316	65.944	10	F
148504	2016-08-23	23:06	8	19	-65.275	65.926	8.5-9	F
148505	2016-08-26	18:14	2	15	-65.260	65.930	10	M
148506	2016-08-27	15:28	4	14	-65.265	65.929	10	F
126499	2016-08-28	14:45	3	30	-65.286	65.923	11	F
126500	2016-08-28	14:45	2	30	-65.286	65.923	10	F

2.4.2 Telemetry

Eleven animals were equipped with Wildlife Computers SPLASH tags in Cumberland Sound between 20 August and 28 August 2016, but only obtained usable data from 9 tags (Table 2.2). The sex ratio of tagged whales with usable data was 3 males and 6 females (5 males and 6 females tagged in total), with body sizes ranging from 9 to 11 m based on visual estimates of body length (distance between tip of whale’s snout and fluke notch) from the vessel. These estimates suggested that the tagged animals were young juveniles (1-4 years) and sexually immature sub-adults (>4 years and <25 years) (Koski et al. 1993, George, Follmann, et al. 2004, Higdon & Ferguson 2010).

2.4.3 Horizontal movement

I constrained my analysis to telemetry data collected in Cumberland Sound during August and September 2016 to permit comparison with collected prey data. Two locations were predicted per day for each animal using the HSSSM resulting in 454 locations in total. The tags transmitted for 26 ± 10 SD days in Cumberland Sound on average with a total of 50 ± 22 SD predicted locations on average during August and September (range: 7-76 days). During August, I obtained 6 ± 3 SD days (range: 3-12 days) of movement data and 20 ± 9 SD

days for September on average (range: 4-30 days). Five animals spent all of their time during August and September in Kingnait Fiord based on the HSSSM (n=251 Argos locations; n=5 animals). This represents 55% of all predicted locations (n=454 Argos locations; n=9 animals). Three animals spent most of their time in Kingnait Fiord and another left Kingnait Fiord shortly after being tagged and resided in adjacent fiords. From an analysis of the HSSSM behavioural stages (*b*), I found that 0% of the predicted locations were associated with transiting while 98% were consistent with ARM and 2% were of an unknown behaviour. The dominance of ARM behaviour suggests that the tagged bowheads engaged in feeding-related activities daily (Fig. 2.2).

2.4.4 Vertical movement

The 9 tagged whales dove a total of 5,762 times (using >10 m dive definition) over 41 days in Cumberland Sound during the day and night in August and September 2016 (after excluding the data from the day the animal was tagged). The whales conducted predominately 77.1% Square (n = 4,613) and 18.9% U-shaped dives (n = 1,133), whereas V-shaped and unclassified-shaped dives represented only 3.93% (n = 235) and 0% of the total, respectively (Table 2.1). I inspected the summary dive statistics (e.g., range, mean \pm SD) for unusually high values that would exceed the physiological diving limits of the species and found no biologically improbable dives that exceeded 75 minutes in duration or 700 meters in depth.

I found that 56.4% (total dives n=1,477 day and night) and 51.0 % (n=4,504 day and night) of all classified dives occurred during the day in August and September, respectively (Table 2.3). The tagged whales conducted proportionally more Square-shaped dives than U- or V-shaped dives during August (66.1%; total classified daytime dives n=976) and September (83.2%; n=2,297). Furthermore, I found that Square shaped dives were consistently deeper and longer in duration than any other dive shape (Figs 2.3 & 2.4; Table 3.3). The whales dove to comparable mean depths during September (215.5 m \pm 38.76 SD) and August (214.5 m \pm 28.73 SD), but stayed longer at depth during September (September 21.3 mins \pm 2.61 SD; August 18.4 \pm 1.52 SD) based on weighted averages (Fig. 2.4). However, during August, 16.39% (total Square dives n=537) of all Square-shaped dives occurred in the top 50 m of the water column at 22.48 m \pm 4.51 SD and 79.89% (n=429) occurred below 100 m at an average of 260.42 m \pm 35.83 SD suggesting that the whales alternate between shallow and deep feeding

Table 2.3: The total number of dives (n dives) and SPLASH tagged animals (n animals) during daylight hours (between sunrise and sunset) by shape and month in Cumberland Sound and Kingnait Fiord. During August two animals (Ptt 126500 and 148506) conducted only a single V-shaped dive in Cumberland Sound (CS). Similarly, Ptt 148505 conducted only one U and V-shaped dive during September in Kingnait Fiord (KF). Depth and duration reflect the weighted mean maximum dive depth (m) and associated minimum dive duration (mins).

Month	Location	Shape	Depth (m)	Duration (mins)	n dives	n animals
August	CS	Square	214.52 ± 28.74	18.36 ± 1.52	537	8
August	CS	U	72.41 ± 29.03	9.01 ± 2.20	255	7
August	CS	V	69.20 ± 42.40	11.10 ± 3.00	41	7
September	CS	Square	215.54 ± 38.77	21.29 ± 2.61	1910	9
September	CS	U	84.37 ± 18.66	10.13 ± 1.68	322	8
September	CS	V	120.16 ± 60.85	14.13 ± 3.60	65	8
August	KF	Square	207.73 ± 13.44	18.08 ± 1.66	241	4
August	KF	U	76.17 ± 25.32	9.65 ± 1.63	176	3
August	KF	V	76.67 ± 38.81	11.66 ± 2.74	29	3
September	KF	Square	240.01 ± 19.69	22.89 ± 1.94	1125	5
September	KF	U	94.68 ± 18.76	10.48 ± 1.68	172	4
September	KF	V	169.46 ± 58.94	16.69 ± 2.87	28	4

dives. Furthermore, U-shaped dives consistently occurred at a similarly shallow depth during August (72.41 ± 29.03 SD) and September (84.37 ± 18.66 SD) based on a weighted average (Table 2.3).

I found that 4 out of the 9 tagged animals spent their time (2-8 days) exclusively in Kingnait Fiord during August and 5 animals resided exclusively (3-30 days) in Kingnait Fiord during September based on the predicted HSSSM locations. While in Kingnait Fiord, the whales conducted greater numbers of deeper dives (63.0% ≥ 100 m; n=202 dives) than shallow dives (37.5% ≤ 50 m; n=121). For example, individuals alternated between deep (≥ 100 m) Square (267.4 m ± 29.15 SD; n=170 dives) and U-shaped (242.7 m ± 25.82 SD; n=32 dives) dives and shallow (≤ 50 m) Square and U-shaped dives that occurred at 24.67 m ± 2.06 SD (n=32 dives) and 28.9 m ± 3.22 SD (n=89 dives), respectively, on average (Fig. 2.4).

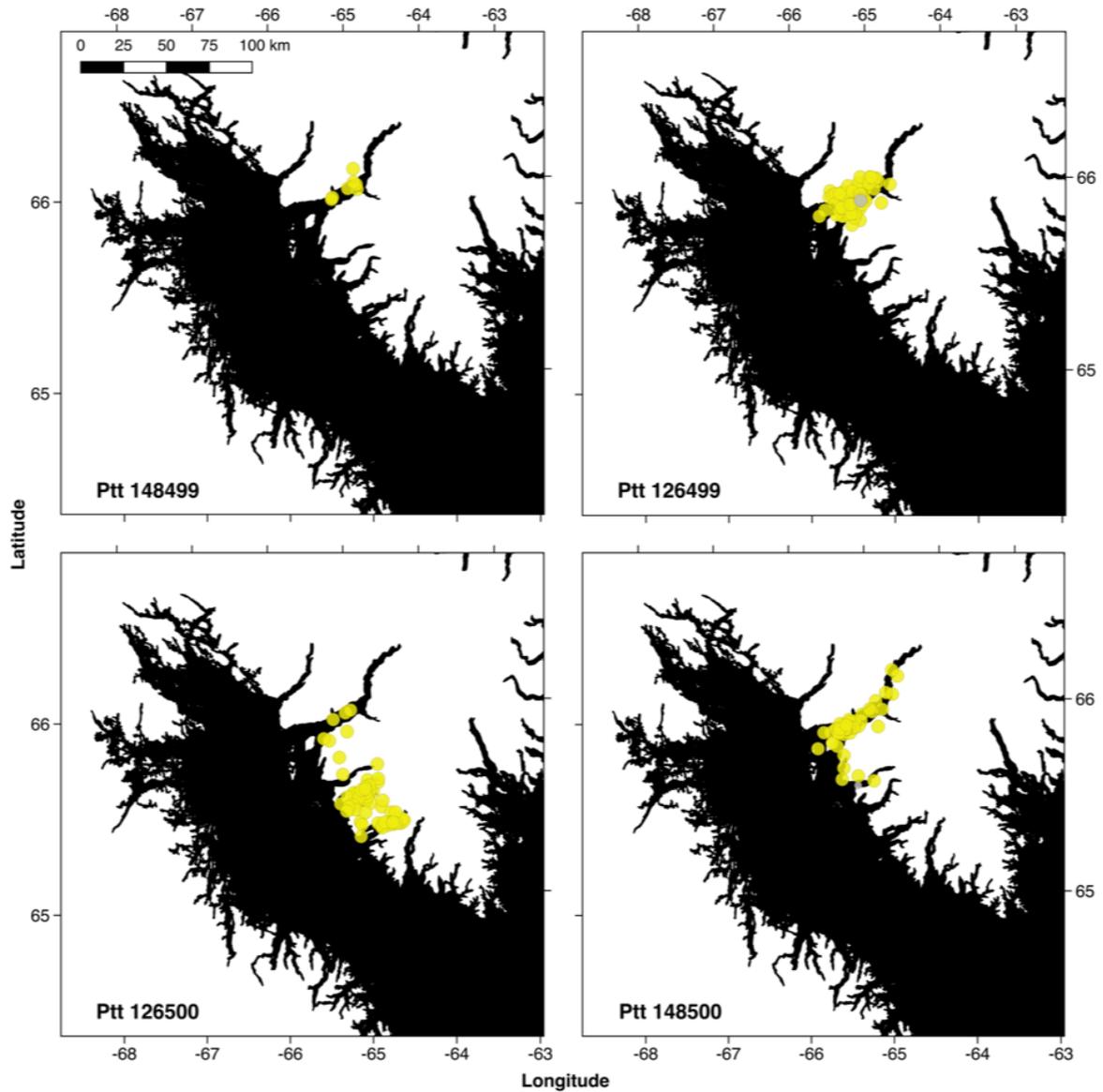


Figure 2.2: Locations (2 per day) of 4 bowhead whales (Ptt 126499, 148499, 126500, 148500) tagged with SPLASH tags in Kingnait Fjord during August 2016. Locations were predicted using a hierarchical switching state-space model (HSSSM), and were categorized by behavioural states — area-restricted movement (i.e., probable feeding) (yellow) and an unknown behavioural state (grey).

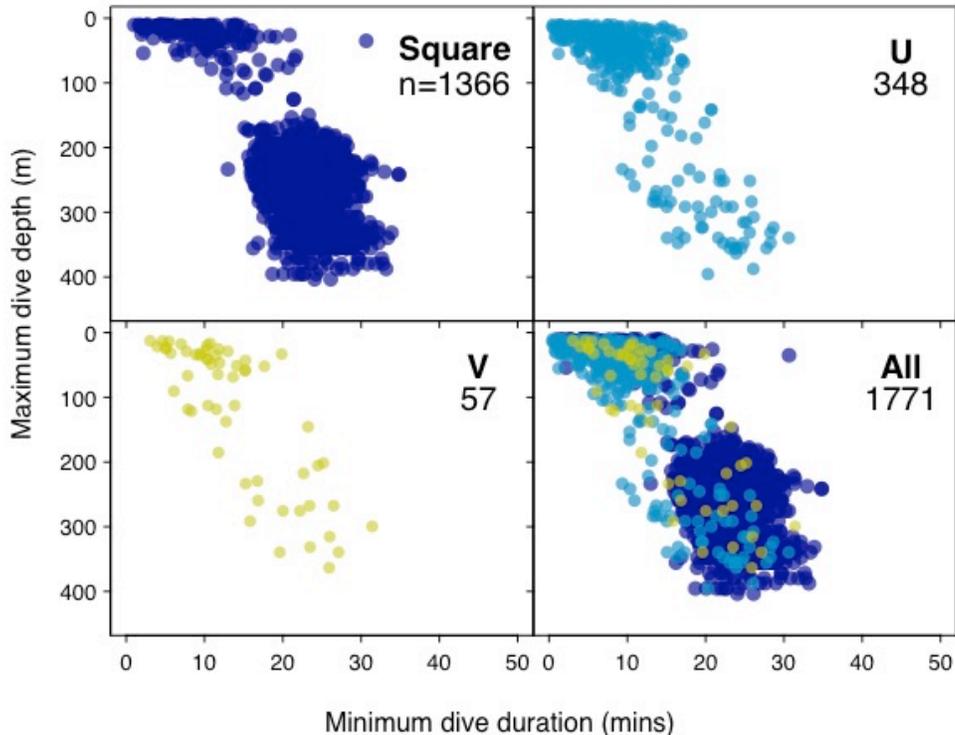


Figure 2.3: All daytime dives for 5 SPLASH tagged bowhead whales (Ptt 126499, 148499, 148502, 148504, 148505) that resided in Kingnait Fiord during August and September 2016. Dive types are differentiated in the panels by colour (Square–dark blue; U–light blue; V–green).

2.4.5 Unmanned aerial systems behavioural observations

I obtained high-resolution aerial images (n=1143) and video of tagged and untagged whales using a small unmanned aerial system (UAS), the DJI Phantom 3 Professional. The position of the encountered whale was automatically recorded each time an image was captured using the built-in global positioning system (GPS). The UAS flight altitude was simultaneously recorded as well using the altimeter and, on average, the UAS was flown at an altitude of 12.9 m (± 5.4 SD). The maximum distance flown from the survey vessel was 1000 m and the UAS was hand-deployed and hand-retrieved from the ~8 m aluminum vessel. Flight times lasted ~8-12 min.

By conducting focal follows of tagged animals with the UAS I was able to opportunistically and qualitatively observe how bowhead whale behaviour changed in response to my vessel. On numerous occasions, I found that when my engines went from neutral to engaged, the tagged animal's behaviour would change such that it would transition

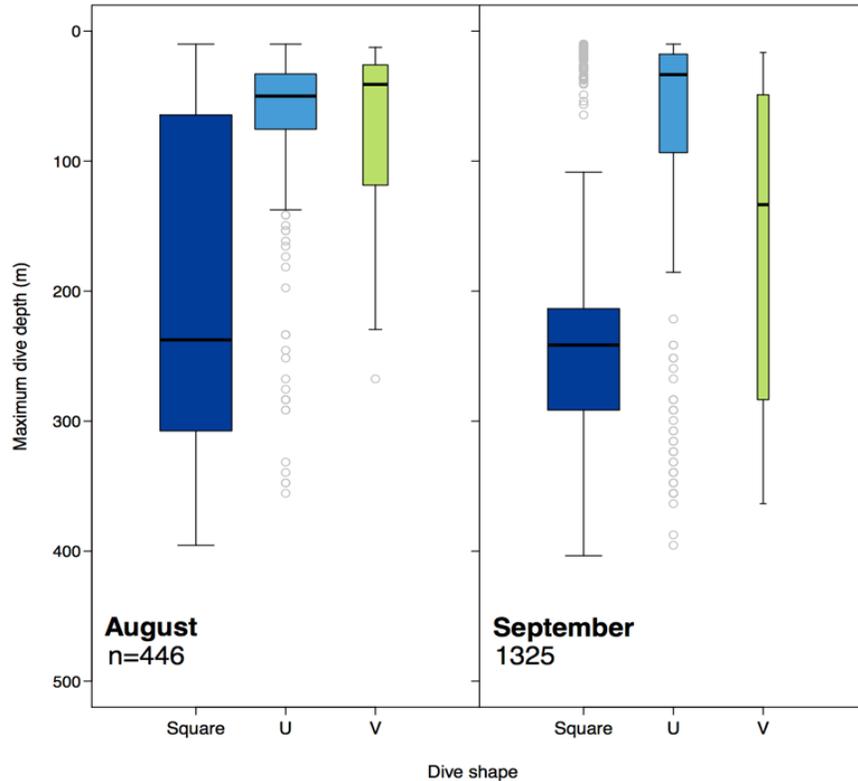


Figure 2.4: Daytime diving depths by shape of the dives (Square, U and V) made by 4 SPLASH tagged bowhead whales that were in Kingnait Fiord during August (n=446 dives) and 5 during September 2016 (n=1325 dives). The width of each boxplot is proportional to the numbers of recorded dives. The median maximum dive depth in August was 238 m for Square shaped, 50 m for U and 41 for V-shaped dives. Similarly, the median dive depth during September was 242 m for Square dives, 34 m for U and 134 for V-shaped dives.

abruptly from either resting at the surface or conducting short and shallow dives in the top few meters of the water column to traveling directly away from the vessel quickly. Examination of the fine-scale dive data for the focal followed animals similarly demonstrated that the whales were conducting principally short and shallow dives. Furthermore, I did not record any near surface feeding events. However, I did obtain still images with animals that had slightly agape mouths (Fortune et al. 2017). These animals were occupying shallow, coastal waters where prior prey sampling revealed extremely low abundances of zooplankton, and Fortune et al. (2017) suggested that these whales were likely regulating their temperature by passing water over their oral rete. Consequently, it appears unlikely that the whales were in fact feeding while I conducted focal follows.

2.4.6 Optical plankton counter particle size, abundance and biomass

Of the 72 vertical OPC casts in Kingnait Fiord, 52 were made in association with bowhead whales. The depth stratum with the highest abundances of particles ≥ 1.0 mm (2146.9 particles $m^{-3} \pm 778.3$ SD; range = 1050-3950 particles m^{-3}) was between 30 and 40 m ($n=16$). I detected two prey layers (i.e., depth strata where zooplankton abundances approached or exceeded 1000 particles m^{-3} which is representative of prey concentrations that elicit feeding in North Atlantic right whales ;Baumgartner & Mate 2003)—a shallow (5-55 m) and deep (190-225 m) layer. Particle abundances were highly variable in the shallow layer and ranged from 50 to 3950 particles m^{-3} (Mean particle abundance: 294.1 ± 542.2 SD) compared with abundances at depth that varied from 50 to 1150 particles m^{-3} (mean particle abundance: 285.4 ± 175.4 SD) (Fig. 2.5). I found that mean ECD was 1.46 ± 0.53 SD when averaged across the entire water column and that particle size increased with increasing depth. Particle sizes were 25% larger at depth whereby the ECD averaged 1.21 mm ± 0.49 SD between 5 and 55 meters, and averaged 1.63 mm ± 0.52 SD between 190 and 225 m (Fig. 2.5). When particle sizes were converted to biomass (wet weight m^{-3}) for each cast (Fig. 2.5), I found that estimated biomass was 10% higher and less variable on average in deeper layers (190-225 m; 979.39 mg $m^{-3} \pm 378.25$ SD) compared with shallow layers (5-55 m; 886.79 mg $m^{-3} \pm 2853.88$ SD). Furthermore, when I plotted biomass concentration in an area where bowheads appeared to frequently engage in feeding behaviour (e.g., high fluking and long dives) during daytime in Kingnait Fiord behind Kekertukdjuak Island (Fig. 2.6) I found that particle biomass was high near the surface (5-55 m) and comparatively higher at depth (190-225 m). High biomass appears to occur because of greater particle abundance (Fig. 2.7 A) in the surface and because of larger particles on average at depth (Fig. 2.7 B), which is consistent with what I observed elsewhere in Kingnait Fiord.

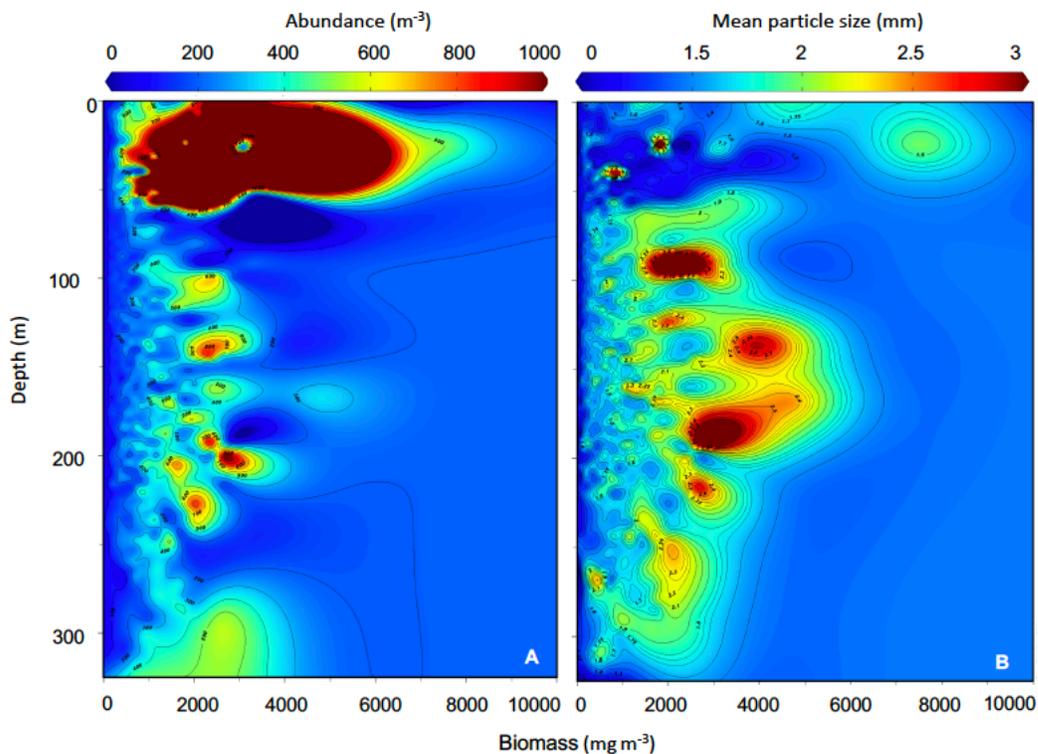


Figure 2.5: Biomass (mg m^{-3}), abundance (m^{-3}) and mean size (mm) (i.e., equivalent circular diameter) of particles based on 4 m aggregated depth bins for all OPC casts ($n=72$) inside Kingnait Fiord. **A) High biomass is associated with greater particle abundances (e.g., ≥ 1000 particles m^{-3}) near the surface and relatively lower particle abundances at depth, whereby blue contours represent low particle abundances (e.g., 0-200 particles m^{-3}) while red represents higher abundances (e.g., 800-1000 particles m^{-3}). **B)** Biomass at depth is associated with larger mean particle sizes compared with biomass measurements near the surface where blue contours represent small ECD measurements (e.g., 0-1.5 mm) and red represents larger (e.g., 2.5-3 mm) particle sizes.**

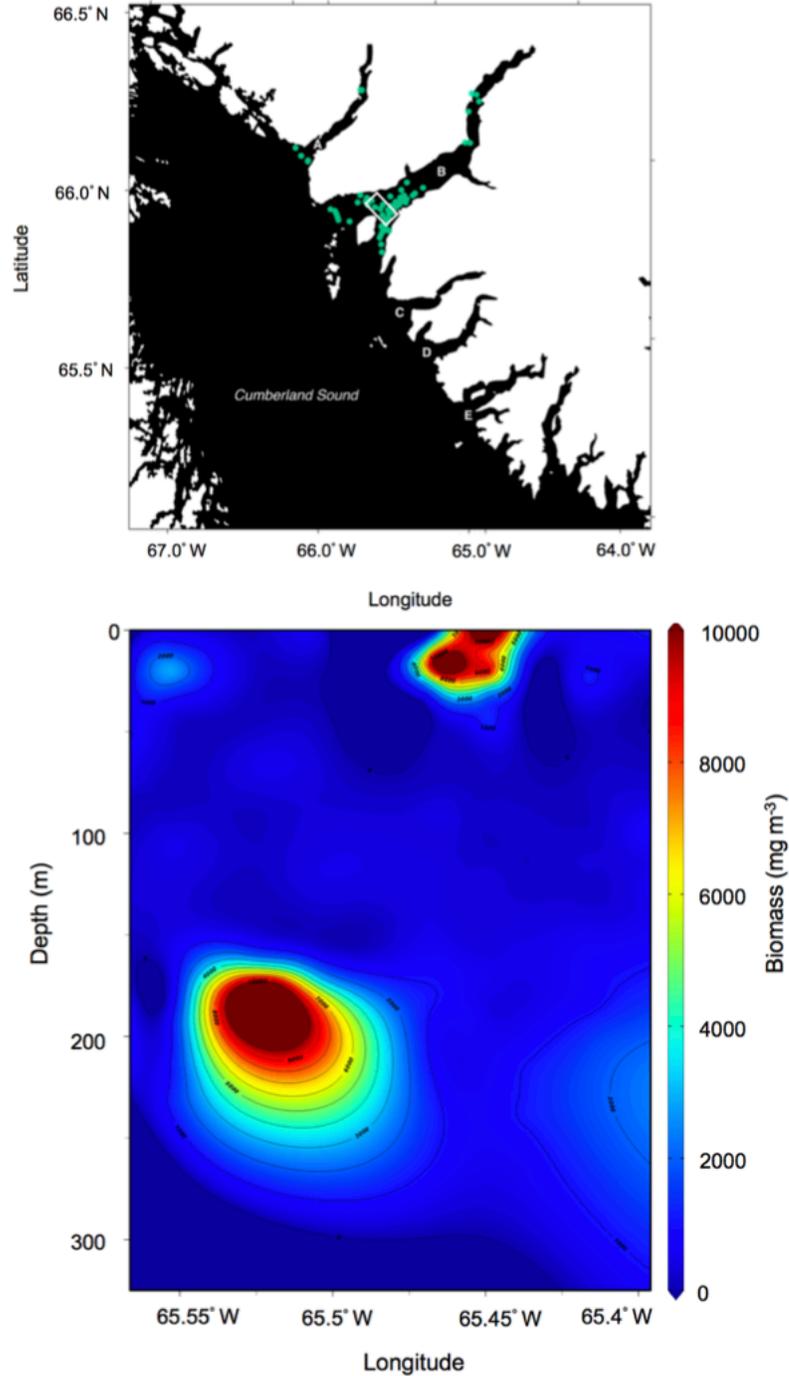


Figure 2.6: Top: Locations of all OPC vertical casts (•) in 2016, and a sub-set of the casts (n=16) (white box) across Kingnait Fiord behind Kekertukdjuak Island where bowhead whales made long, high-fluking dives and were presumed to feed. For reference, I identified fiords of interest where: **A**=Pangnirtung Fiord, **B**=Kingnait Fiord, **C**=Iqalujjaq Fiord, **D**=Unnamed, **E**=Kumlien Fiord and **F**=Ujuktuk Fiord. Bottom: Vertical particle biomass concentrations within the sub-set area were particularly high (≥ 1000 particles/m³) for some of the OPC casts at the surface and at depth.

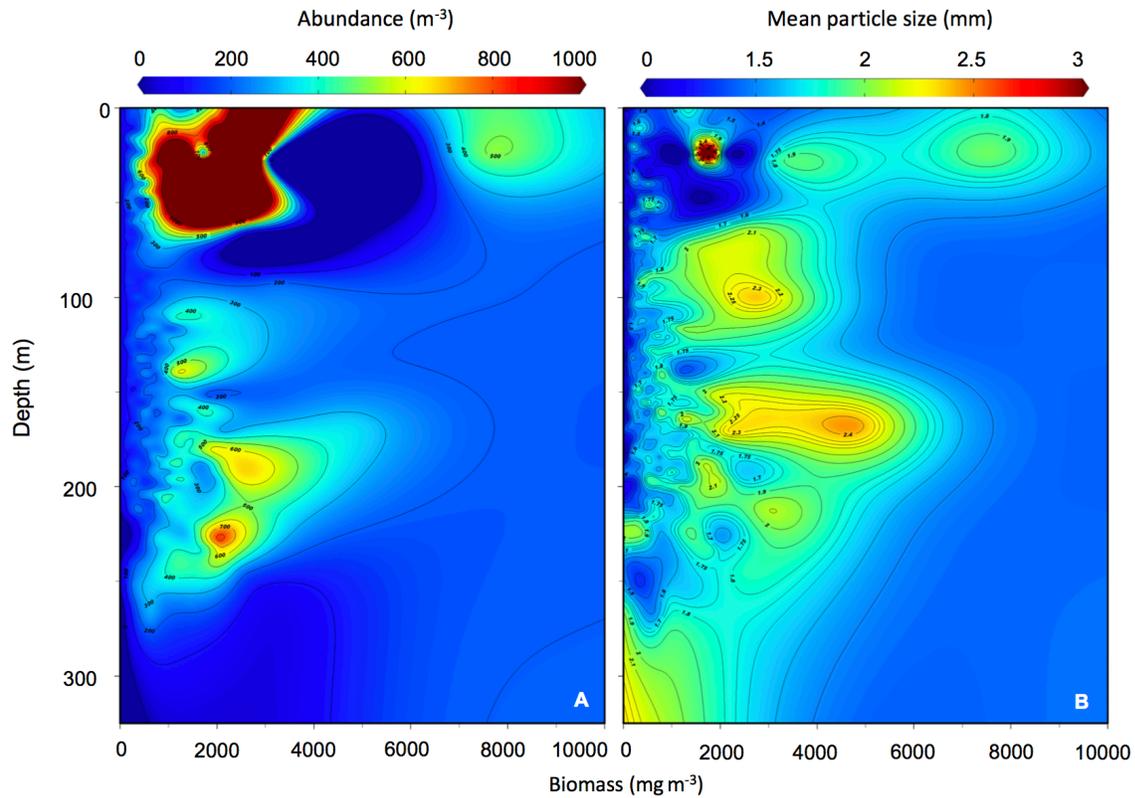


Figure 2.7: Biomass (mg m^{-3}), abundance (m^{-3}) and mean size (mm) (i.e., equivalent circular diameter) of particles based on 4 m aggregated depth bins for $n=16$ OPC casts made behind Kekertukdjuak Island inside Kingnait Fiord (Fig 2.6) where bowheads display behaviours consistent with feeding. **A) High biomass is associated with greater particle abundances near the surface compared with at depth. **B)** Biomass at depth is associated with larger mean particle sizes compared with biomass measurements near the surface.**

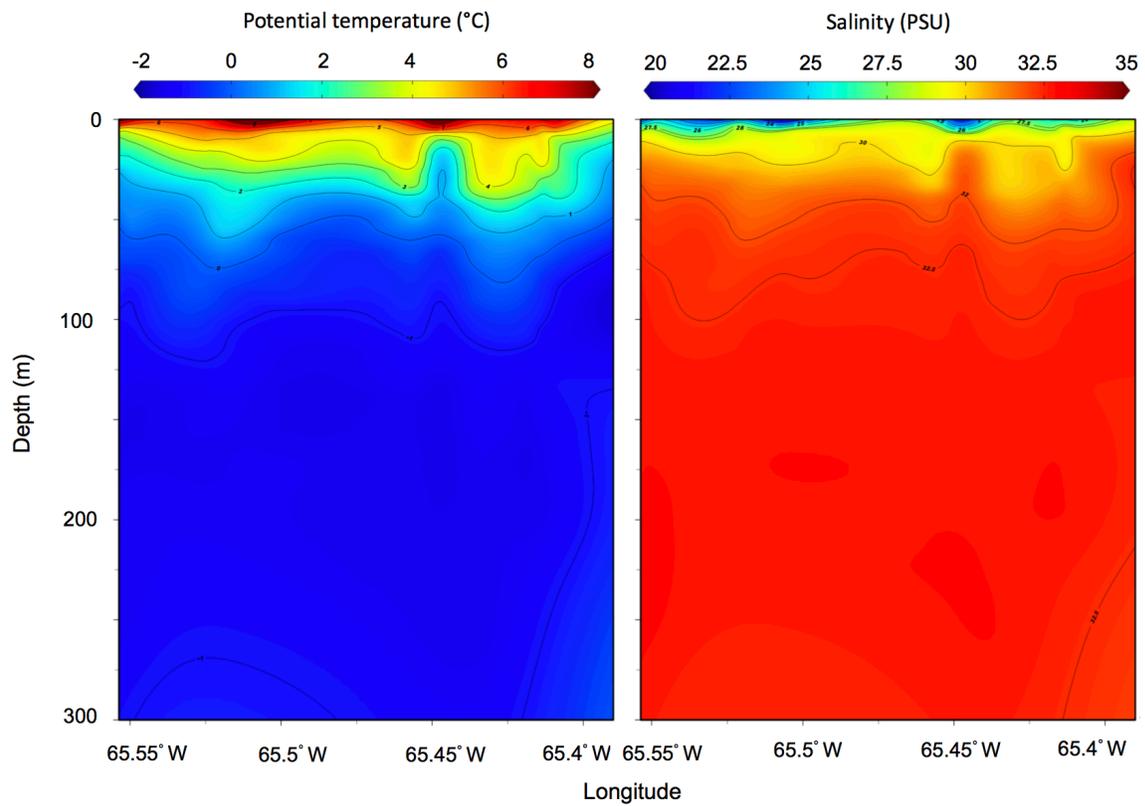


Figure 2.8: Potential temperature (°C) and salinity (PSU) contour plots for n=16 CTD profiles made across Kingnait Fiord behind Kekertukdjuak Island where bowhead whales made long, high-fluking dives and were presumed to feed (Fig. 2.6).

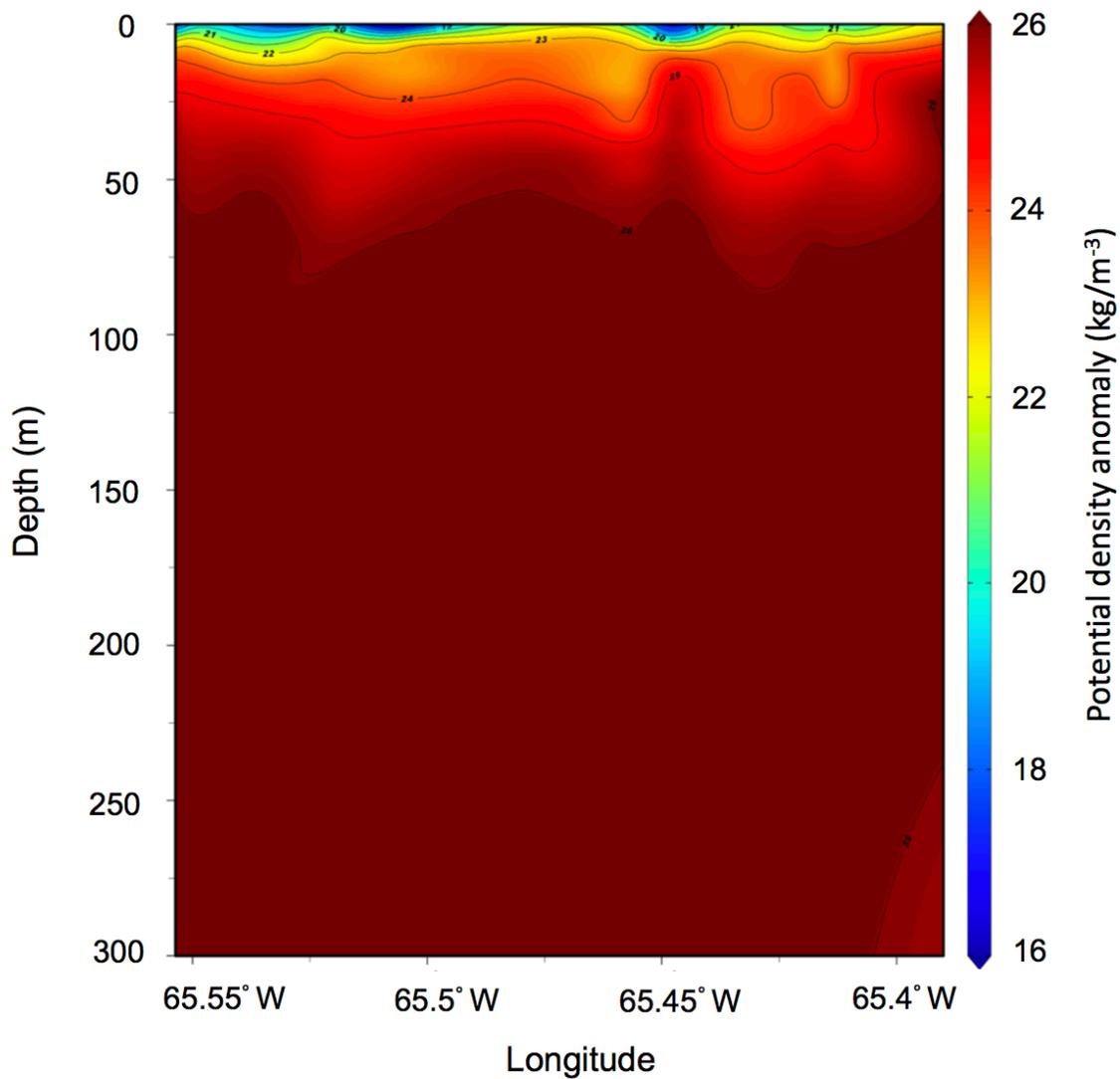


Figure 2.9: Potential density anomaly (kg m^{-3}) contour plot for $n=16$ CTD profiles made across Kingnait Fiord behind Kekertukdjuak Island where bowhead whales made long, high-fluking dives and were presumed to feed (Figs. 2.6 & 2.7).

I obtained 11 vertical OPC casts in Pagnirtung Fiord where the maximum sampling depth ranged from 52 to 112 m. I found that particle abundances ≥ 1000 particles m^{-3} occurred between 8 and 36 m ($25.7 \text{ m} \pm 12.41 \text{ SD}$) ($n=4$ casts and $n=7$ layers) and ranged from 1000 to 3000 particles m^{-3} ($1607.1 \text{ particles } m^{-3} \pm 707.9 \text{ SD}$). Only one prey layer was detected, and it occurred between 5 and 40 m ($325 \text{ particles } m^{-3} \pm 458.3 \text{ SD}$; range: 50-3000 particles m^{-3}). Particle abundances were considerably less at depth (90-110 m) and ranged from 50 to 250 particles m^{-3} ($106.3 \text{ particles } m^{-3} \pm 72.89 \text{ SD}$). The average integrated water column ECD was $1.33 \text{ mm} \pm 0.41 \text{ SD}$ and particle size increased with increasing depth whereby the average ECD for particles between 5-40 m was $1.26 \text{ mm} \pm 0.36 \text{ SD}$ and $1.38 \text{ mm} \pm 0.34 \text{ SD}$ between 90-110 m. Unlike Kingnait Fiord, I found that estimated biomass was 45% greater at the surface ($527.02 \text{ mg } m^{-3} \pm 404.25 \text{ SD}$; 5-40 m; $n=11$) than at depth ($291.82 \text{ mg } m^{-3}$; 90-110 m; $n=1$).

2.4.7 Temperature and salinity profiles

I conducted 72 co-located CTD and OPC casts in Kingnait Fiord during August. I found strong water column stratification consistent with sub-Arctic fiords during summer whereby the surface (1 m) or local water (i.e., freshwater inputs from rivers) was considerably fresher ($26.84 \text{ PSU} \pm 2.28 \text{ SD}$) and warmer ($6.57 \text{ }^\circ\text{C} \pm 1.20 \text{ SD}$) compared with the intermediate (100 and 200 m) or advected coastal water (i.e., Cumberland Sound and Davis Strait) that was considerably cooler ($-0.83 \text{ }^\circ\text{C} \pm 0.75 \text{ SD}$ at 100 m and $-1.25 \text{ }^\circ\text{C} \pm 0.56 \text{ SD}$ at 200 m) and higher in salinity ($32.41 \text{ PSU} \pm 1.23 \text{ SD}$ at 100 m and $32.26 \text{ PSU} \pm 1.81 \text{ SD}$ at 200 m). When examining temperature and salinity measurements ($n=16$) from the middle of Kingnait Fiord where bowheads appeared to engage in feeding activities during the daytime, it appears as though the temperature gradient was stronger than the salinity gradient (Fig. 2.7), and that vertical differences in temperature may have driven the apparent vertical density differences (Fig. 2.8) found in the top 50 m of the water column. Furthermore, I found that the average base depth of mixed layer occurred at $17.06 \text{ m} \pm 9.09 \text{ SD}$ for CTD casts made in the middle of Kingnait Fiord.

Table 2.4: Summary of all quantitative net samples collected using a 333 µm mesh net. Samples were obtained in the presence and absence of bowhead whales and some were collected directly in the fluke print (i.e., location where an animal conducted a fluking dive). Two hauling methods (vertical and oblique depending on the cable angle) were used to obtain prey samples as indicated by the “Tow type” in Pangnirtung and Kingnait Fiord.

Date	Whales	Fluke print	Tow type	Latitude	Longitude	Location
2016-08-05	no	no	vertical	66 15.235	065 33.507	Pangnirtung Fiord
2016-08-05	no	no	vertical	66 15.368	065 33.370	Pangnirtung Fiord
2016-08-05	no	no	vertical	66 15.441	065 33.327	Pangnirtung Fiord
2016-08-05	no	no	vertical	66 15.984	065 33.102	Pangnirtung Fiord
2016-08-07	no	no	vertical	66 04.018	065 56.524	Pangnirtung Fiord
2016-08-10	no	no	vertical	66 06.140	066 01.880	Pangnirtung Fiord
2016-08-10	yes	yes	vertical	65 55.529	065 23.573	Kingnait Fiord
2016-08-15	no	no	vertical	65 55.819	065 33.200	Kingnait Fiord
2016-08-15	no	no	oblique	65 57.663	065 19.839	Kingnait Fiord
2016-08-16	yes	yes	vertical	65 55.736	065 26.904	Kingnait Fiord
2016-08-16	no	no	oblique	65 55.997	065 16.612	Kingnait Fiord
2016-08-16	no	no	oblique	65 56.074	065 16.973	Kingnait Fiord
2016-08-16	no	no	oblique	65 56.194	065 16.872	Kingnait Fiord
2016-08-19	yes	no	vertical	65 55.025	065 28.001	Kingnait Fiord
2016-08-19	yes	no	vertical	65 58.061	065 18.925	Kingnait Fiord
2016-08-20	no	no	vertical	65 55.919	065 17.473	Kingnait Fiord
2016-08-19	yes	no	vertical	65 57.045	065 23.657	Kingnait Fiord
2016-08-23	no	no	vertical	65 55.407	065 30.296	Kingnait Fiord
2016-08-23	no	no	vertical	65 53.524	065 24.833	Kingnait Fiord
2016-08-23	no	no	vertical	65 56.154	065 21.622	Kingnait Fiord
2016-08-23	no	no	vertical	65 51.710	065 26.923	Kingnait Fiord
2016-08-23	no	no	vertical	65 52.042	065 28.044	Kingnait Fiord
2016-08-26	no	no	vertical	65 49.055	065 28.513	Kingnait Fiord
2016-08-27	no	no	vertical	65 54.822	065 24.909	Kingnait Fiord
2016-08-27	no	no	vertical	65 53.208	065 26.288	Kingnait Fiord
2016-08-28	no	no	vertical	65 56.566	065 31.442	Kingnait Fiord

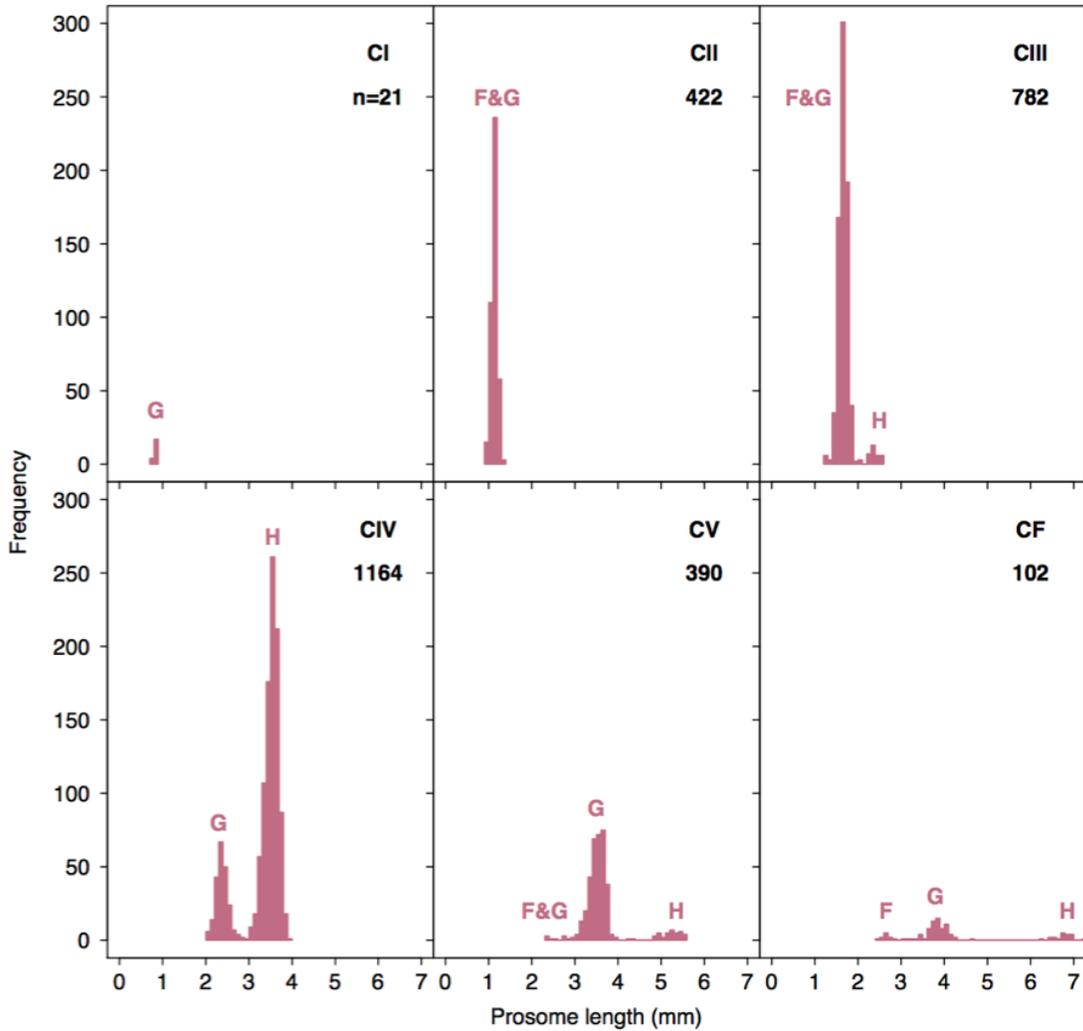


Figure 2.10: Distribution of prosome lengths by life-stages for all 3 *Calanus* spp. identified and enumerated from 20 net samples collected in Kingnait Fiord. These measurements differentiated the three morphologically similar *Calanus* spp. based on the species-specific size ranges determined by Madsen *et al.* (2001) for *Calanus finmarchicus* (F), *C. glacialis* (G) and *C. hyperboreus* (H). Overlap in size ranges is likely between species, making identifications particularly challenging for early-stages such as CII and CIII *C. finmarchicus* and *C. glacialis*.

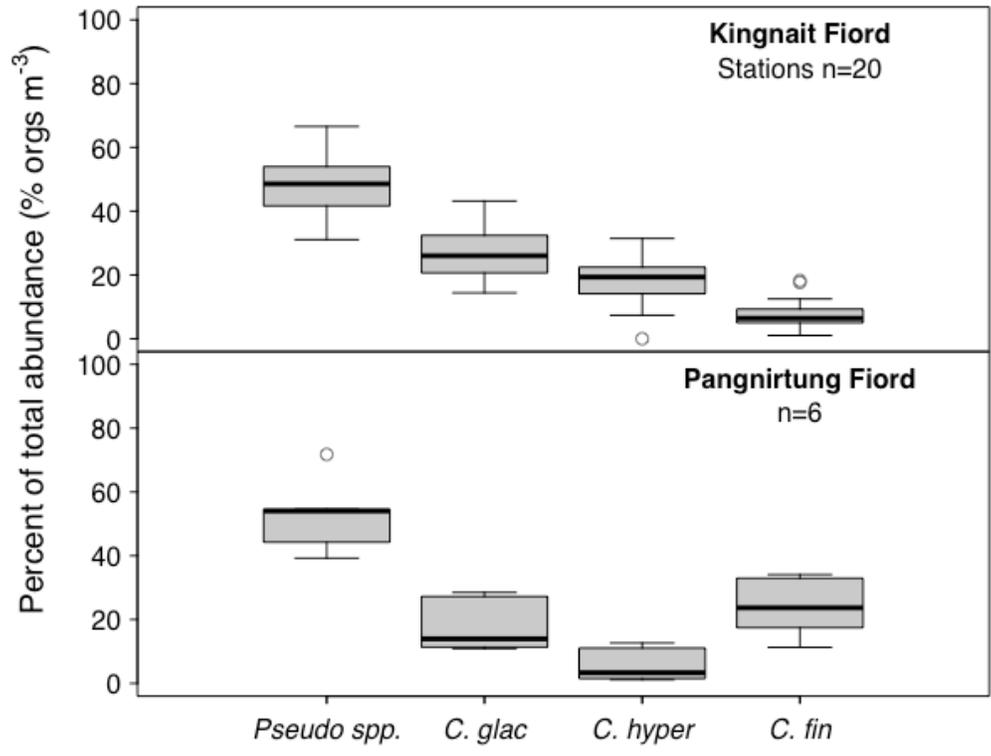


Figure 2.11: Proportion of total abundance of most common individual calanoid copepods (4 species) sampled from 6 net tows in Pangnirtung Fiord and from 20 tows in Kingnait Fiord. Species included *Pseudocalanus* spp., *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia* spp., *Oithona* spp. and *Acartia longiremis*.

Table 2.5: Proportion (Mean \pm SD) of total abundance (orgs m^{-3}) of the four most common zooplankton species (*Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus* and *Pseudocalanus* spp.) by life stage for net samples collected in Kingnait Fiord. Early life stage includes copepodites stage I to IV and late represents life-stages between V and adult (male and female).

Species	Life stage	Proportion
<i>Calanus hyperboreus</i>	Early	17.13 \pm 7.04
<i>Calanus hyperboreus</i>	Late	1.11 \pm 1.20
<i>Calanus glacialis</i>	Early	18.74 \pm 11.60
<i>Calanus glacialis</i>	Late	7.40 \pm 5.39
<i>Calanus finmarchicus</i>	Early	7.10 \pm 4.90
<i>Calanus finmarchicus</i>	Late	0.28 \pm 0.40
<i>Pseudocalanus</i> spp.	Early	5.02 \pm 2.46
<i>Pseudocalanus</i> spp.	Late	43.21 \pm 10.11

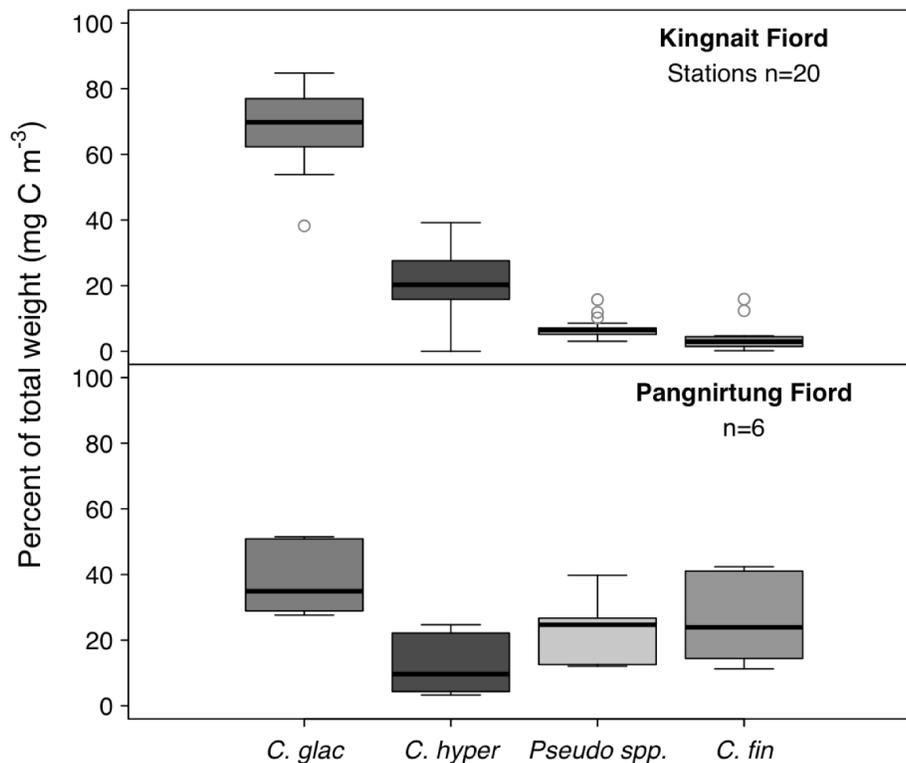


Figure 2.12: Proportions of 4 species of calanoid copepods by estimated weight at 6 stations in Pangnirtung Fiord and at 20 stations in Kingnait Fiord. Species included *Calanus glacialis* (n=863), *C. hyperboreus* (n=1754), *C. finmarchicus* (n=1135) and *Pseudocalanus* (Liu & Hopcroft 2008). The boxplots are shaded according to the relative total caloric content per individual of each species from lowest energy prey (*Pseudocalanus* spp.) to greatest energy content (*C. hyperboreus*) (DeLorenzo Costa et al. 2006, Falk-Petersen et al. 2009).

Table 2.6: Percent of total abundance (orgs m⁻³) and biomass (mg C m⁻³) for the most common species from net collected samples in Pagnirtung Fiord (n=6) and Kingnait Fiord (n=20). Mean values and standard deviations are reported. Biomass was calculated by determining the abundance of early (CI-CIV) and late (CV-Adult) stage organisms for each species and then multiplying the total number of organisms (m⁻³) by the mean biomass (mg C m⁻³) of each stage grouping (i.e., early or late).

Species	Location	% Abundance	% Biomass
<i>Pseudocalanus spp.</i>	Pagnirtung Fiord	52.9 ± 11.15	23.4 ± 10.3
<i>Calanus hyperboreus</i>	Pagnirtung Fiord	5.5 ± 5.15	12.3 ± 9.65
<i>Calanus glacialis</i>	Pagnirtung Fiord	17.7 ± 8.13	38.1 ± 10.9
<i>Calanus finmarchicus</i>	Pagnirtung Fiord	23.9 ± 9.16	26.2 ± 14.3
<i>Pseudocalanus spp.</i>	Kingnait Fiord	48.2 ± 10.21	6.90 ± 2.93
<i>Calanus hyperboreus</i>	Kingnait Fiord	18.2 ± 7.02	20.8 ± 9.3
<i>Calanus glacialis</i>	Kingnait Fiord	26.1 ± 8.13	68.6 ± 10.8
<i>Calanus finmarchicus</i>	Kingnait Fiord	7.4 ± 4.79	3.7 ± 3.9

Table 2.7: Percent (% *Calanus* spp.) of all *Calanus* spp. organisms enumerated (n=323) from bowhead whale stomach contents by species and life-stage by species.

	Total	% <i>Calanus</i> spp.
<i>Calanus hyperboreus</i>		
early	85	26.3
late	8	2.5
unstaged	4	1.2
<i>Calanus glacialis</i>		
early	26	8.0
late	79	24.5
unstaged	4	1.2
<i>Calanus finmarchicus</i>		
early	0	0
late	4	1.2
unstaged	0	0
<i>Calanus</i> spp.		
unstaged	113	35.0

2.4.8 Zooplankton net sample abundance and biomass

Twenty six zooplankton net samples were collected in Pangnirtung (n=6) and Kingnait Fiord (n=20) between 5 August and 28 August 2016 (Table 2.4, Table A.1 & Table A.2). I found that, on average, the samples contained 91% (± 8.8 SD) calanoid copepods of which 48% (± 11.4 SD) consisted of *Calanus* spp. Of these *Calanus* spp., 78% (± 19.7 SD) were Arctic taxa (e.g., *Calanus hyperboreus* and *C. glacialis*) and 22% (± 19.7 SD) were of temperate/subarctic origin (e.g., *Calanus finmarchicus*). Other species such as *Metridia lucens*, *M. longa*, *Acartia* spp. and *Oithona* spp. represented less than 5% (4.88%) of the enumerated organisms and were excluded from my biomass calculations due to their relatively small contribution to zooplankton assemblages in both Kingnait and Pangnirtung Fiord. Furthermore, small taxa such as *Oithona* spp., *Acartia* spp. and early life-stages of *Pseudocalanus* spp. may be quantitatively underestimated from net samples due to the large mesh size (333 μm) of the net. When net samples were converted into abundance (total number of organisms m^{-3}) for the most common species, I found that *Pseudocalanus* spp. was similarly the most numerous species in Pangnirtung (52.98 % ± 11.15 SD; 55.56 orgs $\text{m}^{-3} \pm 41.87$ SD) and Kingnait Fiord (48.23 % ± 10.21 SD; 13.98 orgs $\text{m}^{-3} \pm 4.45$ SD). However, the second most abundant species were *C. finmarchicus* (23.86 % ± 9.16 SD; 28.26 orgs $\text{m}^{-3} \pm 29.71$ SD) in Pangnirtung Fiord and *C. glacialis* (26.14% ± 8.13 SD; 8.06 orgs $\text{m}^{-3} \pm 4.19$ SD) in Kingnait Fiord (Fig. 2.11; Table A.1).

Using my prosome measurements and previously established species-specific size ranges for *Calanus* spp. (Madsen et al. 2001), I found that all *Calanus* spp. were dominated by early life stages (CI-CIV) (Fig. 2.10; Table 2.5) and that this was particularly true for *Calanus finmarchicus* (96.1 ± 6.5 early stage). Numerically, *Pseudocalanus* spp. was the most abundant taxa in Pangnirtung and Kingnait Fiord representing 47% (± 9.3 SD) of all calanoid copepods, followed by *Calanus glacialis* (23.0 % ± 8.9 SD), *C. hyperboreus* (14.3% ± 8.0 SD) and *C. finmarchicus* (10.8% ± 9.2 SD) (Fig. 2.11).

When I compared the species composition between fiords (Fig. 2.11), I found that Pangnirtung Fiord (n=6) contained a higher proportion of *Pseudocalanus* spp. 52.3% (± 11.2 SD) compared with Kingnait Fiord (n=20) 48.2% (± 10.0 SD). I also found that *C. finmarchicus* was more dominant in Pangnirtung Fiord (23.9% ± 9.2 SD) than Kingnait Fiord

(7.4 % ± 4.8 SD) and that *C. glacialis* (26.1% ± 8.1 SD) and *C. hyperboreus* (18.2% ± 7.0 SD) were more dominant in Kingnait Fiord compared with Pagnirtung Fiord (*C. glacialis*: 17.7% ± 8.1 SD and *C. hyperboreus*: 5.5% ± 5.1 SD) (Fig. 2.11). However, when converted to weight (mg C m⁻³), I found that *C. glacialis*—an Arctic taxa—comprised the greatest proportion of total *Calanus* spp. and *Pseudocalanus* spp. biomass in Kingnait Fiord (Fig. 2.12).

In terms of biomass, 4,359 *Calanus* spp. organisms were staged during enumeration and identification (n=26 stations) and 86% had undamaged exoskeletons permitting prosome measurement (i.e., n=3752) (Fig. 2.11). Of those measured, biomass was calculated using previously established allometric relationships between prosome length (µm) and weight (mg C). Unlike total numerical abundance, I found that zooplankton biomass was dominated by *Calanus glacialis* (68.6% ± 10.8 SD in Kingnait Fiord and 38.1% ± 10.9 SD in Pagnirtung Fiord) and *C. hyperboreus* (20.8% ± 9.3 SD in Kingnait Fiord and 12.3% ± 9.7 SD). This was particularly true for Kingnait Fiord (Fig. 2.12 & Table 2.6).

2.4.9 Species composition of bowhead whale stomach sample

The sub-adult female harvested in Kingnait Fiord (65°48'23" N and 65°28'12" W) on 14 September 2016 measured 11.76 m (straight line distance from snout to fluke notch). The 500 mL sub-sample of stomach contents contained a total of 6 zooplankton species. Of the 477 organisms I enumerated, 67.7% (n=323) were *Calanus* spp., 18.7% (89) were *Metridia* spp., 9.6% (n=46) were unidentified copepods, 1.89% (n=9) were *Pseudocalanus* spp., 1.89% (n=9) were amphipods and 0.21% (n=1) were mysids. I found that the *Calanus* spp. were dominated by early-stage (CI-CIV) *Calanus hyperboreus* (26.3%, n=85) and late-stage (CV-Adult) *C. glacialis* (24.5%, n=79) and *C. finmarchicus* (1.2%, n=4) (Table 2.8).

2.5 Discussion

My analysis of multi-scale bowhead whale diving behaviour and fine-scale zooplankton distribution and abundance provides new insights into the diet and feeding ecology of bowhead whales that previous studies were unable to capture in the Canadian Arctic. Most notably, I found that bowheads employed a more plastic feeding strategy than previously thought. Whales appeared to exploit two discrete prey layers during the daytime—

a shallow layer that consisted of higher abundances of smaller prey, and a deep layer that was of comparatively lower abundance but higher in biomass. Furthermore, differences in zooplankton species composition between two adjacent fiords provide evidence that the whales principally occupied Kingnait Fiord because of the dominance of large, lipid rich Arctic copepods such as *Calanus glacialis*. These findings are the first to confirm that Cumberland Sound, Nunavut is a summertime feeding habitat for Eastern Canada-West Greenland bowhead whales.

2.5.1 Habitat use patterns

The discovery and exploitation of bowhead whales in Cumberland Sound during the mid-19th century was essential to the resurgence of the commercial hunt after bowheads were overharvested in the high Arctic (Reeves et al. 1983). Scottish whalers, under the direction of William Penny, established the Kekerten Island Whaling Station on Qikiqtaq Island near the mouth of Kingnait Fiord in 1857 (Holland 1970). The station was strategically placed to allow the whalers to spot bowheads from shore using a telescope and to overwinter in preparation for the spring hunt (Holland 1970). The Kekerten Island Whaling Station became one of the most significant and longest operating whaling stations in Cumberland Sound—making Kingnait Fiord a historically important habitat for bowhead whales.

Eastern Canada-West Greenland bowhead whales continue to occupy Kingnait Fiord while their population recovers to pre-exploitation stock sizes (Higdon 2010). Systematic boat-based surveys consistently found whales in this habitat compared with neighbouring fiords such as Pagnirtung Fiord during summer (July and August) (Diemer et al. 2011, Matthews et al. 2012). Furthermore, my analysis of horizontal movement showed that bowheads have a high residency period in Kingnait Fiord, as over half of all predicted HSSSM locations occurred within this habitat during August and September. Five of the tagged animals remained exclusively within Kingnait Fiord during this time period. Almost all (98%) of the HSSSM locations were associated with area-restricted movement suggesting that the whales utilize Kingnait Fiord for feeding purposes. Although some animals made excursions to Iqalugaju Fiord (65°38'58.6" N 65°17'10.6 W; a neighbouring fiord to Kingnait Fiord), no tagged animals appeared to occupy Pagnirtung Fiord. Consequently, it appears as though

Kingnait Fiord continues to be an important summertime habitat for bowheads over other fiords in Cumberland Sound.

2.5.2 Multi-depth feeding strategy

Bowheads appeared to exploit shallow and deep prey layers despite the deeper layer containing 10% more biomass. I found that while in Kingnait Fiord, SPLASH tagged animals partitioned their time between shallow Square (~25 m) and U-shaped (~30 m) dives and deep Square (~267 m) and U-shaped (~242 m) dives, which has been similarly observed for North Atlantic right whales in the Great South Channel (Baumgartner et al. 2017). Furthermore, I found that fine-scale tagged animals also alternated between shallow and deep probable foraging dives. However, the proportion of deep feeding dives were lower compared with the SPLASH tags. Differences in the proportion of time spent conducting deep foraging dives between the two tags may be attributed to temporal variability in dive behaviour as I lacked fine-scale dive data from sunrise to noon when deep foraging dives would be most likely to occur under a diel vertical migration scenario.

I also found that the mean dive depth coincided with the depths of maximum zooplankton abundance both at the surface (30-40 m) and at depth (190-225 m) (Fig. 2.5). The average maximum depth of deep probable foraging dives was somewhat deeper than the depth of the prey layers. Differences between the maximum dive depth and depth of maximum zooplankton biomass may be attributed to: 1) lack of spatio-temporal co-location between dive data and prey samples; and 2) spatial variability in bathymetry (Laidre et al. 2007), whereby the whales may have been conducting the majority of their dives in a deeper region of Kingnait Fiord than where the bulk of my prey samples were collected. Furthermore, the maximum depth of the dive may not correspond perfectly with the depth of prey ingestion as animals may adjust their depth during the bottom phase of their dive, as was observed during deep dives for animals equipped with the fine-scale TDR.

As in my study, bowheads were similarly found to alternate between a shallow and deep prey layer during the spring in Disko Bay (Western Greenland). Considerable variability in feeding dive depth (53-109 m) (Laidre et al. 2007) was observed whereby the whales appeared to exploit a prey layer between 30 and 60 m that had biomass dominated by Arctic taxa (*Calanus glacialis* and *C. hyperboreus*) and a deeper layer between 75 and 115 m that

had biomass dominated by a temperate/subarctic species (*C. finmarchicus*). It was suggested that the deep layer included pre-ascension *C. finmarchicus* and that the shallower layer represented organisms that had ascended to support reproductive and feeding activities (Laidre et al. 2007). In my study, however, I found evidence of the reverse whereby the deep layer likely represented descended Arctic taxa and the shallower layer includes actively feeding temperate/subarctic species and non-overwintering life-stages of *C. glacialis* and *C. hyperboreus*. These differences in vertical distribution of *Calanus* spp. are consistent with what is known about seasonal ontogenetic movement (e.g., Unstad & Tande 1991, Hirche & Niehoff 1996, Madsen et al. 2008, Darnis & Fortier 2014).

The dominance of Arctic copepods (e.g., *Calanus glacialis* and *C. hyperboreus*) relative to temperate/subarctic species suggests that prey quality may be higher in Cumberland Sound than Disko Bay. However, it is also possible that the high abundance of smaller-bodied temperate/subarctic species (e.g., *Calanus finmarchicus*) in Disko Bay (Laidre et al. 2007, Heide-Jørgensen et al. 2013) is sufficient to outweigh the comparatively lower energy content. Due to the morphological similarity and size overlap between the three *Calanus* spp. (Parent et al. 2011) I could not accurately convert the particle size measurements from the OPC into species and life-stage specific measurements. Consequently, future studies seeking to conduct quantitative comparisons of the prey quality between both habitats should collect prey samples using depth-stratified net or pump sampling methods to permit species identification and enumeration.

2.5.3 Zooplankton species composition

Bowhead whales may select Kingnait Fiord over other areas because of improved feeding conditions. Zooplankton species composition from net collected samples revealed that smaller bodied taxa such as *Pseudocalanus* spp. (representing ~48% and ~53% of total abundance on average in Kingnait and Pangnirtung Fiord) and *Calanus finmarchicus* (~24% total abundance in Pangnirtung Fiord) were considerably more abundant than Arctic *Calanus* spp. (Fig. 2.11 & Table 2.6). Differences in zooplankton assemblages translated into considerably lower biomass estimates (mg C m^{-3}) for larger-bodied, higher energy Arctic species such as *Calanus glacialis* and *C. hyperboreus* in Pangnirtung Fiord (50% of total biomass per cubic meter on average) compared with Kingnait Fiord (89%) (Fig. 2.11 & Table

2.6). Arctic species of *Calanus* are higher in energy content (e.g., *Calanus glacialis* contains 0.38-0.45 mg of lipid per late-stage individual; Falk-Petersen et al. 2009) compared with temperate/sub-Arctic species (e.g., *Calanus finmarchicus* contains 0.04-0.08 mg of lipid per late-stage individual; Falk-Petersen et al. 2009). Consequently, the quality of prey available to bowhead whales appears to be greater in Kingnait Fiord compared with Pangnirtung Fiord due to the presence of large-bodied and energy-rich Arctic taxa in Kingnait Fiord.

Biomass estimates from OPC data showed that the near surface prey layers were comparable between fiords with Kingnait Fiord having only marginally higher biomass than Pangnirtung Fiord. However, the absence of a deep layer that is consistently high in biomass in Pangnirtung Fiord may help explain why whales appear to prefer Kingnait Fiord. The opportunities for feeding appear to be greater in Kingnait Fiord with the presence of a shallow and deep prey layer. Furthermore, the quality of prey appears to be higher in Kingnait Fiord due to the greater abundance and biomass of Arctic taxa.

Similar to the net sampling, my analysis of stomach contents found that mostly *Calanus* spp. were consumed—representing two-thirds of the total number of zooplankton identified. Of the *Calanus* species, *C. hyperboreus* (30.0%) and *C. glacialis* (33.7%) were the most numerous. However, I was unable to identify down to the species level for 35.0% of all *Calanus* spp. due to missing urosome segments needed to stage individuals and identify species based on prosome size. Some of the unidentified species might be *C. finmarchicus*, which I found in the net samples. Other studies similarly found that the numerical abundance of bowhead whale stomach contents were dominated by copepods of the Calanidae family in the Beaufort Sea and Hudson Strait. However, they were unable to make species level identifications due to differences in preservation methods (freezing vs. formalin) (Pomerleau, Ferguson, et al. 2011).

Psuedocalanus spp. was poorly represented in my stomach sample compared with the net samples. This may reflect diet selection of larger, more energy-rich organisms such as *Calanus* spp. or it may be an artefact of the small size of the organisms and the presumably quicker time required for digestion (e.g., effects of differential digestion; Hyslop 1980). As a consequence, it is possible that smaller species and earlier life-stages are underestimated from stomach content analysis and that these results represent the minimum number of species consumed. However, the species identifications from the stomach sample provide

confirmation that the whales were consuming *Calanus glacialis* and *C. hyperboreus*, which is consistent with my interpretation of the vertical distribution of particles and foraging behaviour of the whales.

2.5.4 Zooplankton vertical distribution

The presence of two discrete prey layers in Kingnait Fiord likely reflects the oceanographic conditions, zooplankton species diversity and life-history characteristics. The depth of maximum particle biomass in the surface waters occurred near the estimated mixed layer depth that was between 8 and 26 m (17 m on average based on n=16 stations behind Kekertukdjuak Island) (Fig. 2.6). Under stratified conditions, phytoplankton concentrations should be greatest in warm, low-density, nutrient-rich surface waters near the mixed layer where light penetration is high (Dunweber et al. 2010, Swalethorp et al. 2011). As a result, actively feeding herbivorous copepods, such as early stage *Calanus finmarchicus*, would be expected to co-occur near the mixed layer where feeding conditions are presumed greatest.

As the summer progresses and phytoplankton concentrations decrease due to grazing, later developmental stages of *Calanus finmarchicus* (e.g., CIV and CV) and early to late stages of multi-generational Arctic species such as *C. glacialis* (e.g., CIV and V) and *C. hyperboreus* (e.g., CIII, CIV and CV) may begin their seasonal descent to near bottom depths for diapause (Visser & Jónasdóttir 1999, Scott et al. 2000, Hirche 2013, Baumgartner & Tarrant 2017). Diapause is a form of dormancy, whereby copepods suppress their metabolic rates by occupying cooler water masses following the phytoplankton bloom and reduce their swimming activity as a means to conserve their lipid reserves until the following spring when they ascend to surface waters to feed (Madsen et al. 2001, Heide-Jørgensen et al. 2007, Laidre et al. 2007, Darnis & Fortier 2014, Baumgartner & Tarrant 2017).

The deeper prey layer included particles that were comparatively larger (1.63 mm ECD) than those found in the near surface layer (1.21 mm ECD). These larger particle size measurements were presumably the larger bodied Arctic copepods identified in the net tows. Particle measurements from OPC's are typically smaller than the actual copepod prosome measurements due to differences in the orientation and transparency of the organisms as they pass through the light beam (Baumgartner 2003). For example, previous studies found that *Calanus finmarchicus* CV ECD was underestimated by ~30% using the OPC (Herman 1992).

Given the likelihood of underestimation, it is feasible that the CIV and CV *C. glacialis* (2.03-2.93 mm and 2.73-3.9 mm) and the CIII-CV *C. hyperboreus* (>1.95 mm and >3.90 mm) organisms found in the net tows were represented by the comparatively larger particles detected by the OPC in the deep layer (190-225 m).

Predator avoidance and adaptation to seasonally predictable fluctuations in phytoplankton availability may explain why Arctic copepods have either initiated diapause or undergone diel vertical migration. Diel vertical migration is a form of predator avoidance whereby small prey species such as zooplankton descend to depth (below the euphotic zone) during daylight hours to avoid predation from visual predators (Bollens & Frost 1989, Hays 1995, Falk-Petersen et al. 2008, Baumgartner et al. 2011). It may be particularly beneficial for larger copepods that have accumulated considerable lipids to undergo diel vertical migration because the risk of predation outweighs the benefit of feeding during daylight hours (Huntley & Brooks 1982).

In the absence of day and night sampling, I can only speculate as to which mechanism was regulating copepod vertical movement. However, the Arctic species identified based on prosome lengths (Fig. 2.9 & Table 2.5) represent diapausing stages (e.g., CIV-CV for *C. glacialis* and CIII-CV for *C. hyperboreus*). Furthermore, previous studies in Disko Bay, Greenland found that both *C. glacialis* and *C. hyperboreus* terminated feeding even when phytoplankton remained available (Swalethorp et al. 2011), providing support that these organisms were engaged in diapause as opposed to diel vertical migration at the time of sampling.

2.5.5 Energetic trade-offs between prey layers

The variability in bowhead foraging dive depth may reflect a balancing of energetic trade-offs associated with diving and prey consumption. Bowheads may use shallow feeding dives to partially off-set the presumably increased energy expenditure associated with deeper feeding. Although the aerobic dive limit is unknown for baleanids, the proportion of the total dive duration spent at the surface post-dive (PCST) is considered to be an indicator of whether or not an animal has incurred a build-up of lactate in the blood due to anaerobic metabolism that is being cleared during the post-dive surface interval (Kooyman et al. 1980, 1983).

I examined the proportion of total dive duration spent at the surface post-dive for fine-scale tagged animals and found that it did not increase with increasing dive duration or depth. However, the majority of feeding dives were shallow ($25.7 \text{ m} \pm 28.09 \text{ SD}$; $n=78$) precluding my ability to determine whether the time at the surface increased during deep foraging dives. North Atlantic right whales (*Eubalaena glacialis*) were found to be within their ADL when conducting foraging dives to $\sim 120 \text{ m}$ (Baumgartner & Mate 2003, Baumgartner et al. 2017). However, I know based on my longer-term SPLASH tag data that bowhead whales routinely conducted foraging dives to depths more than double that of North Atlantic right whales (267 m) on average. Consequently, it is feasible to assume that after long periods of successive deep diving, bowheads may require additional time at the surface to recover energetically. Access to shallow aggregations of prey may provide animals with an energetic respite while feeding almost continuously (Baumgartner et al. 2017).

2.6 Conclusions

This is the first confirmation that Cumberland Sound is a summertime foraging habitat for ECWG bowhead whales—at least under current environmental conditions. The comparison of two adjacent fiords—one with whales and one without—revealed bowhead whale prey preferences. Most notably, it suggests that the whales preferred Kingnait Fiord over Pangnirtung Fiord because it had a deep prey layer with a higher biomass of Arctic taxa. Bowhead whales feeding in Kingnait Fiord may offset the presumably increased energy costs incurred from repeated deep dives by intermittently exploiting shallowly aggregated prey layers when they occur in high-abundances. Using the vertical prey sampling and multi-scale tagging thus revealed that the bowhead whales exploit multi-depth prey layers and are flexible foragers.

My results further suggest that although prey quality and quantity are important to bowhead whale feeding, biomass is ultimately the most influential. The whales appeared to preferentially target deep aggregations of high biomass, which were likely comprised of a relatively low numerical abundance of higher energy Arctic taxa (e.g., *Calanus glacialis* and *C. hyperboreus*). This finding contrasts with Disko Bay where animals appeared to prefer higher numerical abundances of lower energy temperate/subarctic prey (e.g., *Calanus finmarchicus*) at depth (Laidre et al. 2007). Bowhead feeding depth in both habitats coincided

with the depth of maximum biomass, suggesting that this is the best metric for determining where whales are likely to feed in the water column and for assessing habitat quality.

How bowhead whale foraging behaviour and energy balance may be affected by future changes in the species composition and abundance of their prey is unknown. There is a need to predict how future changes in environmental conditions are likely to alter the distribution and abundance of temperate/subarctic and Arctic copepods through the range of ECWG bowhead whales. One possible scenario may include a shift in species composition whereby *Calanus hyperboreus* and *C. glacialis* experience a poleward shift and *C. finmarchicus* dominates zooplankton assemblages in Cumberland Sound. If temperate/subarctic species dominate, will the abundance of lower quality prey be sufficient to support the energetic requirements of the population at its current numbers? Or will bowheads mirror range shifts in Arctic calanoid copepods and preferentially occupy feeding habitats in the high Arctic (e.g., Gulf of Boothia)? Addressing these questions through modeling simulation will help us understand whether Cumberland Sound will continue to be an important summertime habitat for this segment of the population in the face of climate change.

Chapter 3: Seasonal foraging behaviour of bowhead whales in Cumberland Sound, Nunavut

3.1 Summary

Climate change may affect the foraging success of bowhead whales (*Eubalaena mysticetus*) by altering the diversity and abundance of zooplankton species available as food. I collected seasonal movement and dive-behaviour data for 25 Eastern Canada-West Greenland bowheads using time-depth telemetry tags and used state-space models to examine whale movements and dive behaviours. Zooplankton samples were also collected in Cumberland Sound (CS) to determine species composition and biomass. I found that CS was used seasonally by 14 of the 25 tagged whales (43% of locations occurred during fall, 26% summer, 20% spring and 11% winter). Area restricted movement was the dominant behaviour in CS, suggesting that the tagged whales allocated considerable time to feeding. Prey sampling data suggested that bowheads were exploiting energy-rich Arctic copepods such as *Calanus glacialis* and *C. hyperboreus* during summer. Dive behaviour changed seasonally in CS. Most notably, probable feeding dives were substantially shallower during spring (110.5 m \pm 99.9 SD) and summer (100.7 m \pm 113.6 SD) compared to fall (236.0 m \pm 107.3 SD) and winter (272.12 m \pm 90.28 SD). These seasonal changes in dive depths likely reflect changes in the vertical distribution of calanoid copepods, which are known to suspend development and overwinter at depth during fall and winter when phytoplankton availability is presumed to be low. Overall, CS appears to be an important year-round foraging habitat for bowheads, but is particularly important during the late summer and fall. Whether CS will remain a reliable feeding area for bowhead whales under climate changes is not yet known.

3.1 Introduction

The Arctic is warming at a rate more than double the global average (Screen et al. 2012), and is experiencing unprecedented decreases in the extent and thickness of sea ice (Stroeve et al. 2007, Kwok et al. 2009). Such environmental changes are likely affecting the community structure, distribution and abundance of Arctic zooplankton, which are sensitive to changes in water temperature (Hays et al. 2005, Chust et al. 2014). Continued warming of Arctic waters may result in the large-lipid rich Arctic species being replaced with smaller temperate/subarctic species that thrive in warmer conditions and are comparatively lower in

energy content (Beaugrand et al. 2002, Beaugrand 2009). Such ecosystem changes will likely alter the stability of current food web structures (McMeans et al. 2013) and impact the foraging success of marine predators that feed on zooplankton in the Arctic.

Bowhead whales (*Balaena mysticetus*) are considered to be moderately vulnerable to future environmental changes that will likely alter their current prey resource (Moore & Huntington 2008). The replacement of large-bodied zooplankton with comparatively smaller species has already been documented during short-term warming events in the Arctic (Lalande et al. 2013). Long-term trends in decreasing body size have also been observed in the North Sea (Beaugrand 2009), and changes in the abundance, distribution, and diversity of zooplankton species available to bowhead whales are also likely to change in the future. Such potential changes to the feeding regime of bowhead whales in the Eastern Canadian Arctic makes understanding how they forage under current environmental conditions essential to evaluating the sensitivity of the species to future changes in prey quality and quantity.

Much of what is known about the foraging strategy of Eastern Canada-West Greenland (ECWG) bowhead whales is the result of archival tagging and prey sampling studies in Disko Bay on the western coast of Greenland, in late winter and early spring (Madsen et al. 2001, Laidre et al. 2007, Heide-Jørgensen et al. 2010, 2013, Swailethorp et al. 2011, Laidre & Heide-Jørgensen 2012). However, the sex ratio in these studies was heavily skewed towards non-lactating adult females (85:15 female:male), and is thus not representative of the entire population (Laidre et al. 2007, Heide-Jørgensen et al. 2010). During the spring (February-May), adult females in Disko Bay consumed predominately temperate/subarctic calanoid copepods such as *Calanus finmarchicus* (Laidre et al. 2007). These female bowhead whales made deep, long dives during late winter and comparatively shallower dives during spring (Heide-Jørgensen et al. 2013). Such temporal differences in diving behaviour were likely due to seasonal vertical movements of their prey. The tagged whales were presumed to feed on dormant (i.e., diapausing) copepods at depth during winter, and on active copepods during spring (Heide-Jørgensen et al. 2013), suggesting that adult females seasonally-adjusted their foraging strategy to maximize prey consumption. Whether other demographic groups of bowhead whales employ similar strategies elsewhere during other seasons is unknown.

Little is known about the foraging ecology of bowhead whales in other regions of the ECWG population range. For example, despite the long history of bowhead whale occupancy

and commercial exploitation that occurred in Cumberland Sound (Reeves et al. 1983), few foraging studies have been conducted. In Cumberland Sound, the sex ratio of whales between 2011 and 2013 was 80:125 (female:male), closer to parity than in Disko Bay, but somewhat biased towards males (Frasier et al. 2015). It is also known that males predominate along the east coast of Baffin Island (Southwell 1898), which suggests that many of these males and those in Cumberland Sound are likely counterparts to the adult females found in Disko Bay (Heide-Jørgensen et al. 2010). Given the apparent importance of Cumberland Sound to all demographic groups, including juveniles and mother-calf pairs, assessing diets, foraging behaviour and habitat use in this region fills an important gap in knowledge about the foraging ecology of the Eastern Canada-West Greenland bowhead population.

Differences in zooplankton species abundance have been attributed to the strong influence of the Baffin Island Current, which is of Arctic origin in Cumberland Sound (Dunbar 1951, Aitken & Gilbert 1989, McMeans et al. 2012), along with the West Greenland Current, which is of Atlantic Origin in Disko Bay (Heide-Jørgensen et al. 2013). However, both locations are likely to contain some Arctic and Atlantic fauna because the Baffin Island Current and West Greenland Current are known to mix in both regions (McMeans et al. 2012, Heide-Jørgensen et al. 2013). This may be particularly true along the Davis Strait sill, which may sometimes bring the West Greenland Current to Cumberland Sound (Bedard et al. 2015). Consequently, the quality and quantity of bowhead prey and thus their feeding ecology is likely to differ between habitats and seasonally due to physical oceanographic processes.

Zooplankton communities are expected to differ between Disko Bay and Cumberland Sound, which in turn should influence the feeding behaviour and relative quality of prey consumed by bowhead whales. For example, bowheads in Disko Bay feed predominately on a smaller temperate/subarctic calanoid copepod (*Calanus finmarchicus*), rather than on the less abundant, but larger bodied Arctic copepods (*C. hyperboreus* and *C. glacialis*) (Laidre et al. 2007). Laidre, Heide-Jørgensen, & Gissel Nielsen (2007) collected zooplankton at 25 stations in Disko Bay and found the mean biomass concentration (mg C m^{-3}) of *Calanus finmarchicus* was 49 ± 39 SD compared with 12.3 ± 14.9 SD for *C. hyperboreus* and 2.8 ± 2.3 SD for *C. glacialis*. Conversely, zooplankton species in Cumberland Sound are likely to be dominated by Arctic copepods, but it is not known whether they are preferred by the bowhead whales that feed there. Furthermore, differences in the life-histories of the Arctic and temperate/subarctic copepods likely require different feeding strategies to capture them.

To examine the seasonal foraging behaviour of different demographic groups of ECWG bowhead whales in Cumberland Sound, I used time-depth telemetry tags that recorded horizontal and vertical movements. I examined spatiotemporal trends in movement to determine how bowhead whales used Cumberland Sound throughout the year. I characterized how feeding behaviour (dive depth, shape and duration) changed by day, month, year and over diel time-scales. I then analyzed bowhead whale dive shape, depth and duration and combined information on the species composition and biomass of zooplankton obtained through net collections to determine the importance of Cumberland Sound as a foraging ground. Overall, this research improves understanding of the diet and seasonal foraging characteristics of an understudied segment of the ECWG bowhead whale population.

3.2 Methods

3.2.1 Telemetry

Twenty five bowhead whales were equipped with long-term satellite telemetry tags containing time-depth recorders and Argos transmitters (Wildlife Computers SPLASH MK10) to record horizontal and vertical movements; however, one tag only transmitted for a single day in Cumberland Sound and was thus removed from my analysis. The SPLASH tag provided information on date, time, location, and summary dive behaviour (e.g., depth, duration and shape). To increase longevity of the tag, the Platform transmitter terminals (Ptts) were programmed to transmit up to 400 times a day every second hour during summer, and less frequently during winter (i.e., 100 times every second day). For my study, summer included June to August, fall was between September and November, winter ranged from December to February and spring occurred between March and May.

The whales were tagged in Foxe Basin and Cumberland Sound during summer (2012 and 2013; Table 1). Juvenile and non-lactating adult animals were selected for tagging, which meant excluding animals < 9 m long that were likely calves and those in mother-calf pairs. Each tag was attached with a ~ 20 cm stainless steel anchor, and a skin and blubber sample was simultaneously collected from a 4-cm biopsy tip attached to the tag deployment device. The anchor and biopsy tip were both sterilized with 1:10 bleach/water solution prior to use. Biopsy samples were collected to genetically determine sex and individual id. The tags were deployed from a wooden canoe freighter using an 8-m fiberglass hand-held tagging pole. The

tags were attached dorsally and behind the blow holes to improve data transmission by maximizing the time the transmitter was out of water during a surfacing event.

Table 3.1: Summary information for all 25 bowhead whales tagged in Cumberland (CS) and Foxe Basin (FB) with Wildlife Computers SPLASH Tags (MK10) between 2012 and 2013. Ptt is the platform transmitter terminal used to identify unique individuals. The start date represents the day the animal was tagged and the end date indicates when the tag stopped transmitting. Location is the habitat where the animal was tagged, and length is the estimated body length in meters from the tagging vessel. Animals that visited Cumberland Sound are in bold.

Ptt	Start	End	Duration (days)	Location	Length (m)	Sex
114494	2012-07-03	2013-05-21	322	FB	12	F
114495	2012-07-03	2014-06-26	723	FB	11-12	F
114496	2012-07-03	2013-12-13	528	FB	11	F
114497	2012-07-06	2013-05-10	308	FB	12	M
114498	2012-07-06	2013-02-17	226	FB	11	M
114499	2012-07-06	2013-06-08	337	FB	13-14	F
114500	2012-07-06	2014-02-21	595	FB	12-13	M
114501	2012-07-07	2013-01-05	183	FB	-	-
114502	2012-08-06	2013-07-10	338	CS	10	M
114503	2012-08-06	2014-06-26	689	CS	10	F
114504	2012-08-07	2013-07-19	346	CS	10-11	F
114505	2012-08-08	2013-06-22	318	CS	11-12	M
114506	2012-08-08	2012-08-27	19	CS	13-14	F
114507	2012-08-12	2013-09-19	403	CS	10	M
114508	2012-08-12	2014-08-19	737	CS	9-10	M
114509	2012-08-12	2013-05-26	287	CS	9-10	M
128145	2013-07-03	2014-11-13	498	FB	11-12	F
128146	2013-07-03	2015-05-22	688	FB	13-14	F
128148	2013-07-09	2014-06-06	332	FB	13	F
128149	2013-07-09	2013-07-22	13	FB	12-13	-
128150	2013-07-09	2015-07-08	729	FB	10	F
128151	2013-07-09	2015-07-01	722	FB	9-10	M
128152	2013-07-09	2015-05-24	684	FB	9-10	M
128153	2013-07-03	2014-07-16	378	FB	12-13	M
128154	2013-07-03	2014-05-18	319	FB	11-12	M

3.3 Horizontal movement analysis

The raw Argos data were re-processed with the Square Root Unscented Kalman Filter (SRUKF) by Service Argos. The SRUKF algorithm uses a correlated random walk model that predicts the future position of an animal and its estimated error based on the individual's previous location and estimated error (Silva et al. 2014). I chose the Kalman Filter over Least-Squares algorithm because it tends to increase the number of useful positions and improves the accuracy of low quality Argos locations (e.g., 0, A and B), which are common for large whale tagging studies (Silva et al. 2014, Lowther et al. 2015). As a result of the diving behaviour of the whales (e.g., short surface intervals) and environmental factors (e.g., seasonally ice covered), the bowhead whale telemetric data included many low-quality locations.

The SRUKF filtered data were subsequently run through a speed filter using the `vmask` function in the `argosfilter` package in R (R Development Core Team 2016). This function filters Argos satellite tracking data and is especially designed for marine animals with poor location quality. I used a speed threshold of 2 m s^{-1} , and Argos locations that resulted from swimming speeds above this threshold were subsequently removed.

I fit a hierarchical switching-state-space model (HSSSM) (Jonsen et al. 2005, 2013) to my filtered telemetry data to: 1) estimate the movement of individual animals; 2) determine individuals' behavioural states (area restricted movement and transient); and 3) quantify error in predicted locations. The `bsam` package in R (R Development Core Team 2016) provided in the supplement of Jonsen et al. (2013) was used to fit a correlated random walk model (CRW) that switched between two CRWs that reflected area restricted movement and traveling behavioural states (Jonsen et al. 2005). The two CRWs and the associated behavioural states differ in mean turn angle and swimming speed (Jonsen et al. 2005), whereby, area restricted movement (ARM) reflected instances of low swimming speeds and high turning angles (consistent with foraging behaviour) and traveling consisted of faster, more linear movements. The model (HSSSM) was fit to each data set ($n = 25$) containing individual specific location data with 40,000 Monte Carlo Markov Chain (MCMC) iterations, dropping the first 30,000 (i.e., burn-in) and retaining every 10th sample from the remaining 10,000, resulting in a total of 1,000 samples per chain ($n = 2$ chains).

The HSSSM was chosen because it yields regularly spaced location estimates and categorizes movement behaviour, which is necessary for evaluating the seasonal foraging behaviour of bowhead whales. Behavioural states (b) were classified based on mean estimates from the MCMC samples, which assumed that $b = 1$ was transiting and $b = 2$ was area restricted movement. Consequently, the cut off points I used were the same as previous studies (Jonsen et al. 2007, Silva et al. 2014) and locations with mean estimates of $b > 1.75$ were assumed to indicate ARM; $b < 1.25$ reflected transient behaviour; values between $b > 1.25$ & $b < 1.75$ were unclassified.

Many empirical studies describe the movement of predators relative to the distribution and abundance of their prey. Feeding (or expected feeding based on prior experiences) has been inferred from area restricted movement (or area restricted search) over different spatial scales in fish (Hill et al. 2000), birds (Paiva et al. 2010), and terrestrial (Byrne & Chamberlain 2012) and aquatic mammals (Thums et al. 2011). Predators exhibiting area restricted movement alter their movement pattern to increase the time spent in productive areas by increasing their turning rate after detecting prey (or anticipating the detection of food) and reducing their speed if prey abundance is high (Tinbergen et al. 1967, Kareiva & Odell 1987, Haskell 1997, Fauchald & Tveraa 2003, Higdon & Ferguson 2010, Anderwald et al. 2012). Consequently, feeding animals are thought to spend more time in a given area if they are feeding or searching for food. However, it is also possible that animals conducting other non-feeding behaviours such as mating (Würsig et al. 1993, Richardson et al. 1995) and rock-rubbing (Fortune et al. 2017) can produce similar movement patterns (e.g., low swimming speed and high tortuosity). Therefore, it is important to consider vertical movements when inferring feeding behaviour from horizontal movement patterns.

3.4 Vertical movement analysis

We analyzed the vertical movement of SPLASH tagged animals to determine how foraging effort changed seasonally in Cumberland Sound using the time-depth-recorder dive data. For example, dive duration, shape (V, U, Square or unknown), and minimum and maximum dive depth were recorded with the time-depth recorder (TDR). Dives were classified as vertical excursions to depths ≥ 8 m. The dive shape was classified according to three broad categories defined by Wildlife Computers: V-shaped dives represented those where ≤ 20 % of dive duration was spent at maximum depth, U-shaped dives occurred when > 20 % and ≤ 50

% of the dive duration was spent at maximum depth, and Square dives included those where > 50 % of the dive duration was spent at maximum depth. Previous studies that examined dive profiles of balaenid whales (North Atlantic right whale, *Eubalaena glacialis*, and bowhead whale) in relation to prey availability found that V-shaped dives reflected search behaviour (i.e., non-feeding dives), whereas Square and U-shaped dives where whales maximized their bottom time were most likely representative of foraging dives (Baumgartner & Mate 2003, Laidre et al. 2007, Heide-Jørgensen et al. 2013). For example, during springtime in Disko Bay, bowhead whales conducted deep U-shaped dives near the sea bottom where high abundances of pre-ascension *Calanus finmarchicus* occurred (Laidre et al. 2007). Furthermore, temporal changes in dive behaviour have been documented for bowhead whales, suggesting that individuals adjust their foraging behaviour according to the vertical distribution of their prey (Heide-Jørgensen et al. 2013). Consequently, foraging behaviour may be inferred by examining bowhead whale dive characteristics.

I filtered the bowhead whale dive behaviour data based on the SRUKF Argos location data and only dives occurring within Cumberland Sound were included in my analysis. I then filtered the predicted locations from the HSSSM by removing gaps exceeding four consecutive days based on the SRUKF data as a way to exclude inaccurate data. I merged the behavioural data with the Argos location data by matching dates when tagged animals were inside Cumberland Sound. I assumed that animals did not make short (< 24h) excursions outside of Cumberland Sound and that if there was an Argos location within Cumberland Sound on a particular day, all dives occurring during that same day were conducted inside Cumberland Sound.

I investigated whether there were diel and seasonal impacts on bowhead diving behaviour (e.g., dive depth and duration) using linear-mixed effects models with the lme statistical package in R (R Development Core Team 2016). I fitted several nested linear mixed-effects models and used likelihood ratio tests to examine how season and time of day affect bowhead whale dive depth and duration, along with Akaike's information criterion (AIC) to indicate model support. Since there were multiple dive records per animal (i.e., repeated measures), I included a hierarchical error structure of individual, year, month, and day, along with a continuous autoregressive process within day since measures were irregularly spaced in time (i.e., CAR(1) process; Pinheiro & Bates 2000). I found support for this random effects

structure (i.e., lower AIC and supported by Likelihood Ratio Tests) relative to other more simple random effect error structures for all models.

3.5 Prey Sampling

We collected prey samples to understand why bowhead whales may be utilizing Cumberland Sound as a summertime habitat and how the species composition of zooplankton may differ from Disko Bay (69° 15' N, 53° 33' W). Zooplankton samples were collected in the fluke print of diving bowhead whales using vertical hauling methods and a 333- μ m conical mesh net with a 60-cm diameter mouth opening. The net was outfitted with a General Oceanics helical flow meter and a Sensus Ultra time-depth recorder to determine the sampling distance used to calculate the volume of sampled water. All samples were obtained between 23-26 August 2013 from Kingnait Fiord (65°55' N and -65°25' W) where bowhead whales are regularly observed conducting deep and long dives. Once the vertical tow was completed, the net was sprayed down with the seawater on the deck and all collected organisms were concentrated into the cod end bucket at the end of the net. The concentrated organisms were then filtered through a 333- μ m mesh sieve and transferred to a 250-mL sample jar and fixed with 5% buffered formalin for preservation.

Zooplankton species composition and abundance was determined using taxonomic identification and enumeration methods in the laboratory. Each sample was filtered through a 333- μ m mesh sieve, and subsequently rinsed with freshwater and transferred to a beaker and diluted with water. The sample volume was recorded and a Hensen-stemple pipette was used to obtain a homogenous aliquot (i.e., sub-sample of known volume). A Folsom plankton splitter was used to sub-sample dense samples and the total number of times each sample was split depended on the total number of sample organisms. Each aliquot contained a minimum of 200 calanoid copepods and each organism was identified to the lowest possible taxon (e.g., species and genus for calanoid copepods) and life-stage for *Calanus* spp. and *Pseudocalanus* spp. using a dissecting microscope. I discriminated between morphologically similar *Calanus* species (e.g., *Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus* ; Grainger 1961, Jaschnov 1970) by measuring prosome lengths (e.g., Unstad & Tande 1991, Hirche et al. 1994) for all *Calanus* spp. with undamaged exoskeletons using a dissecting microscope, stage micrometer and ocular micrometer. To minimize measurement variability, I measured all

organisms from the same orientation (right lateral side down). I used species-specific prosome size ranges reported by Madsen et al. (2001) to differentiate species. However, *Calanus* spp. are known to overlap in prosome length, which is particularly likely to introduce error into the identification of early life-stages of *Calanus glacialis* resulting in an over-estimation of *Calanus finmarchicus* (Parent et al. 2011).

Zooplankton biomass was estimated for all *Calanus* organisms with prosome measurements using known relationships between prosome length (mm) and body weight (mg C) using:

$$C_{mg} = a * PL_{mm}^b$$

where $a = 0.0048$ and $b = 3.5687$ for *Calanus finmarchicus* and *C. glacialis* (Madsen et al. 2001) and $a = 0.0014$ and $b = 3.3899$ for *C. hyperboreus* (Hirche & Mumm 1992, Thor et al. 2005). I estimated the individual carbon content of early (CI-CIV) and late (CV-Adult) *Pseudocalanus* spp. by assuming that early stage organisms had mean prosome lengths of 0.597 mm and late stage organisms measured 1.009 mm (Liu & Hopcroft 2008).

Previously collected vertical zooplankton data were also used to further elucidate whether Square-shaped dives were feeding dives and whether temporal shifts in dive depth reflected changes in the vertical distribution of prey. I compared the maximum depth of Square-shaped dives with the depth of maximum zooplankton biomass in Disko Bay (Madsen et al. 2001).

3.6 Results

3.6.1 Telemetry

The sex ratio of the tagged whales occupying Cumberland Sound was somewhat biased towards males (57:43 %), and body lengths ranged from 9.5 to 13.5 m. Age-class was broadly inferred based on previous studies (George et al. 1999, 2011, Higdon & Ferguson 2010, Koski et al. 2010) using boat-based estimates of body lengths that approximated the distance between the tip of the whale's snout to the fluke notch. These estimates revealed that 33% ($n = 3$) of the females were probably adults (> 13 m & > 25 yrs), and 66 % ($n = 4$) were sub-adults (≥ 10 & ≤ 12.5 m and < 25 yrs). No estimated female body lengths were within the range of calves (< 7.5 m & 0-1 yrs) or young juveniles (≥ 7.5 & < 10 m and 1-4 yrs). However, I found that

62.5% (n = 5) of all males were sub-adults and 37.5% (n = 3) were young juveniles. Consequently, my body length estimates suggested that young juveniles, sub-adults and adult animals utilize Cumberland Sound. However, my tagged whale data was biased towards reproductively immature animals for both sexes (particularly males as no adults appear to have been tagged) because the average body length was 10.9 m (\pm 1.3 SD).

Animals tagged in 2012 transmitted for 397 days on average, while those tagged in 2013 transmitted for 485 days (Table 3.1). The HSSSM predicted two daily locations for each animal, resulting in 16,587 locations throughout the Eastern Canadian Arctic. A portion of these locations occurred within Cumberland Sound (12 %). However, of the 14 animals that visited Cumberland Sound, almost one quarter (24 %) of their 8,546 locations were inside the Sound. Furthermore, one animal stayed nearly an entire year (from 9 August 2012 to 18 July 2013) inside Cumberland Sound and just outside the mouth of the Sound. These findings suggest that whales can have a relatively long residency time in Cumberland Sound that occasionally includes overwintering (n = 1).

Seasonal patterns in Cumberland Sound occupancy times were found for SPLASH tagged whales. When data for all years were combined, bowhead whales (n = 14) had the greatest number of locations (two per day) in Cumberland Sound during the fall (n = 890, 43 %), followed by summer (n = 543, 26 %), spring (n = 415, 20 %) and winter (n = 224, 11 %) (Fig. 3.1). When data were separated by year, tagged animals had the highest occupancy in Cumberland Sound during the fall of 2012 (n = 849 locations), summer of 2012 (n = 297) and spring 2013 (n = 251) (Fig. 3.2). Tagged bowhead whales spent the least amount of time in Cumberland Sound during the winter (range 21-116 days between 2012 and 2015). The low occupancy during winter may be partially an artifact of the tag settings, as fewer transmissions were scheduled during winter months to increase tag longevity. Consequently, my results are likely minimum estimates for bowhead whale winter residency in Cumberland Sound.

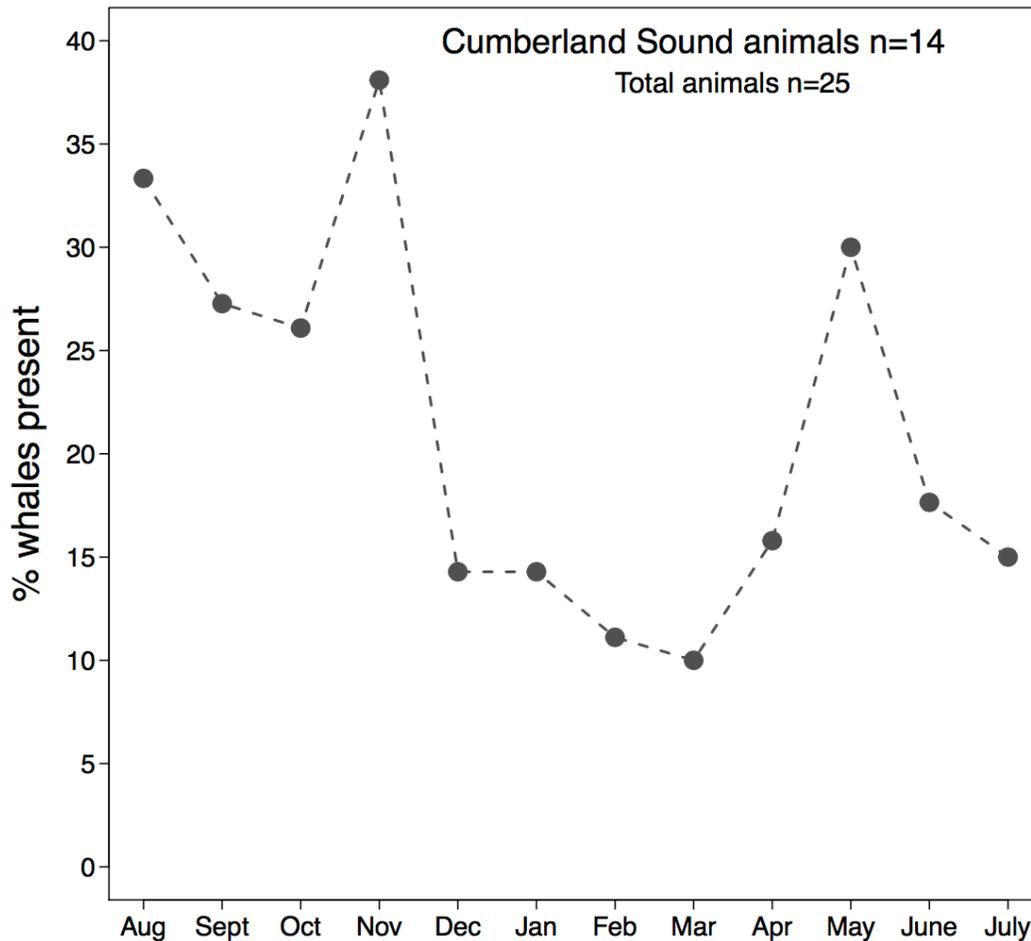


Figure 3.1: The proportion of SPLASH tagged bowhead whales in Cumberland Sound by month across all years (2012–2015). All animals were tagged during the summer in Foxe Basin (July) and Cumberland Sound (August) during 2012 and 2013. One tag transmitted for only 13 days (Ptt 128149) during July 2013 after deployment, making August the month with the maximum number of tagged animals (n=24) when all years are combined.

3.6.2 Behaviour

The bowhead whales in Cumberland Sound displayed pronounced differences in behavioural states (*b*) as determined by the HSSSM. The majority of all estimated locations in Cumberland Sound (n = 2072) were associated with ARM (presumably foraging behaviour) based on the weighted average ($91.4\% \pm 10.72\text{ SD}$) (Fig. 3.3), whereby the percentage of HSSSM locations with ARM for an individual whale was weighted by the total number of HSSSM locations for that whale when calculating the weighted average. Traveling behaviour rarely occurred and represented only 2.17% ($\pm 3.69\text{ SD}$) of all locations. The remaining 6.32% ($\pm 7.59\text{ SD}$) of locations were of an unknown behavioural state. Furthermore, I found

seasonal differences in the proportion of locations assumed to be associated with ARM behaviour. Most notably, ARM was greatest during the fall ($95.3\% \pm 7.99$ SD of all locations based on weighted mean), followed by the spring ($91.3\% \pm 19.61$ SD), summer ($89.3\% \pm 12.65$ SD) and winter ($81.3\% \pm 27.6$ SD). The high percentages of ARM behaviour suggest that bowhead whales consistently allocate time to foraging activities while occupying Cumberland Sound.

3.6.3 Diving

Of the 14 tagged whales that visited Cumberland Sound, one (Ptt 114498) had only a single location within the Sound and no associated dives. The remaining 13 whales dove a total of 21,144 times over 456 days in Cumberland Sound (Fig. 3.4). The whales conducted predominately Square (68.2% , $n = 14,419$) and U-shaped dives (22.2% , $n = 4,692$), whereas V-shaped (8.5% , $n = 1,805$) and unclassified-shaped dives (1.1% , $n = 228$) were a small portion of the total (Table 3.2). I inspected the summary dive statistics (e.g., range, mean \pm SD) for unusually high values that would exceed the physiological diving limits of the species. I found two V-shaped dives that were extraordinarily deep and long in duration, such that the maximum depth was 976 m and the minimum dive duration was 114 hours. I subsequently removed these biologically improbable outliers from my analysis. Furthermore, only two tagged animals occupied Cumberland Sound during February ($n=354$ Square dives) and March ($n=427$ Square dives).

When evaluating whether bowheads allocated more or less time to probable feeding dives during different seasons, I found an interaction between season and dive shape for dive duration (Table 3.3; log-likelihood ratio test LRT = 1269.9, $p < .0001$). In particular, Square dives had the longest duration, particularly during winter (Fig. 3.5). To permit inferences about the seasonal vertical movement of zooplankton based on the assumed connection between the zooplankton depth and bowhead whale probable feeding depth, I examined impacts of dive shape and season on dive depth. As with dive duration, I found an interaction between dive shape and season (Table 3.3; LRT = 1295.5, $p < .0001$). For example, Square-shaped dive depth was shallow (≤ 50 m) during spring and early to mid-summer and comparatively deeper (≥ 150 m) during fall and winter (Fig. 3.5). I also found that the maximum depth of Square-shaped dives agreed well with the seasonal depths of maximum zooplankton biomass in Disko

Bay (Madsen et al. 2001) (Fig. 3.6), providing further evidence that the depth where bowhead whale feeding occurs changes seasonally in Cumberland Sound.

Through initial examination of bowhead whale dive depths during the day and night (Figs. 3.5 – 3.7), I found evidence of diel diving behaviour for eight animals during early and late August 2012. During early August (August 1-15), I found that the maximum depth (Table 3.4; LRT = 20.2, $p < .0001$) and minimum dive duration (Table 3.4; LRT = 29.7, $p < .0001$) of Square-shaped dives differed for periods of daylight (day) versus darkness (night). However, these results concerning diel effects should be interpreted with caution since the changes in AIC compared to the null model were relatively small. During early August, the maximum depths of Square dives were 122 m (± 80 SD) during the day and 59 m (± 46 SD) during the night based on the average depth of each individual's mean Square-shaped dive depth. Similarly, I found that the depth (Table 3.4; LRT = 36.4, $p < .0001$) and duration (Table 3.4; LRT = 69.9, $p < .0001$) of Square-shaped dives differed substantially in late August (August 16-31) during the day and night. Although less pronounced than during early August, the depths of Square dives were considerably deeper during the day (250 m ± 32 m SD) compared with the night (159 m ± 59 m SD) during late August. Bowhead whales similarly conducted longer dives during the daytime (18.85 min ± 1.936 min SD) than the nighttime (14.61 min ± 2.664 SD) during late August.

We also found evidence of diel diving behaviour during April when data from 2013 and 2015 were pooled together for three animals (Table 3.4; LRT = 20.6, $p < .0001$). Square-shaped dives were substantially deeper during the day (193 m ± 57 SD) and somewhat shallower at night (131 m ± 55 SD). Overall, I found that bowhead whales conducted deeper and longer Square-shaped dives during daylight hours in August (Figs. 3.7 & 3.8) and to a lesser extent in April. However, there was considerable variability in dive depth that is likely due to individual variation in foraging strategies and variability in the vertical distribution of prey (Fig. 3.8). It is important to consider that these diel diving models were constructed for specific time periods based on initial examination of the dive data.

We found that bowhead whales spent a portion of their day (21-22%) conducting Square and U-shaped dives in Cumberland Sound during summer. Overall, the whales appeared to allocate the most time to probable feeding dives during summer (5.0 ± 1.52 hrs) and the least during spring (2.5 ± 0.76 hrs) (Table 3.5). However, the time bowheads allocated

to probable foraging dives on a daily basis was quite variable during summer. For example, the maximum time individual animals spent conducting Square dives ranged from 9.7 to 14.2 hours in 2012 and between 5.8 and 11.7 hours in 2013. These results suggest that individuals occasionally allocated considerable time to feeding activities—but tended to use a relatively small portion of the day to feed on average (i.e., 20.8% or 5 hrs).

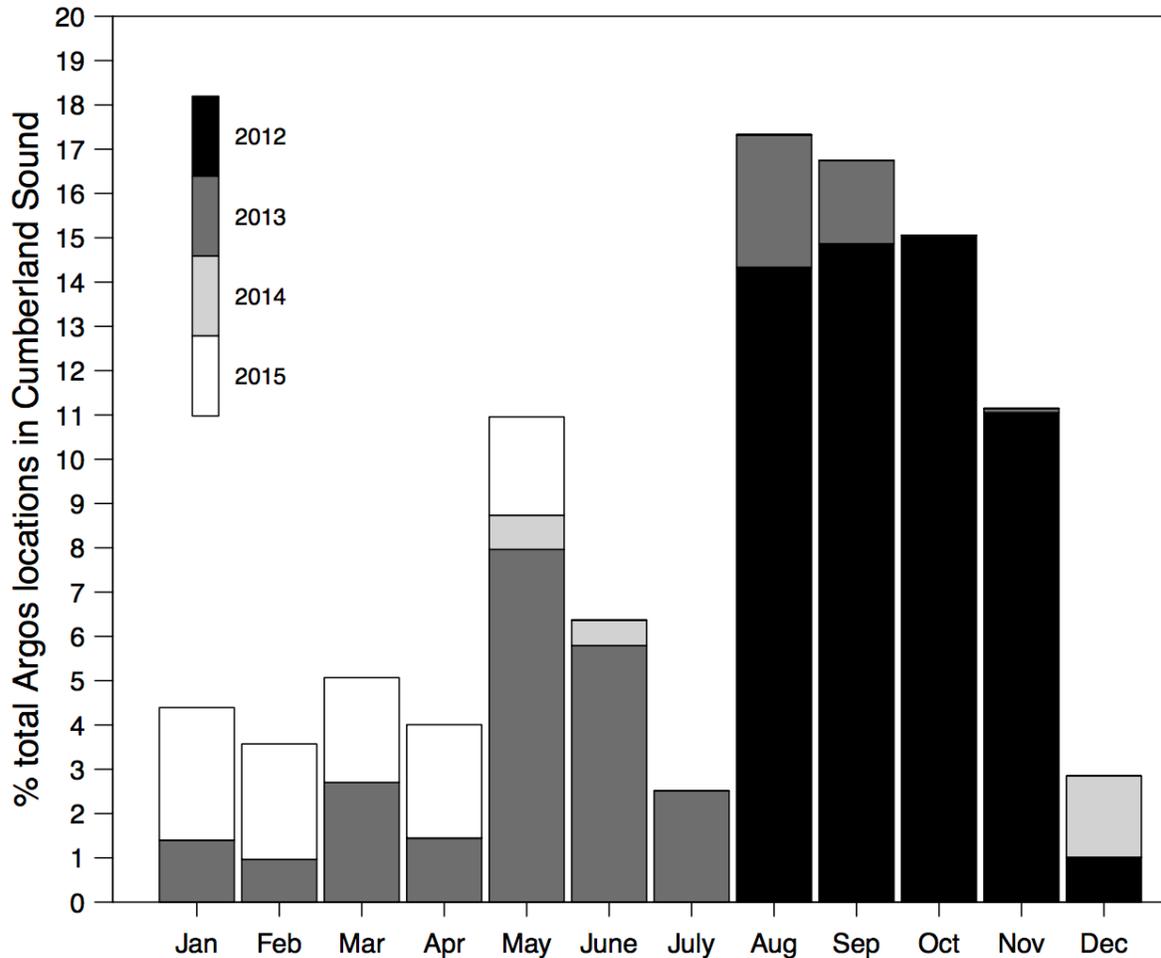


Figure 3.2: Total number of locations 14 SPLASH tagged bowhead whales (n = 2072) spent in Cumberland Sound by month and year based on HSSSM predicted locations. No animals were found in Cumberland Sound during the spring of 2012 as the whales were first tagged during the preceding summer of 2012.

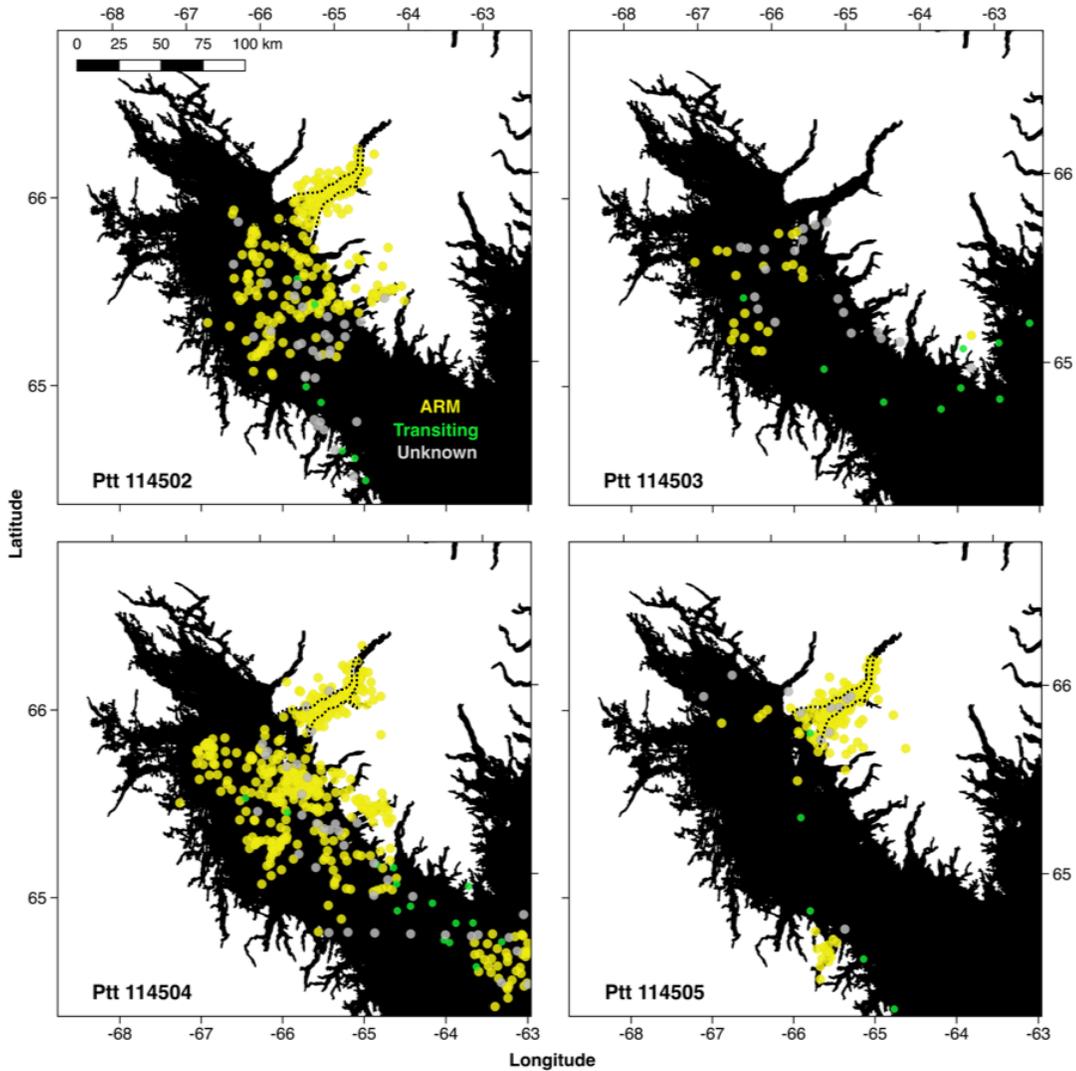


Figure 3.3: Argos satellite locations for 4 SPLASH tagged bowhead whales (Ptt 114502, 114503, 114504, 114505) derived from hierarchical switching state-space models (HSSSM) in Cumberland Sound with two locations per day. HSSSM predicted locations resulting from gaps in Kalman filtered Argos data exceeding 4 consecutive days were considered less reliable than predictions made from locations closer in time, and were removed from analysis. Three behavioural states derived from the HSSSM are indicated with yellow, green, and grey circles reflecting area-restricted movement (i.e., probable feeding), traveling behaviour, and an unknown behavioural state, respectively.

Table 3.2 Summary dive statistics for Square-, V- and U-shaped dives in Cumberland Sound between 2012 and 2015 for 13 bowhead whales. Data were pooled across months and years. Two V-shape dives (> 700 m depth and > 75 minutes in duration) were considered erroneous and removed from the analysis.

Maximum dive depth (meters)				
Shape	Range (min-max)	Mean ± SD	Skew	Kurtosis
Square	8-655.5	165.23± 128.81	0.101	1.53
U	8-543.5	61.82 ± 88.30	3.310	15.34
V	8-451.5	45.91 ± 58.81	2.216	7.21
Minimum dive duration (minutes)				
Square	0.42-47.4	16.46 ± 8.31	-0.080	2.15
U	0.12-40.3	6.68 ± 6.70	1.629	6.86
V	0.58-50.8	8.07 ± 6.36	1.599	5.45

Table 3.3: Linear mixed-effects models for the impacts of dive shape and season on dive duration and maximum depth. The change in AIC (Δ AIC) and likelihood ratio tests (LRT) are relative to the model earlier in the list for dive duration and for maximum depth. These indicate that there are interactions between dive shape and season for both dive duration and maximum depth.

Model	Fixed	df	AIC	LR test	Δ AIC
Dive duration (mins)					
null	~1	20212	310158.6	~	~
1	~Shape	20209	306052.7	4111.883 (p<.0001)	4105.9
2	~Shape+Season	20209, 31	306031.3	27.39382 (p<.0001)	21.4
3	~Shape*Season	20200,31	304779.4	1269.908 (p<.0001)	1251.9
Maximum dive depth (m)					
null	~1	20212	244571.1	~	~
4	~Shape	20209	243113.0	1464.026 (p<.0001)	1458.1
5	~Shape+Season	20209, 31	243103.2	15.849 (p=0.0012)	9.8
6	~Shape*Season	20200,31	241841.5	1295.518 (p<.0001)	1261.7

Table 3.4: Linear mixed-effects models for the impacts of time of day (i.e., day or night based on sunset and sunrise during early and late August 2012) on Square dive duration and maximum depth. The change in AIC (Δ AIC) and likelihood ratio tests (LRT) are relative to the model earlier in the list for dive duration and for maximum depth and indicate that there are diel effects on both dive duration and maximum depth.

Model	Fixed	df	AIC	LR test	Δ AIC
Early August Maximum Square dive depth (m)					
null	~1	1314	14336.3	~	~
7	~day.night	1313	14318.2	20.102 (p<.0001)	18.1
Early August Minimum Square dive duration (mins)					
null	~1	1314	18643.8	~	~
8	~day.night	1313	18616.1	29.663 (p<.0001)	27.7
Late August Maximum dive depth (m)					
null	~1	1495	18706.6	~	~
9	~day.night	1494	18672.2	36.353 (p<.0001)	34.4
Late August Minimum dive duration (mins)					
null	~1	1495	22703.9	~	~
10	~day.night	1494	22636.0	69.879 (p<.0001)	67.9

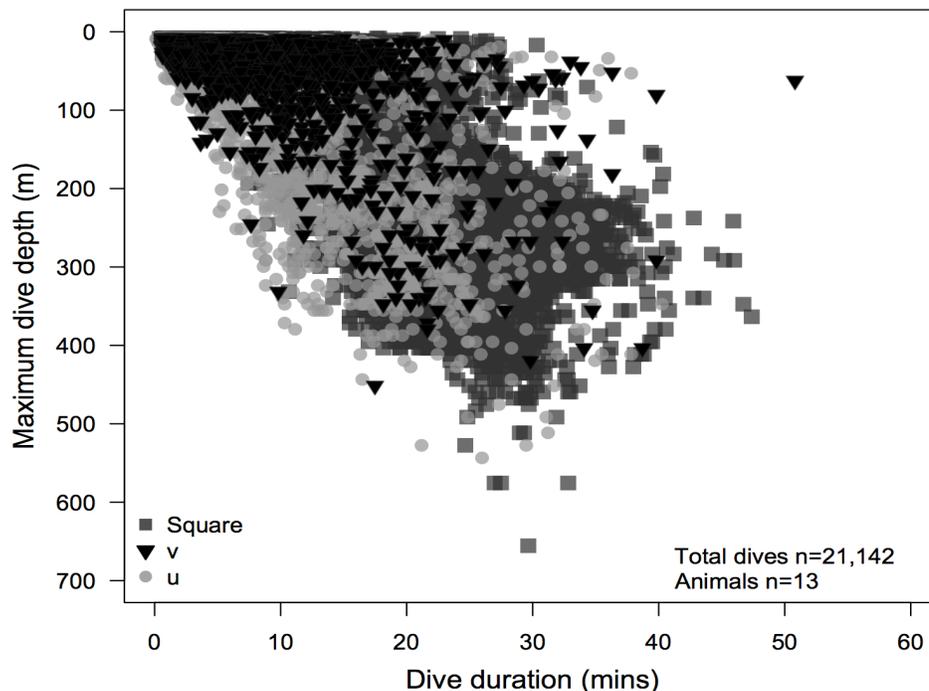


Figure 3.4: Maximum depth and duration for Square-, U- and V-dives for 13 bowhead whales equipped with SPLASH tags while in Cumberland Sound between 2012 and 2015. Data were pooled across months and seasons. Square-shaped dives were considerably deeper and longer in duration compared to V-shaped dives, suggesting that they reflect feeding behaviour.

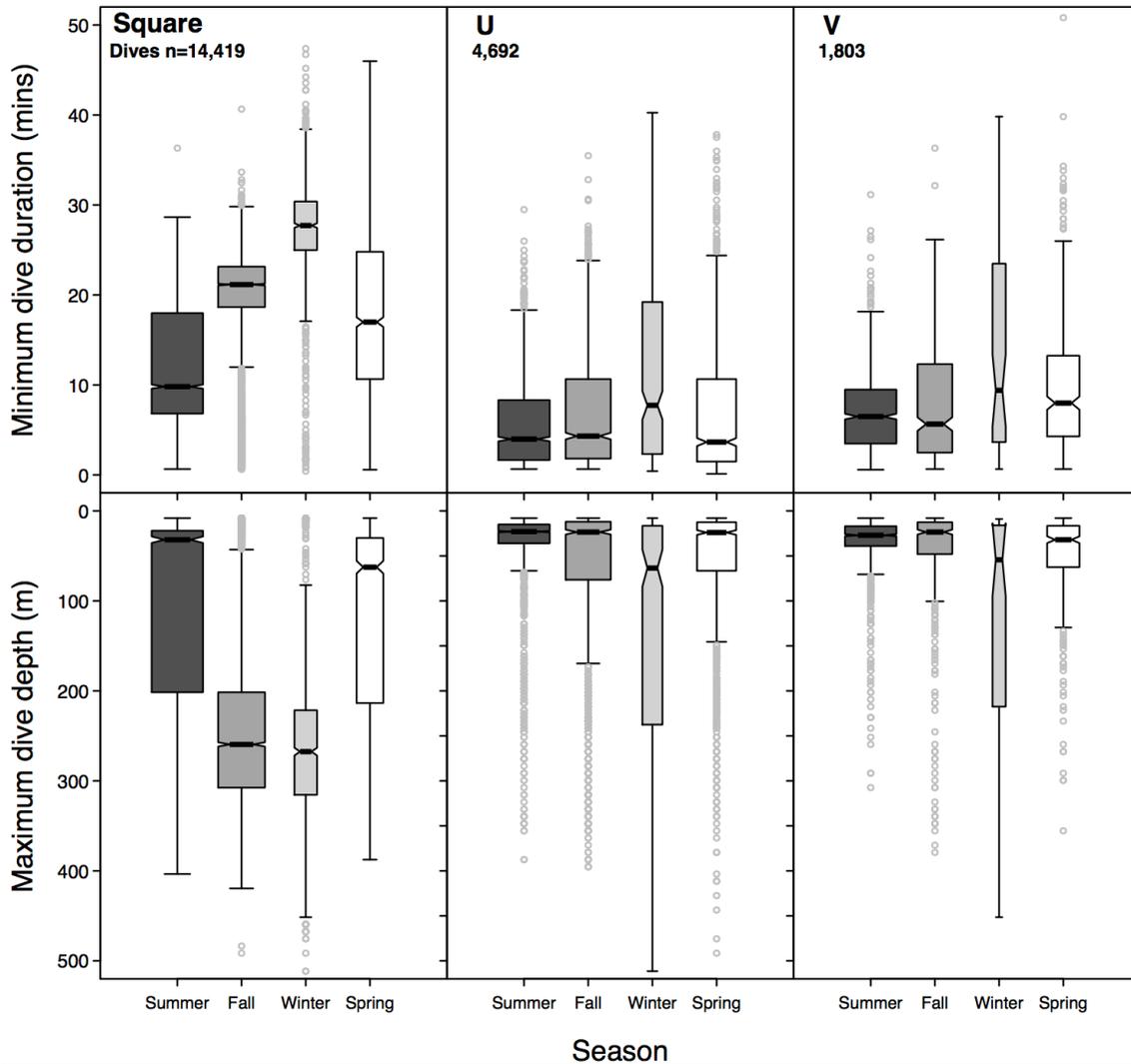


Figure 3.5: Minimum dive duration (minutes) and maximum dive depth (meters) by season and type of dive (Square, U and V) for 13 bowhead whales that occupied Cumberland Sound. The greatest temporal differences observed between dive depth and duration occurred for Square-shaped dives, which likely reflect foraging behaviour. U- and V-shaped dives showed little seasonal variation and remained consistently shorter and shallower than Square dives. The width of the boxes is proportional to the Square-root of the number of dives per month (i.e., the wider the box, the greater the sample size). Instances where the notches of two boxes do not overlap provides evidence that the medians differ. The black bar represents the median, the box represents the interquartile range, the whiskers reflect the non-extreme maximum and minimum values and the grey dots indicate extreme values.

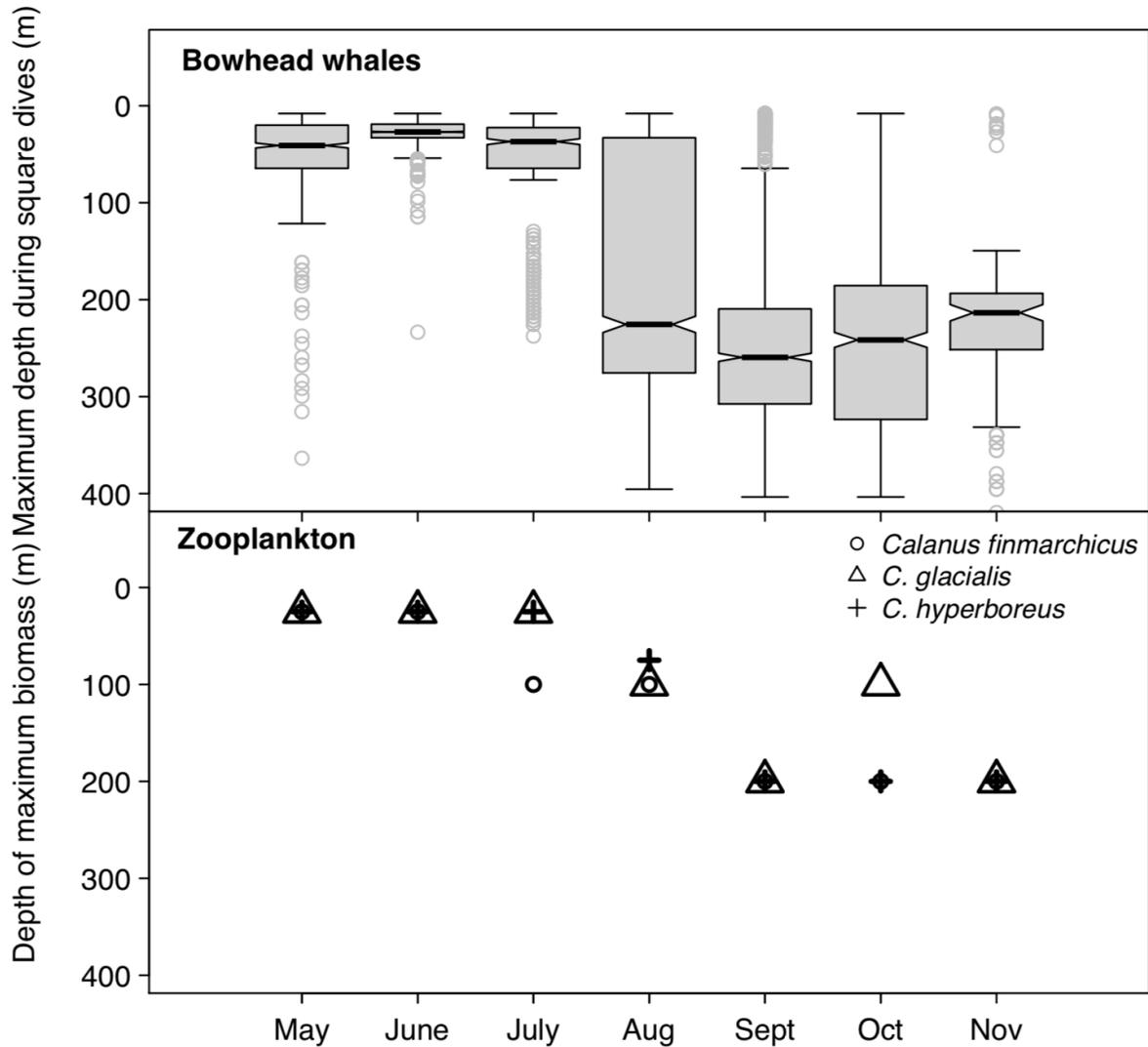


Figure 3.6: Comparison of the maximum depth (meters) of Square-shaped dives for bowhead whales during the daytime in Cumberland Sound (n = 13 animals) and the depth of maximum zooplankton biomass (meters) of three dominant calanoid copepod species (*Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*) collected in Disko Bay—a habitat along western Greenland at a similar latitude to Cumberland Sound. The plotted zooplankton data were collected and reported by Madsen et al. (2001).

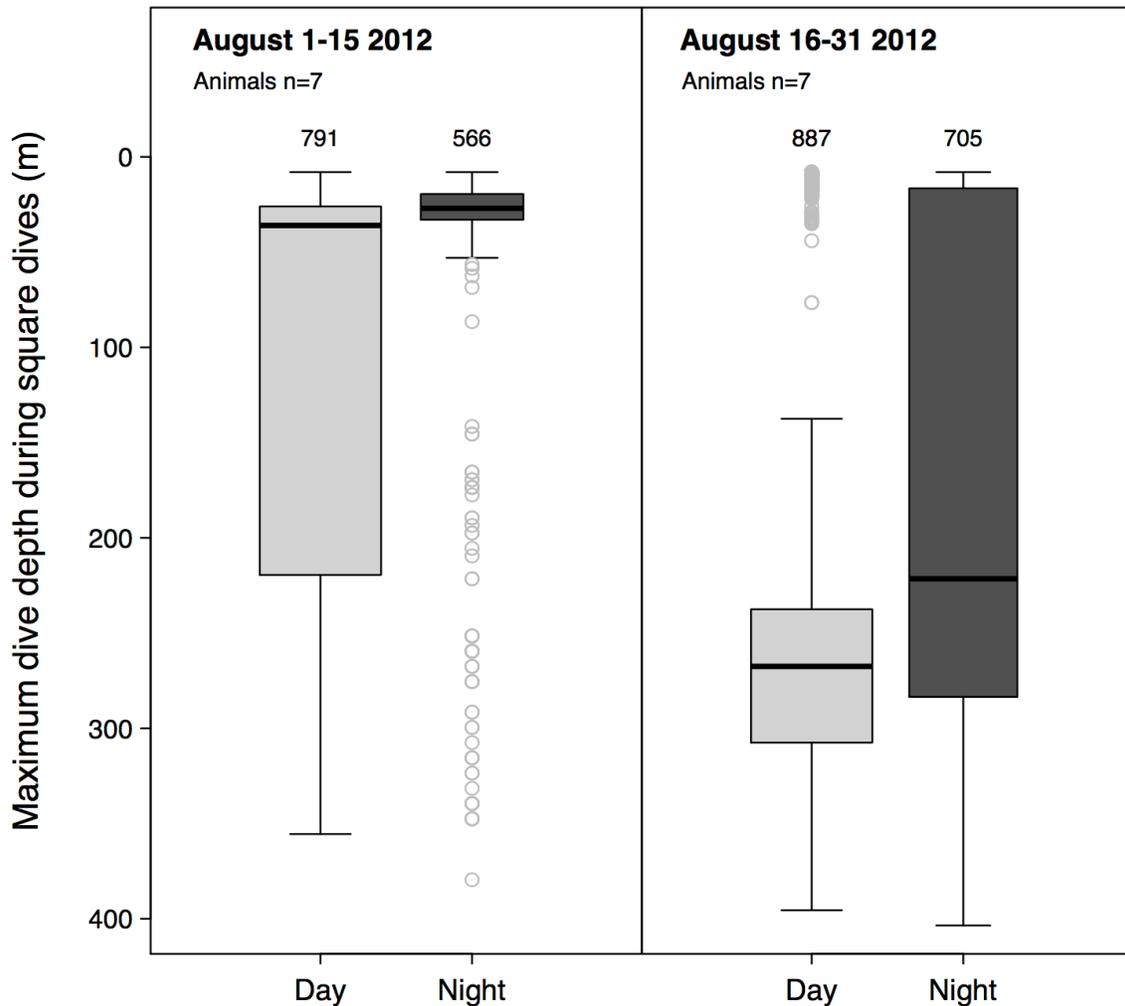


Figure 3.7: Maximum dive depth during Square dives (meters) for 8 bowhead whales in Cumberland Sound during early (Aug 1-15) and late (Aug 16-31) August 2012. Diel vertical migration of calanoid copepods appears to occur particularly during late August based on the median depth of bowhead whale Square dives being considerably deeper during the day and shallower at night. During early August, Square-shaped dives occurred near the surface during both the day and night. However, dive depth remained deepest during the day. This change in bowhead whales dive behaviour (i.e., increasingly deep dives during the day and night) during late August may reflect the initiation of diapause for some calanoid copepods.

3.6.4 Zooplankton

We collected seven zooplankton samples near diving bowhead whales in Kingnait Fiord during August 2013. Species identification revealed that the full water-column tows consisted almost exclusively of calanoid copepods ($94 \% \pm 0.03$ SD). Of the copepods, *Pseudocalanus* spp. was the most common ($55 \% \pm 0.05$ SD) followed by *Calanus* spp. ($36 \% \pm 0.57$ SD) (Fig. 3.9). Due to the prevalence of *Pseudocalanus* spp. and *Calanus* spp., I only calculated abundance (orgs m^{-3}) for these organisms. I found that *Pseudocalanus* spp. represented the greatest proportion of total abundance ($61 \% \pm 5.9$ SD) on average followed by *Calanus glacialis* ($27 \% \pm 5.8$ SD), *C. finmarchicus* ($8.4 \% \pm 2.0$ SD) and *C. hyperboreus* ($4.2 \% \pm 1.5$ SD) (Fig. 3.10). I measured prosome lengths for 91 % ($n = 623$) of all staged *Calanus* spp. ($n = 682$). Prosome measurements were variable within and between taxa due to species-specific and ontogenetic variation in size. On average, an individual copepod was estimated to contain 0.015 mg C ind^{-1} (± 0.036 SD) for *C. finmarchicus* as compared with 0.107 mg C ind^{-1} (± 0.159 SD) for *C. glacialis* and 0.124 mg C ind^{-1} (± 0.122 SD) for *C. hyperboreus*. I used mean estimates of weight (mg C ind^{-1}) for early (CI-CIV) and late (CV-Adult) individuals per species and their associated abundance per tow to calculate mean dry weight per cubic meter (mg C m^{-3}). I found that estimated dry weight was dominated by *C. glacialis* ($72 \% \pm 7.9$ SD; 0.87 mg $m^{-3} \pm 0.41$ SD), followed by *Pseudocalanus* spp. ($12 \% \pm 4.7$ SD; 0.13 mg $m^{-3} \pm 0.04$ SD), *C. hyperboreus* ($11 \% \pm 5.6$ SD; 0.13 mg $m^{-3} \pm 0.11$), and *C. finmarchicus* ($5 \% \pm 2.4$ SD; 0.06 mg $m^{-3} \pm 0.02$) (Fig. 3.10). Absolute abundances and weights of *Calanus* and *Pseudocalanus* spp. are reported in the Appendix (Table A3).

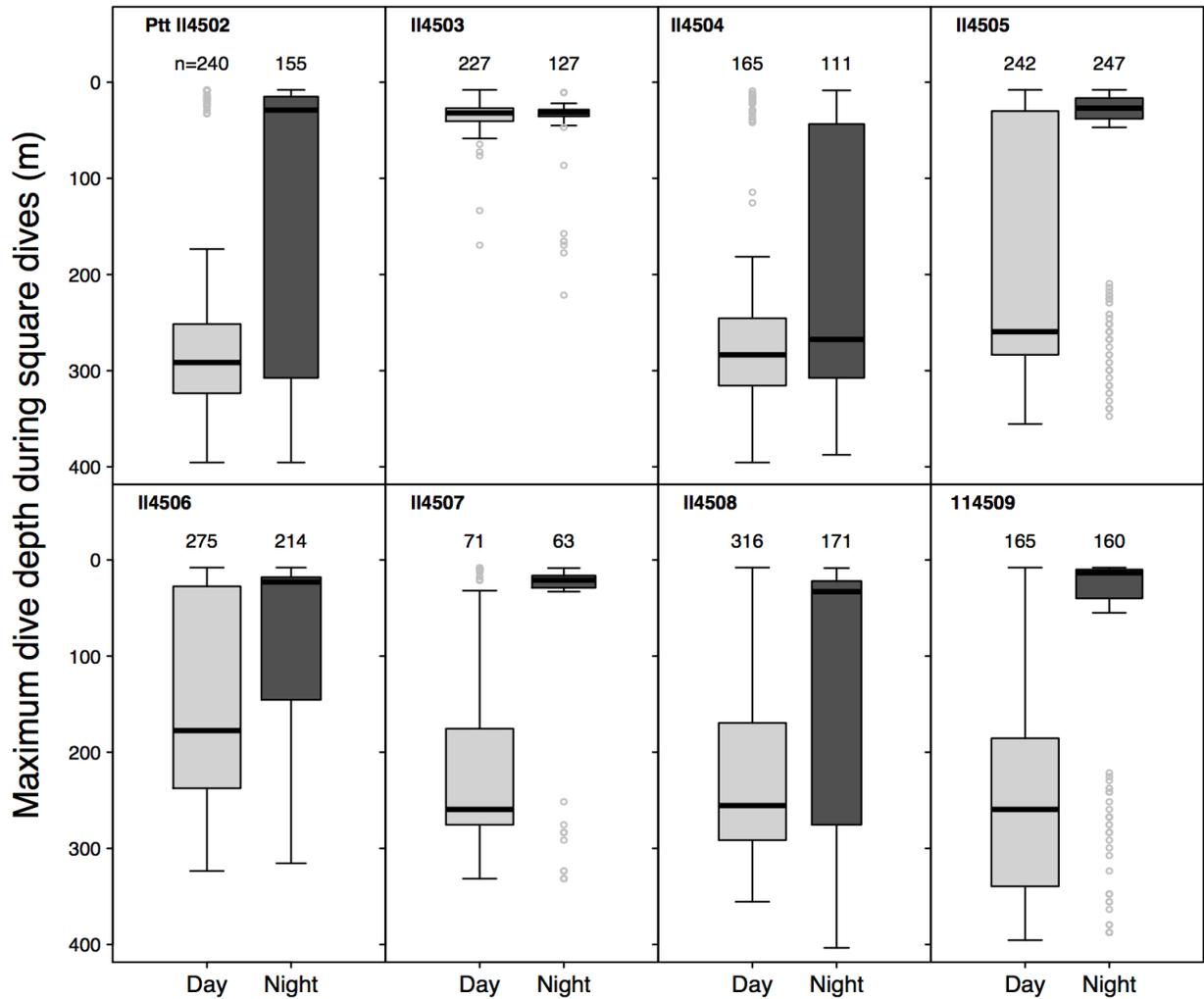


Figure 3.8: Maximum dive depth (meters) of Square-shaped dives during the day and night for 8 bowhead whales in Cumberland Sound during August 2012. Diel dive patterns were observed for all animals (with the exception of Ptt 114503), whereby the maximum depth of Square dives was deepest during the day and shallowest at night. There was considerable variation in the diel diving patterns between the individual tagged whales.

Table 3.5: Average time spent making Square-shaped dives per day in Cumberland Sound. Dive durations were pooled across years for each animal that spent a minimum of 5 days in Cumberland Sound per season. Dive durations were first averaged to provide a mean daily dive time per individual, and then averaged across individuals.

Season	Square dives (mean \pm SD)	Years	# Animals
Summer	5.0 \pm 1.52 hrs	2012 & 2013	9
Fall	4.5 \pm 1.53 hrs	2012 & 2013	6
Winter	4.6 \pm 2.44 hrs	2012-2015	4
Spring	2.5 \pm 0.76 hrs	2013 & 2015	5

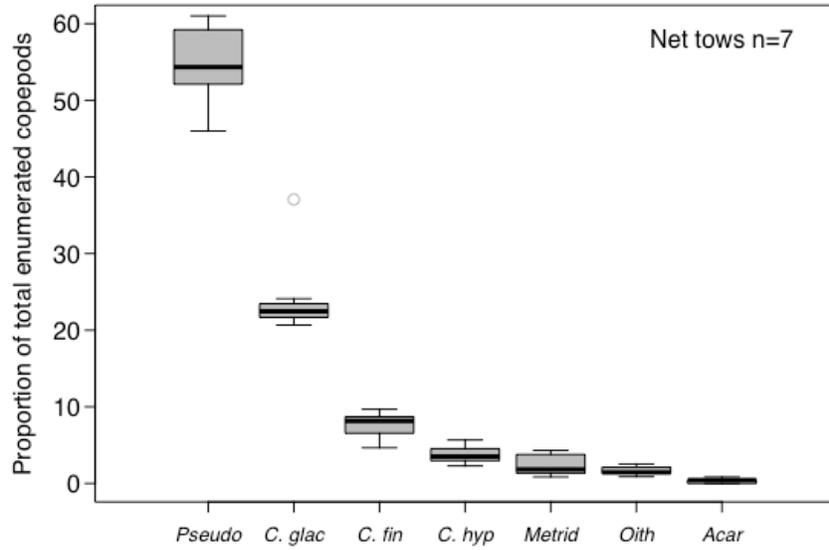


Figure 3.9: The proportion of enumerated calanoid copepods per sample for *Pseudocalanus* spp., *Calanus glacialis*, *C. finmarchicus*, *C. hyperboreus*, *Metridia* spp., *Oithona* spp., and *Acartia longiremis* with all life-stages grouped together.

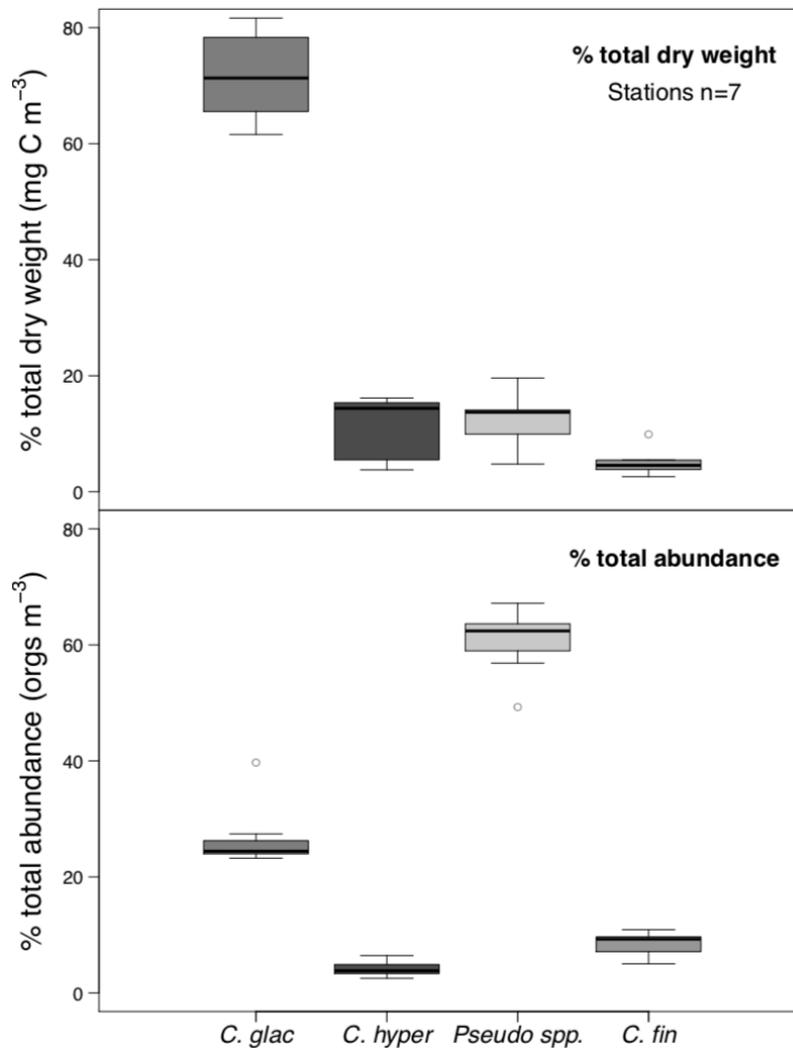


Figure 3.10: Percent contribution by species to total biomass (mg C m⁻³) (top) and total abundance (orgs m⁻³) (bottom) based on 7 net tows in Kingnait Fiord during August 2013. Abundance and biomass calculations were made for the most common species identified—*Calanus glacialis*, *C. hyperboreus*, *C. finmarchicus* and *Pseudocalanus spp.* The boxplot shading is relative to the total lipid content per individual species with the darkest shading representing the species with the highest energy content (e.g., *C. hyperboreus*) and the lightest representing the lowest energy prey (*Pseudocalanus spp.*) (DeLorenzo Costa et al. 2006, Falk-Petersen et al. 2009).

3.7 Discussion

Our analysis of long-term (> 365 days) bowhead whale horizontal and vertical movements provides new insights into habitat-use patterns and feeding behaviour that previous studies have not captured using smaller datasets and with biologgers that provided less detailed dive information. Most notably, I found that whales resided in Cumberland Sound during all four seasons with one animal remaining all year. However, peak occupancy occurred during summer

(26 %) and fall (43 %). Furthermore, almost all of the satellite telemetry locations (91 %) were associated with area-restricted movement, suggesting that Cumberland Sound is a year-round feeding area. These findings provide a new understanding of the feeding behaviour of bowhead whales, and the biological significance of Cumberland Sound to the Eastern Canada-West Greenland population.

3.7.1 Evidence of feeding behaviour

The feeding behaviours of bowhead whales and the closely related North Atlantic right whale (*Eubalaena glacialis*) have been inferred from horizontal movement data collected from satellite telemetry tags and from vertical dive data recorded using time-depth recorders. Previous studies that examined dive profiles of balaenid whales in relation to prey availability found that Square- and U-shaped dives where whales maximized their bottom time were representative of foraging dives (Baumgartner & Mate 2003, Laidre et al. 2007, Heide-Jørgensen et al. 2013, Baumgartner et al. 2017). In one study, bowhead whales conducted deep U-shaped dives near the sea bottom in Disko Bay (western Greenland) where high abundances of pre-ascension *Calanus finmarchicus* occurred (Laidre et al. 2007). Other studies of bowhead whales in the Eastern Canadian Arctic found that changes in swimming speed, turning radius and diving frequency could be used to evaluate bowhead whale feeding activity (Pomerleau, Patterson, et al. 2011, Nielsen et al. 2015). Together, these studies demonstrate that biologging can provide considerable information regarding the sub-surface foraging behaviour of large whales.

We observed the tagged whales occupying Cumberland Sound during all months. However, peak foraging likely occurs during late summer and early fall based on high occupancy during that time inferred from hierarchical-switching-state-space models that were parameterized with satellite telemetry data (Figs. 3.2 & 3.3). The greatest number of HSSSM locations occurred during August (2012 = 14.3 % & 2013 = 3 %), followed by September (2012 = 14.9 % & 2013 = 1.9 %), October (2012 = 15.1 % & 2013 = 0 %) and November (2012 = 11.1 % & 2013 = 0.09 %) for 14 animals. The residency period was long (25 days; 6 August to 31 August 2012) for the 8 animals tagged in Cumberland Sound during August 2012, suggesting that this is an important area for a portion of the population. Furthermore, results from the state-space models demonstrated that just over 90 % of all HSSSM locations were associated with behaviours typically thought to reflect feeding activities (e.g., slow swimming speed and high turning angles).

Bowhead whales in Cumberland Sound allocated considerable time to sub-surface foraging activities based on the vertical dive data (≥ 8 m). They made mostly Square- (68 %) and U-shaped (22 %) dives that were consistent with foraging dives recorded for North Atlantic right whales (Baumgartner & Mate 2003) in the western Atlantic. However, unlike North Atlantic right whales that are believed to spend the majority (50-90 %; Goodyear 1996) of their day foraging while occupying their summer feeding grounds such as the Bay of Fundy, bowhead whales spent only a small fraction (21-22 %) of their day conducting Square and U-shaped dives during the summer in Cumberland Sound. This finding provides support that Cumberland Sound is a multi-use habitat that serves functions beyond feeding such as rock-rubbing for exfoliation (Fortune et al. 2017)

Overall, the dive durations for right whales (12.2 min \pm 2.22 SD; Baumgartner & Mate 2003) and bowhead whales (12.0 min \pm 3.3 SD) were remarkably similar during the summer. Both species dove to comparable depths on average (mean dive data averaged across individuals), whereby right whales dove to 121.2 m (\pm 24.2 SD) (Baumgartner & Mate 2003) and bowheads similarly dove to 117.4 m (\pm 52.4 SD). This suggests that the increased time right whales allocated to foraging is unlikely related to differences in the vertical distribution of their prey. Interspecific differences in daily feeding activities may instead reflect disparities in: 1) the quality and quantity of available prey; 2) the spatial-heterogeneity of prey patches; 3) energetic requirements; and 4) environmental conditions.

3.7.2 Seasonal feeding patterns

Some large whales have highly seasonal feeding seasons marked by intense feeding during summer in productive high latitude habitats, and fasting over winter in lower latitude areas (e.g., Corkeron & Connor 1999, Kenney et al. 2001, Christiansen et al. 2013). However, unlike a proportion of right whales that presumably fast for a significant portion of the year while occupying southern calving grounds between December and March (Keller et al. 2012), bowheads appear to feed year round in Cumberland Sound based on > 50 % of their dives each season being probable foraging dives. I found that bowheads allocated the most time to foraging dives during the summer in Cumberland Sound on average (5.0 \pm 1.52 hrs) and the least amount during spring (2.5 \pm 0.76 hrs) (Table 3.5). However, there was a lot of individual variability in the time allocated to probable foraging dives, suggesting that bowheads alternated between days when they spent over half the day feeding (e.g., 60%) and others when they spent only a small fraction of the day

engaged in feeding activities. Variability in individual feeding times may reflect differences in energy requirements based on age, sex, reproductive and nutritive condition (Lockyer 1981, George 2009, Miller et al. 2012, Fortune et al. 2013).

The apparently reduced feeding time during spring may reflect the presence of zooplankton near the surface during the phytoplankton bloom, making it more accessible with less effort by the whales. It is also possible that feeding time was underestimated during spring if whales were exploiting prey patches located between 0 and 7 m in the water column (as North Atlantic right whales do during spring; Baumgartner et al. 2017). Another possible explanation for why bowhead whales allocated less time than right whales to feeding activities during the summer is that they may have comparatively lower daily food requirements, in part because they appear to feed continuously throughout the year. Bowheads also have comparatively thicker blubber stores (Haldiman & Tarpley 1993, Rosa 2006, George et al. 2007) compared with North Atlantic right whales (Moore et al. 2004, Miller et al. 2011) and may opt to catabolize this energy store during lean years, providing a greater capacity to fast. It is also possible that bowhead whales have lower basal metabolic rate (i.e., hypometabolic condition; George 2009), and hence lower daily energy requirements, compared to North Atlantic right whales.

Our conclusion that bowheads feed year-round in Cumberland Sound is consistent with prior telemetry and diet studies. Previous satellite-tagging studies similarly found that bowhead whales occupied Cumberland Sound during winter months. One study reported that predominately adult females, originating from Disko Bay, occupied Cumberland Sound between late July and mid-December (Nielsen et al. 2015). Another study recorded one whale in Cumberland Sound during late July that then traveled to the high-Arctic and subsequently returned to Cumberland Sound in early January and remained within the area until the start of May (Pomerleau, Patterson, et al. 2011). My conclusion that bowhead whales are feeding year round is further supported by dietary stable isotope analysis of Eastern Canada-West Greenland bowhead whales that also reported year round foraging (Matthews & Ferguson 2015). Year-round feeding may be an artifact of 1) a population below carrying capacity and 2) favorable physical and biological oceanographic conditions that support calanoid copepod production throughout their range. Consequently, due to their apparently flexible feeding strategy, bowhead whales may be able to reduce their summertime foraging effort compared to right whales.

The plasticity of bowhead whale's feeding strategy is also reflected by seasonal adjustments in dive behaviour. The depth of probable foraging dives (i.e., Square dives) varied seasonally, suggesting that the vertical distribution of zooplankton fluctuates seasonally in Cumberland Sound. This was seen in the maximum depth of Square dives becoming increasingly deeper during summer ($122.7 \text{ m} \pm 59.3 \text{ SD}$), fall ($218.9 \text{ m} \pm 22.5 \text{ SD}$) and winter ($253.1 \pm 111.5 \text{ SD}$)—and becoming shallower during spring ($73.5 \pm 50.4 \text{ SD}$; all years combined for all individuals that spent a minimum of 5 days inside Cumberland Sound per season; Fig. 3.5).

Inferences may be made about the vertical distribution of bowhead prey in Cumberland Sound based on the life-history characteristics of calanoid copepods and zooplankton sampling research conducted in an adjacent habitat, Disko Bay, Greenland. The composition of zooplankton in Disko Bay is similarly dominated by herbivorous calanoid copepods, such as *Calanus finmarchicus*, *C. hyperboreus* and *C. glacialis*, which occur in maximum numbers at depths that change seasonally (Madsen et al. 2001). However, I found that biomass in Cumberland Sound was dominated by larger-bodied Arctic species on average (*C. glacialis* 72%, *C. hyperboreus* 11% and *C. finmarchicus* 5%), which differs from Disko Bay where *Calanus* spp. biomass was dominated by a *C. finmarchicus* (76%), a temperate/subarctic species, followed by *C. hyperboreus* (20%) and *C. glacialis* (4%). Interestingly, depths of maximum zooplankton biomass from Disko Bay were similar across taxa and compared well with seasonal differences in the depths of bowhead whale foraging dives in Cumberland Sound (Fig. 3.6). This agreement between zooplankton depth distribution and bowhead diving behaviour suggests that *Calanus* spp. have similar seasonal vertical movements at similar latitudes on either side of Davis Strait, and that bowhead whales likely adjust their foraging behaviour (e.g., deep vs. shallow Square dives) in response to changes in the vertical distribution of their prey. However, the seasonal timing of changes in copepod vertical distribution may be somewhat different in Cumberland Sound than in Disko Bay because of oceanographic differences. Consequently, future research is necessary to address spatio-temporal gaps between bowhead whale dive data and zooplankton vertical distribution data.

Calanoid copepods of the Calanidae and Eucalanidae families have life cycles that correspond with seasonal changes in physical and biological oceanographic conditions and feature pronounced vertical movements. In response to reductions in food availability following the spring phytoplankton bloom and increasing predator abundance, lipid-rich life stages of *Calanus* spp. descend to deeper waters (below the winter convective mixed layer for organisms in fiords and shelf seas; Irigoien 2004). Once organisms have vertically migrated, they commence diapause (a

form of dormancy) whereby the cooler water temperatures and reduced activity suppress metabolic rates to decrease catabolism of lipid reserves (Madsen et al. 2001, Heide-Jørgensen et al. 2007, Laidre et al. 2007). Some species (e.g., *Calanus finmarchicus* and *C. glacialis*) may ascend prior to or at the start of the spring phytoplankton bloom to either refuel their lipid reserves to permit spawning or replenish their energy reserves after egg production (Tande 1982, Tande et al. 1985, Niehoff et al. 2002, Madsen et al. 2008, Baumgartner & Tarrant 2017). Larger bodied and longer-lived species such as *Calanus hyperboreus*, however, employ a different reproductive strategy and spawn during the winter while at depth using stored energy (Hirche & Niehoff 1996). The lipid-rich and positively buoyant eggs develop to feeding stage nauplii as they ascend to the surface waters, ready to begin grazing at the start of the phytoplankton bloom (Jung-Madsen et al. 2013).

Zooplankton biomass should be high in the surface waters during the spring phytoplankton bloom and decrease over the late summer months as phytoplankton is grazed down and copepods begin to migrate to depth and enter diapause. The timing and duration of diapause, however, is highly variable and depends on the life-history and reproductive strategy of different species (Falk-Petersen et al. 2009) and on seasonally induced changes in environmental conditions such as ice retreat and solar irradiance (Baumgartner & Tarrant 2017).

Bowhead whale diving behaviour is likely to reflect seasonal movements in the vertical distribution of their prey. Previous studies found that phytoplankton production was highest in Cumberland Sound during late June in 2007 and August 2008 (McMeans et al. 2012). Consequently, I would anticipate surface aggregations of zooplankton to begin forming during early to mid-summer following the retreat of sea ice and persisting until late-summer with diapause commencing during early fall. These seasonal patterns in vertical zooplankton distribution should be reflected in the depth of probable foraging dives of bowhead whales (e.g., Fig. 3.5 & 3.6). I found that tagged bowheads made shallow Square dives during May-August and began making deep dives during the latter half of August—presumably when a pronounced reduction in phytoplankton occurred and zooplankton initiated diapause. Consequently, it appears as though August and September are a transitional period in Cumberland Sound whereby zooplankton begin their vertical migration to depth.

3.7.3 Diel patterns in feeding activity

Zooplankton undergo short-term daily vertical movements in addition to longer-term seasonal shifts in their distribution. For example, *Calanus* spp. make daily excursions below the euphotic zone at dawn to avoid presumed visual predators such as zooplanktivorous fish (Bollens & Frost 1989). Zooplankton will ascend towards the surface after dusk to graze on phytoplankton that is concentrated in the mixed layer (e.g., Bollens & Frost 1989, Durbin et al. 1995, Baumgartner et al. 2011, Sainmont et al. 2013, Vestheim et al. 2013). Such diel vertical migration appears to be a strategy employed to minimize predation risk. However, predator avoidance means foregoing feeding opportunities for part of the day and incurring energetic costs to move through the water column.

Perhaps unsurprisingly, not all copepods undergo diel vertical migration (DVM). One possible reason is that some size classes may be too small to be at risk of being eaten by visual predators and therefore can remain feeding (i.e., smaller copepods are less likely to be visually detected and thus less likely to undergo vertical migration; Hays 1995). However, some copepods are also known to undertake reverse DVM, whereby organisms occupy surface waters during the day and descend to depth at night in response to standard DVM by their invertebrate predators (Ohman et al. 1983). Finally, individuals with full or nearly full oil sacs may conduct DVM to avoid predators, whereas organisms with less full oil sacs may remain in the surface waters to feed during the day and night because the benefit of accumulating more lipid outweighs the potential risk of predation (Huntley & Brooks 1982, Baumgartner et al. 2011). In all likelihood, the avoidance of predators and accumulation of lipid during most years of high primary productivity likely drives strong diel rhythms in copepod vertical distribution in Cumberland Sound during summer.

We observed changes in bowhead whale diving behaviour that were consistent with diel vertical migration of their prey. Interestingly, the depth of Square-shaped dives was consistently deeper during the day compared with the night during August and April, when there are pronounced periods of daylight and darkness (12 hour separation) during the start of spring and fall. Between the end of June and the beginning of July there are over 20 hours of daylight, leaving little darkness to warrant diel vertical migration. I found that Square-shaped dive depth was consistently deeper during the day compared with the night for 8 whales occupying Cumberland Sound during August 2012. During the first two weeks of August, the depth of Square dives was

significantly deeper during the day ($122 \text{ m} \pm 80 \text{ SD}$; mean dive depth averaged for each unique individual) and shallower at night ($59 \text{ m} \pm 46 \text{ SD}$) (Fig. 3.8). Similarly, in late August, bowhead whale dives were significantly deeper during the day ($250 \text{ m} \pm 32 \text{ SD}$) and shallower during the night ($159 \text{ m} \pm 60 \text{ SD}$). However, these late August dives were consistently deeper than dives made earlier that month regardless of time of day. Changes in photoperiod and light intensity may be a circadian cue that initiates diel vertical migration, thus affecting the vertical distribution of bowhead whale prey (Forward 1988).

In contrast to my observation of diel patterns in bowhead diving behaviour in Cumberland Sound, a prior study in the Eastern Canadian Arctic (Pomerleau, Patterson, et al. 2011) found no such behaviour. One possible explanation for this difference is that bowhead whales in the Eastern Arctic study were found at higher latitudes (e.g., Gulf of Boothia) where day length is comparatively longer. Longer daylight (e.g., midnight sun) may diminish or eliminate the mass diel movement of zooplankton (Blachowiak-Samolyk et al. 2006). Further south in Disko Bay, which is at a similar latitude to Cumberland Sound, bowhead whale prey (e.g., *Calanus glacialis* and *C. hyperboreus*) have been reported to undergo diel vertical migrations during late April and early May (Swailethorp et al. 2011).

In the absence of data on the vertical distribution of zooplankton in Cumberland Sound, I can only speculate about what influenced bowhead whale foraging behaviour. It seems unlikely that the shift in dive depths during early and late August was due to temporal differences in day length because there was only about one additional hour of darkness during late August ($\sim 16 \text{ h}$ day length) compared with early August ($\sim 17 \text{ h}$ day length). Of the bowhead Argos locations in Cumberland Sound during early August, only 57.9 % of the locations were in Kingnait Fiord. Conversely, during late August, the spatial distribution of tagged whales changed as they were almost exclusively found in Kingnait Fiord. It is possible that physical oceanographic process differed in Kingnait Fiord thus altering the vertical structure of prey in the water column or that the prey bowhead whales were targeting in Cumberland Sound during early August were following classic DVM due to the co-occurrence of other known zooplanktivorous predators, such as Arctic char (*Salvelinus alpinus*) and capelin (*Mallotus villosus*) (Marcoux et al. 2012), that were otherwise absent in Kingnait Fiord. However, during late August, some copepods (e.g., lipid rich *Calanus glacialis* and *C. hyperboreus*) may have begun their vertical descent to depth to commence diapause.

It is possible that copepods with less accumulated lipid may remain in the surface waters to continue foraging, and only enter diapause once they have accumulated sufficient lipids (e.g., Visser & Jónasdóttir 1999, Rey-Rassat et al. 2002, Campbell & Dower 2003, Irigoien 2004, Maps et al. 2010, 2012, Baumgartner & Tarrant 2017). Asynchronous diapause has been observed for *Calanus finmarchicus* in the North Atlantic Ocean (Tarrant et al. 2008). If diapause were similarly asynchronous in Cumberland Sound, bowheads may exploit deep-water aggregations of diapausing copepods during the day and night while also exploiting shallowly aggregated active prey after dusk. Future zooplankton sampling studies will be required to determine the spatio-temporal variability in diel vertical migration and the relationship between zooplankton depth distribution and bowhead whale dive behaviour (e.g., Baumgartner et al. 2011).

3.8 Conclusions

My findings provide new insight into the flexible feeding strategy of an understudied segment of the Eastern Canada-West Greenland bowhead whale population and the importance of Cumberland Sound as a year-round foraging area. Through analysis of the time spent conducting horizontal (e.g., slow swimming speed and high tortuosity) and vertical (e.g., Square-shaped dives) movements, I found that both sexes likely fed during all months in Cumberland Sound, although late summer and early fall appear to be particularly important feeding times. Unlike Disko Bay where zooplankton biomass appears to be dominated by temperate/subarctic species (e.g., *Calanus finmarchicus*), it appears that bowheads are exploiting mostly Arctic species (e.g., *Calanus glacialis*), which are comparatively larger in size and higher in lipid content (Falk-Petersen et al. 2009). There were also distinct seasonal and diel patterns in bowhead whale dive behaviours that appear to correspond to temporal changes in the vertical distribution of their prey related to well-studied life-history characteristics.

The apparent flexibility of bowhead whales to exploit seasonally available prey throughout the year in Cumberland Sound bodes well for their ability to adapt to climate-induced changes to their habitat. What is less certain, however, is how climate change will alter the species composition and abundance of their primary prey, and whether bowhead whales can adapt their foraging strategies to contend effectively with such changes to their prey base.

Chapter 4: Bowhead whales forage year-round in the eastern Canadian Arctic

4.1 Summary

The eastern-Canada and West-Greenland population of bowhead whales (*Balaena mysticetus*) is widely distributed throughout the Eastern Canadian Arctic (ECA) and is known to migrate seasonally in response to changing sea ice conditions (formation and melt). However, foraging behaviour of this population and the biological importance of their seasonally-occupied habitats are largely unknown. I collected long-term movement (>365 days) and dive behaviour data for 25 bowhead whales equipped with time-depth telemetry tags, and used hierarchical switching-state-space models to quantify their movements and behaviours (feeding and traveling). I found 73% (n=12,200) of the locations were associated with area-restricted movement (ARM) that is consistent with feeding behaviour, while 13% (n=2,205) of the locations were associated with traveling and 14% (n=2,272) were unclassified behaviours. Furthermore, 66% (n=151,314) of all dives ≥ 8 m were associated with ARM and 89% of these dives were probable feeding dives (Square and U-shaped), suggesting that the whales were feeding while engaged in ARM. I also found dives indicative of feeding behaviour increased seasonally from 17% of all Square-shaped dives during winter, to 13% during spring, 40% during summer and 30% during fall. Overall, my diving and Argos location data identify 6 feeding areas (Cumberland Sound, Foxe Basin, Hudson Strait and Frobisher Bay, Hudson Bay, Gulf of Boothia, and Central East Baffin Coast) and indicate that bowhead whales forage throughout the year in the Eastern Canadian Arctic (with probable peak feeding occurring between July and September).

4.2 Introduction

Determining what influences the distributions of marine species is fundamental to understanding their ecology. In the case of cetaceans, distributions of individuals and populations are generally considered to reflect habitat conditions (e.g., physical and environmental), biological constraints (e.g., prey availability, presence of predators and competitors), demography (e.g., population size and demographic composition), species adaptations (e.g., morphological, physical, and behavioural), and interactions with humans (e.g., disturbance and pollution) (Kenney et al.

2001, Cosens & Blouw 2003, Keller et al. 2006, Ford & Reeves 2008, Hlista et al. 2009, Ferguson et al. 2010, Heide-Jørgensen et al. 2010, Moore et al. 2010, Robertson et al. 2013, Gregr et al. 2013, Reinhart et al. 2013). Although cetacean distributions are not equally constrained by each of these factors, the challenge of observing cetaceans has made it difficult to know which are the ultimate factors.

What is known about the distribution and habitat use of whales has largely come from historic whaling data, systematic sighting surveys and tagging studies. Of these three techniques, whaling records have provided insights into the historic distribution and number of whales (Reeves et al. 1983, 1999, 2004, Aguilar 1986, Reeves & Mitchell 1986, Reeves 2001), but have sometimes proven unreliable (e.g., Rastogi et al. 2004). Systematic boat-based and aerial surveys have tended to provide short-term (days to weeks long) pictures of species distribution and demographic composition (Cosens et al. 1997, George, Zeh, et al. 2004, Brown et al. 2007, Nichols et al. 2008, Diemer et al. 2011, Asselin et al. 2012), while telemetry studies provide longer-term (weeks to months) pictures of the distributions of a few individuals based on detailed surface (satellite-linked tags) and underwater (time-depth recorders) location data (Mate et al. 1997, Wiley N & Goodyear D 1999, Baumgartner & Mate 2005, Laidre et al. 2007, Pomerleau, Patterson, et al. 2011, Heide-Jørgensen et al. 2013). Such telemetry tags also provide information about large-scale movements, seasonal patterns in distribution and habitat use.

Satellite tracking tags have shown that bowhead whales (*Balaena mysticetus*) belonging to the eastern-Canada and West-Greenland population are widely distributed throughout their range and make long, seasonal migrations (e.g., Heide-Jørgensen et al. 2003, Ferguson et al. 2010, Pomerleau et al. 2011, Nielsen et al. 2015). This population of bowhead whales is generally found in Hudson Strait, northern Hudson Bay, east Baffin Island and along the ice edge of West Greenland during winter (Reeves & Heide-Jørgensen 1996, Koski et al. 2006)—and along the west coast of Greenland, and the eastern and southern coasts of Baffin Island in Cumberland Sound, Foxe Basin and Lancaster Sound in spring (Ferguson et al. 2010, Pomerleau, Patterson, et al. 2011). By summer, they are widely dispersed between northern fiords and bays in the Canadian High Arctic (such as the Gulf of Boothia; Pomerleau et al. 2011) and southern waters (such as Hudson Bay and Foxe Basin; Cosens et al. 1997, Cosens & Innes 2000, Ferguson et al. 2010, Higdon & Ferguson 2010). However, by winter, they again concentrate along the southern edge of their range as ice forms.

Satellite-telemetry has shown broad-scale movement patterns of bowhead whales in the Eastern Canadian Arctic, but has not revealed what the whales are doing in the different habitats they occupy. Similarly, the small number of bowhead whales tracked to date has prevented determining demographic specific habitat preferences and temporal variations in bowhead whale habitat use patterns (which may reflect inter-annual variation in prey quality and quantity). These short-comings can be addressed by increasing samples sizes and using bio-logging tags that record diving depths as well as locations.

I studied the movement, distribution and habitat use patterns of bowhead whales in the Eastern Canadian Arctic using long-term tags equipped with satellite transmitters and time-depth recorders. I also explored seasonal patterns and inter-annual variability in bowhead habitat use for animals with long tag-attachment times, and compared the residency patterns of different demographic groups within the same habitats. Thus, I sought to identify seasonally important habitats of bowhead whales in the Eastern Canadian Arctic, and to determine when and where different demographic groups feed.

4.3 Methods

4.3.1 Telemetry

A total of 25 bowhead whales were equipped with long-term satellite telemetry tags that included time-depth recorders (Wildlife Computers SPLASH MK10). The SPLASH tag recorded date, time, location and summary dive behaviour (i.e., depth, duration, and shape of dive). The Platform transmitter terminals (Ptts) were programmed to maximize tag longevity to cover as much of the annual whale migrations as possible. Consequently, the tags were programmed to transmit up to 400 times a day every second hour during the summertime and only 100 times every second day during winter.

The 25 bowhead whales were tagged in two habitats, Foxe Basin and Cumberland Sound, during the summer of 2012 and 2013. There were 16 whales tagged during July and August 2012 in Foxe Basin (4 females, 3 males and 1 of unknown sex) and Cumberland Sound (3 females and 5 males). In July 2013, 9 juvenile and adult whales (4 non-lactating females, 4 males and 1 of unknown sex) were tagged in Foxe Basin. Females with newborn calves were not approached for tagging.

A ~20-cm stainless steel anchor was used to attach the tag to the whale's blubber, and a 4-cm biopsy tip to simultaneously collect a skin and blubber sample for genetic analysis and to determine sex. A 1:10 bleach/water solution was used to sterilize the anchor and biopsy tip prior to use. The tags were deployed using an 8-m fiberglass hand-held tagging pole, and attached them in the middle of the back posterior to the blowholes. Placing the tag in this location improved data transmission by maximizing the time the transmitter was above the water.

4.3.2 Horizontal movement analysis

I used the Square Root Unscented Kalman Filter (SRUKF) algorithm developed by Service Argos to re-process the raw Argos data. This algorithm consists of a correlated random walk model that uses the individual's previous location and estimated error to predict an animal's future position (Silva et al. 2014). I selected the Kalman Filter over the Least-Squares algorithm because it typically results in an increased number of positions and improved accuracy of low quality Argos locations (e.g., location classes 0, A and B) that are common for large whale tagging studies (Silva et al. 2014, Lowther et al. 2015). The bowhead whale telemetry data are typically biased towards low-quality locations due to diving behaviour (e.g., short surface intervals between dives) and the environment (e.g., seasonally ice covered).

Argos telemetry data for marine animals often contain some poor quality records. I therefore filtered out the poor data using a speed filter (`vmask` function in the `argosfilter` package in R; R Development Core Team 2009) to remove SRUKF Argos locations that would have resulted from biologically improbable swimming speeds. I set a speed threshold of 2 m/s, and removed locations with swimming speeds greater than this from the data set.

I used the hierarchical switching-state-space Model (Jonsen et al. 2005, Jonsen et al. 2013) to estimate the movement of individual whales and determine the behavioural state associated with each location (e.g., travelling and area-restricted movements). Jonsen et al. (2013) provided the R package 'bsam' (R Development Core Team 2009), which I used to fit a correlated random walk model (CRW). The CRW switched between two CRWs, one that reflected area-restricted-movement (ARM) behaviour and another that reflected traveling behaviour (Jonsen et al. 2005). Mean turn angle and swimming speed were used to differentiate the two CRWs and the associated behavioural states (Jonsen et al. 2005). Low swimming speeds and high turning angles reflected ARM, whereas faster and more linear movements reflected 'traveling' behaviour. ARM behaviour

is assumed to be associated with foraging (e.g., Haskell 1997, Hill et al. 2000, Fauchald & Tveraa 2003, Thums et al. 2011, Byrne & Chamberlain 2012).

I selected the hierarchical switching-state-space model because it provides regularly spaced location estimates and categorizes behaviour, which I needed to determine the seasonal foraging behaviour of bowhead whales in the Eastern Canadian Arctic. I defined seasons as being summer (June, July, August), fall (September, October, November), winter (December, January, February) and spring (March, April, May), and used mean estimates from the Markov Chain Monte Carlo (MCMC) samples to classify behaviour states (b), which assumed that $b=1$ was transiting and $b=2$ was ARM. I used the same cut off points for b as done by others (Jonsen et al. 2007) such that locations with mean estimates of $b > 1.75$ were assumed to reflect ARM and $b < 1.25$ reflected traveling behaviour. Values of b that fell between 1.25 and 1.75 were assigned an unclassified behavioural state.

4.3.3 Vertical movement analysis

I analyzed the diving behaviour of bowhead whales in the Eastern Canadian Arctic using the time-depth-recorder (TDR) dive data to determine: 1) where foraging habitats likely occurred, and 2) how feeding effort changed seasonally throughout their range. The TDR recorded several dive statistics such as dive shape (V, U or Square), maximum dive depth and duration. Dives included excursions to depths ≥ 8 m. The shape of the dive was classified using Wildlife Computers' three broad categories: V-shaped dives included dives where $\leq 20\%$ of total duration was spent at maximum depth, U-shaped dives occurred when $> 20\%$ and $\leq 50\%$ of total duration was spent at maximum depth and Square dives included those where $> 50\%$ of the duration was spent at maximum depth.

Dive shape classification may be used to infer behaviour. Previous foraging ecology studies of balaenid whales have concluded that Square and U-shaped dives that maximize bottom time reflect foraging dives (Baumgartner and Mate 2003, Laidre et al. 2007, Heide-Jørgensen et al. 2013). For example, bowhead whales off the coast of Disko Bay during spring, conducted deep U-shaped dives to depths where high abundances of pre-ascension *Calanus finmarchicus* were concentrated (Laidre et al. 2007). Furthermore, bowhead whales appear to temporally adjust the depth of their U-shape dives, suggesting that individuals alter their feeding behaviour based on the vertical distribution of their prey (Heide-Jørgensen et al. 2013).

I excluded unreliable data from my analysis by removing locations predicted from the state-space model that had gaps exceeding 4 consecutive days (based on the SRUKF data). I subsequently merged the behavioural data with the Argos location data based on matching dates and assumed that animals remained in a specific habitat for the entire day. I also assumed that if there was an Argos location within a habitat on a particular day, all dives occurring during that same day were similarly conducted inside that habitat.

Linear-mixed effects models were used to investigate whether there were seasonal patterns in bowhead whale dive shape, depth and duration using the lme statistical package in R (R Development Core Team 2009). The lme was chosen because it addresses violations of independence (Pinheiro and Bates 2000) associated with having multiple dive records per animal (i.e., repeated measures). I included a hierarchical structure in the random effects whereby individual, year, month and day were nested. Violations of temporal independence in the dive data were accounted for by including a continuous autoregressive process (CAR(1) process for a continuous time covariate), which suits irregularly spaced time-series data.

I fit several linear-regressions to test for differences between fixed-factors (e.g., dive shape, month, habitat, year and sex) for dive depth and duration using maximum likelihood, and used ANOVA ($\alpha=0.05$) to determine the “best” model in terms of fixed-effects factors. Conditional F-tests were used to determine the significance of the model slope, intercept and fixed-effects, and I chose to report F-values for model slopes only as all model intercepts were highly significant ($P \leq 0.001$). Model selection was conducted using log-likelihood ratio tests (LRT) whereby an ANOVA was performed on two nested models (null without fixed-effects and alternative model with fixed-effects). The LRT results were used to determine whether the null model was significantly improved with the addition of fixed-effects. I also used the Akaike’s Information

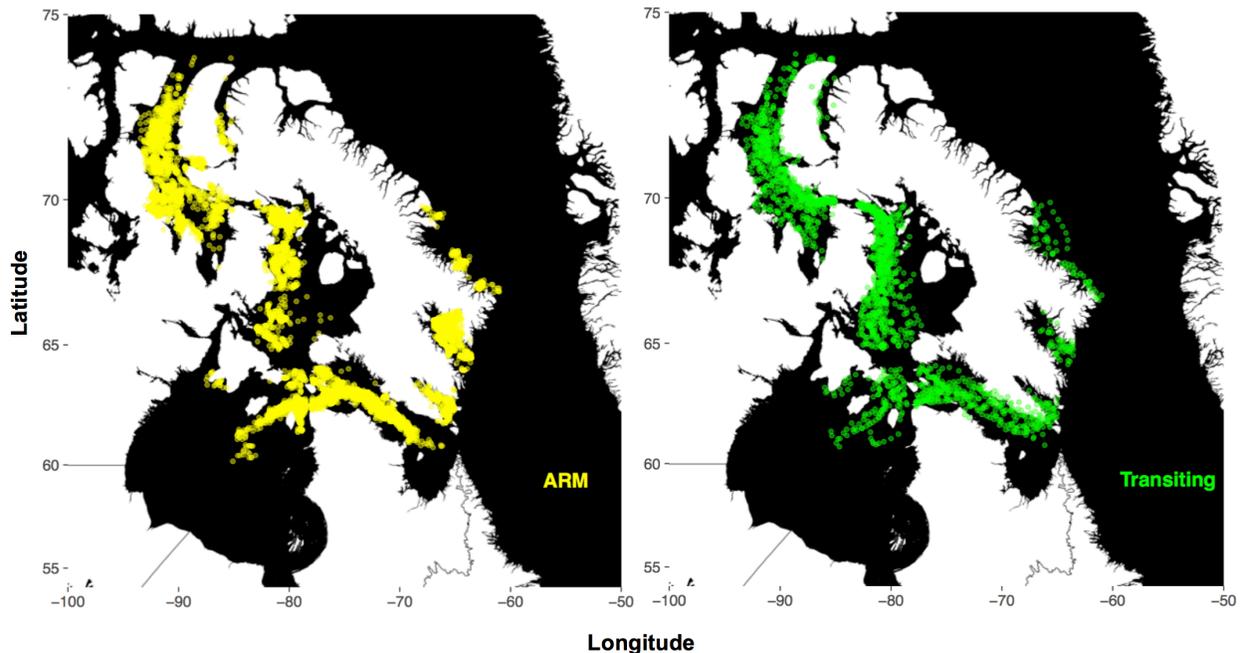


Figure 4.1: Argos Satellite locations for 25 SPLASH tagged bowhead whales in 6 Eastern Canadian Arctic habitats (Cumberland Sound, Foxe Basin, Gulf of Boothia, Hudson Strait and Frobisher Bay, Hudson Bay and Central East Baffin Coast) derived from hierarchical switching state-space models (HSSSM). ARM (●) and transiting (●) behavioural states derived from the HSSSM are plotted for each animal.

Criterion (AIC) to select the ‘best model’, whereby I selected the model with the smallest AIC value.

4.4 Results

The whales tagged in 2012 transmitted data for 397 days on average, while those tagged in 2013 transmitted for 484 days (Table 4.1). The state-space model predicted two daily locations for each animal ($n=25$). The combined data set for all whales contained 16,587 locations throughout the Eastern Canadian Arctic, and the location data were relatively evenly distributed across seasons with 29% ($n=4,737$) in fall, 25% ($n=4,095$) winter, 22% ($n=3,709$) in spring and 24% ($n=4,046$) in summer. Of all the predicted locations, 73% ($n=12,161$) were associated with ARM behaviour and only 13% ($n=2,207$) were associated with transiting behaviour (Fig. 4.1 & Fig. 4.2).

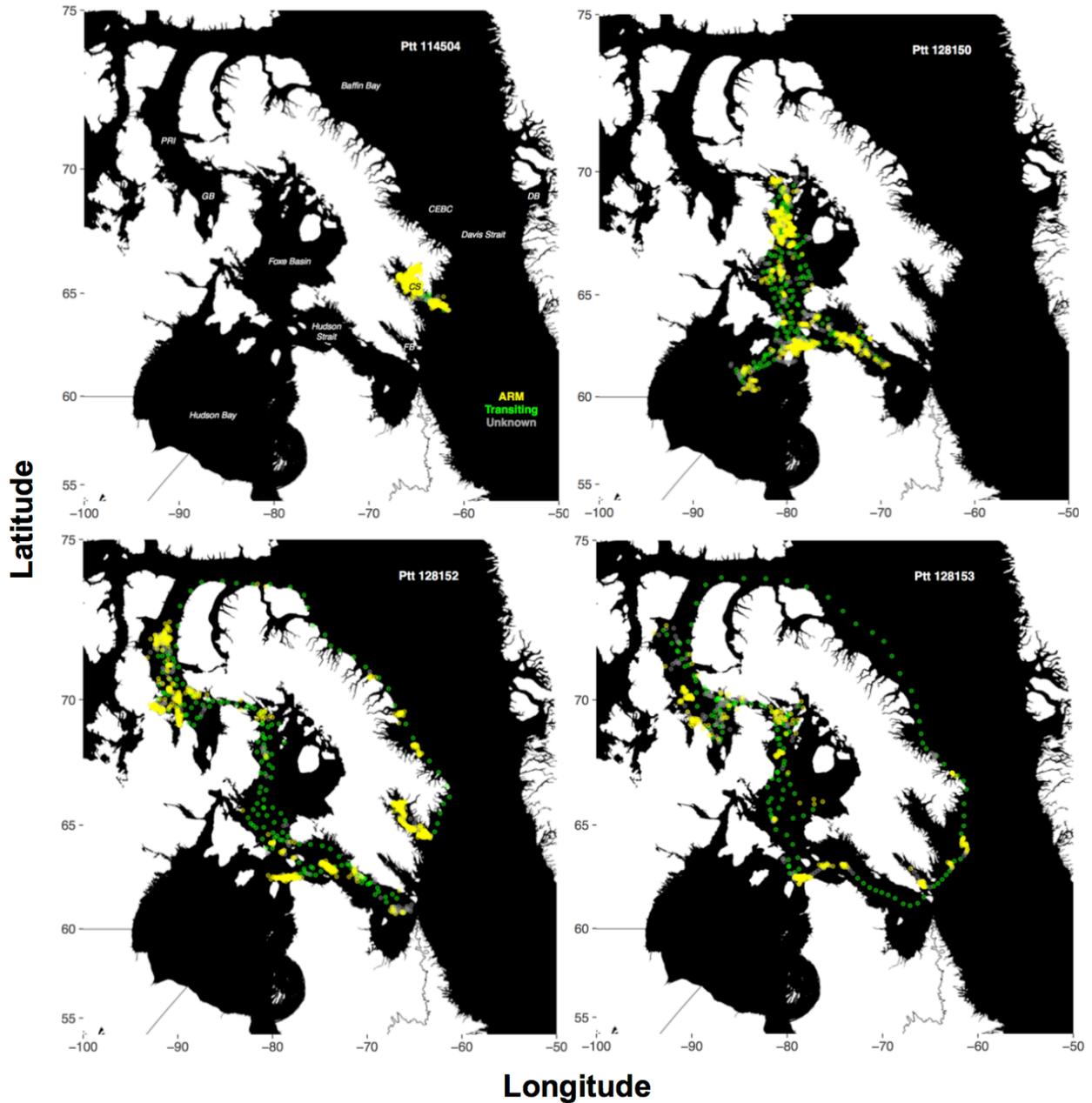


Figure 4.2: Example of individual Argos satellite tracks derived from HSSSM predictions for 4 SPLASH tagged bowhead whales (Ptt 114504, 128150, 128152, 128153) ARM (●), transiting (●) and unknown (●) behavioural states highlighted behavioural states derived from the HSSSM are plotted for each animal.

Table 4.1: Summary information for all bowhead whales tagged in Cumberland (CS) and Foxe Basin (FB) with Wildlife Computers SPLASH Tags (MK10) between 2012 and 2013. Unique animals are identified with the Platform Transmitter Terminal (Ptt). The day the animal was tagged is the ‘start date’ and the day the tag stopped transmitting data is the ‘end date’. The habitat where the animal was tagged is the ‘location’. The ‘body length’ was estimated in meters from observers on board the tagging vessel.

Ptt	Start	End	Duration (days)	Location	Length (m)	Sex
114494	2012-07-03	2013-05-21	322	FB	12	F
114495	2012-07-03	2014-06-26	723	FB	11-12	F
114496	2012-07-03	2013-12-13	528	FB	11	F
114497	2012-07-06	2013-05-10	308	FB	12	M
114498	2012-07-06	2013-02-17	226	FB	11	M
114499	2012-07-06	2013-06-08	337	FB	13-14	F
114500	2012-07-06	2014-02-21	595	FB	12-13	M
114501	2012-07-07	2013-01-05	183	FB	-	-
114502	2012-08-06	2013-07-10	338	CS	10	M
114503	2012-08-06	2014-06-26	689	CS	10	F
114504	2012-08-07	2013-07-19	346	CS	10-11	F
114505	2012-08-08	2013-06-22	318	CS	11-12	M
114506	2012-08-08	2012-08-27	19	CS	13-14	F
114507	2012-08-12	2013-09-19	403	CS	10	M
114508	2012-08-12	2014-08-19	737	CS	9-10	M
114509	2012-08-12	2013-05-26	287	CS	9-10	M
128145	2013-07-03	2014-11-13	498	FB	11-12	F
128146	2013-07-03	2015-05-22	688	FB	13-14	F
128148	2013-07-09	2014-06-06	332	FB	13	F
128149	2013-07-09	2013-07-22	13	FB	12-13	-
128150	2013-07-09	2015-07-08	729	FB	10	F
128151	2013-07-09	2015-07-01	722	FB	9-10	M
128152	2013-07-09	2015-05-24	684	FB	9-10	M
128153	2013-07-03	2014-07-16	378	FB	12-13	M
128154	2013-07-03	2014-05-18	319	FB	11-12	M

The greatest numbers of ARM locations for all bowhead whales (n=25) and years combined was during winter (28%, n=3,405), followed by fall (27%, n=3,297), spring (25%, n=3,017) and summer (20%, n=2,442). The high number of winter and springtime ARM locations corresponds with lower numbers of transiting behaviours observed during winter (12%, n=258) and spring (14%, n=301), while the lower numbers of ARM locations are consistent with the higher number of transiting behaviours that occurred during fall (34%, n=745) and summer (41%, n=903).

4.4.1 Diving Behaviour

The 25 tagged whales made 206,772 dives before 22 of recorded dives were removed as outliers because of dive durations and depths exceeding 75 minutes and 700 meters. I deemed these dives to be biologically unlikely based on previous studies (Heide-Jørgensen et al. 2013), and subsequently removed them from my analyses. I was able to associate 151,279 (73%) of the dives with ARM throughout the Eastern Canadian Arctic. Among these dives, 66% (n=99,780) were Square-shaped, 23% (n=34,852) U-shaped, 10% (n=15,662) were V-shaped, and 0.65% (n=985) were of unknown shape. Of all the Square shaped dives that occurred in association with ARM behaviour, 17% (n=16,699) occurred during winter, 13% (n=13,311) during spring, 40% (n=39,705) during summer and 30% (n=30,065) during fall, suggesting that foraging effort changed seasonally (Fig. 4.3). However, my analysis did not account for surface foraging behaviour, which likely occurred during spring when zooplankton often concentrate at the surface. During transiting behaviour, however, the whales conducted 36,307 dives (3 dives were removed as outliers) where 53% (n=19,263) were Square-shaped, 32% (n=11,523) were U-shaped, 15% (n=5,323) were V-shaped and 0.6% (n=198) were of unknown shape. Furthermore, I found that a high percentage of the total number of Square dives was associated with ARM behaviour: 86% (± 5.87 SD) during winter, 84% (± 5.26 SD) during spring, 70% (± 9.32 SD) in summer and 77% (± 6.43 SD) in fall.

4.4.2 Habitat-use by region

Using the six location filters for each habitat, I found that 84% (n=13,987) of all HSSSM locations were assigned to an area (e.g., Cumberland Sound, Foxe Basin, Gulf of Boothia, Hudson Bay, Hudson Strait and Frobisher Bay and Eastern Central Baffin Island). Consequently, only a small proportion (16%; n=2,600) of all predicted locations occurred outside of a designated habitat.

I also found that the percent of total HSSSM predicted locations that were associated with ARM behaviour varied between habitats (Fig. 4.4). Furthermore, when comparing the average number of ARM and transiting HSSSM locations per animal (pooled across seasons and years), I found that animals allocated more time to probable feeding behaviour (i.e., ARM) in Cumberland Sound than any other habitat (Fig. 4.5).

Bowhead whale diving behaviour differed over spatio-temporal scales. Maximum dive depth of Square-shaped dives differed considerably between habitats, whereby probable foraging dives were deepest off the Central East Baffin Coast and shallowest in Foxe Basin (Fig. 4.6). Furthermore, I found that maximum dive depth was affected by an interaction between dive shape, habitat and month (Table 4.2; log-likelihood ratio test (LRT)= 1661.426 ($p < .0001$)) as was dive duration (Table 4.2: log-likelihood ratio test (LRT)= 885.577 ($p < .0001$)) (Fig. 4.7).

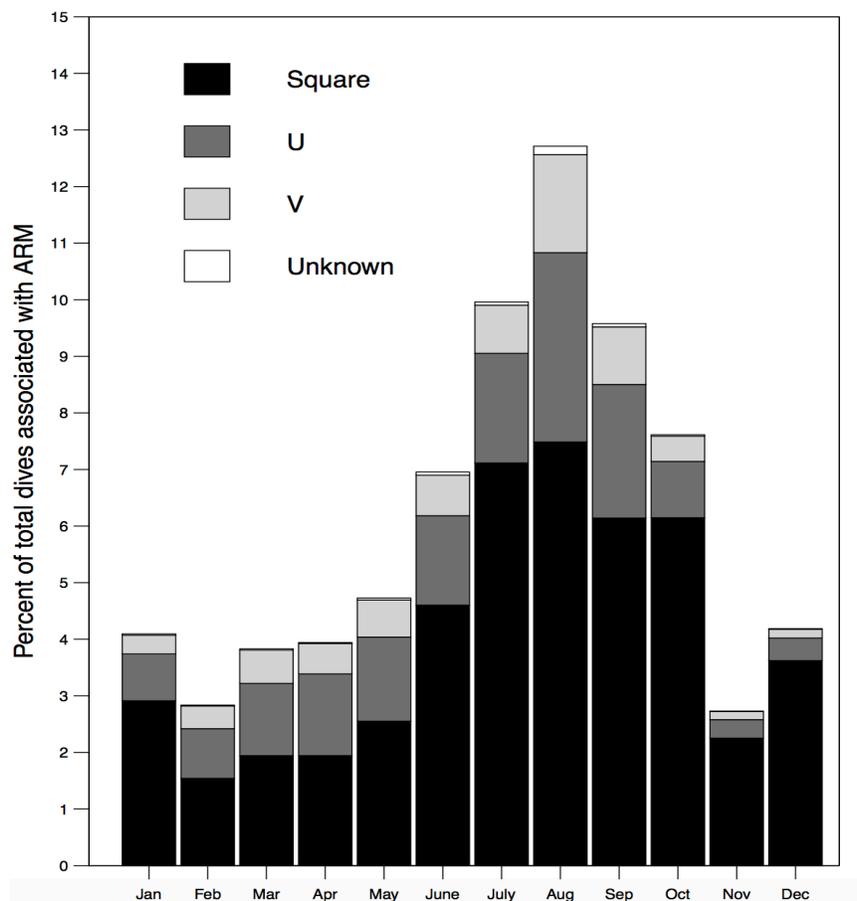


Figure 4.3: Percent of all bowhead whale dives (n=206,748) that occurred on the same day as an ARM Argos location (predicted from the HSSSM) by season and dive shape. Data are pooled across individuals and years.

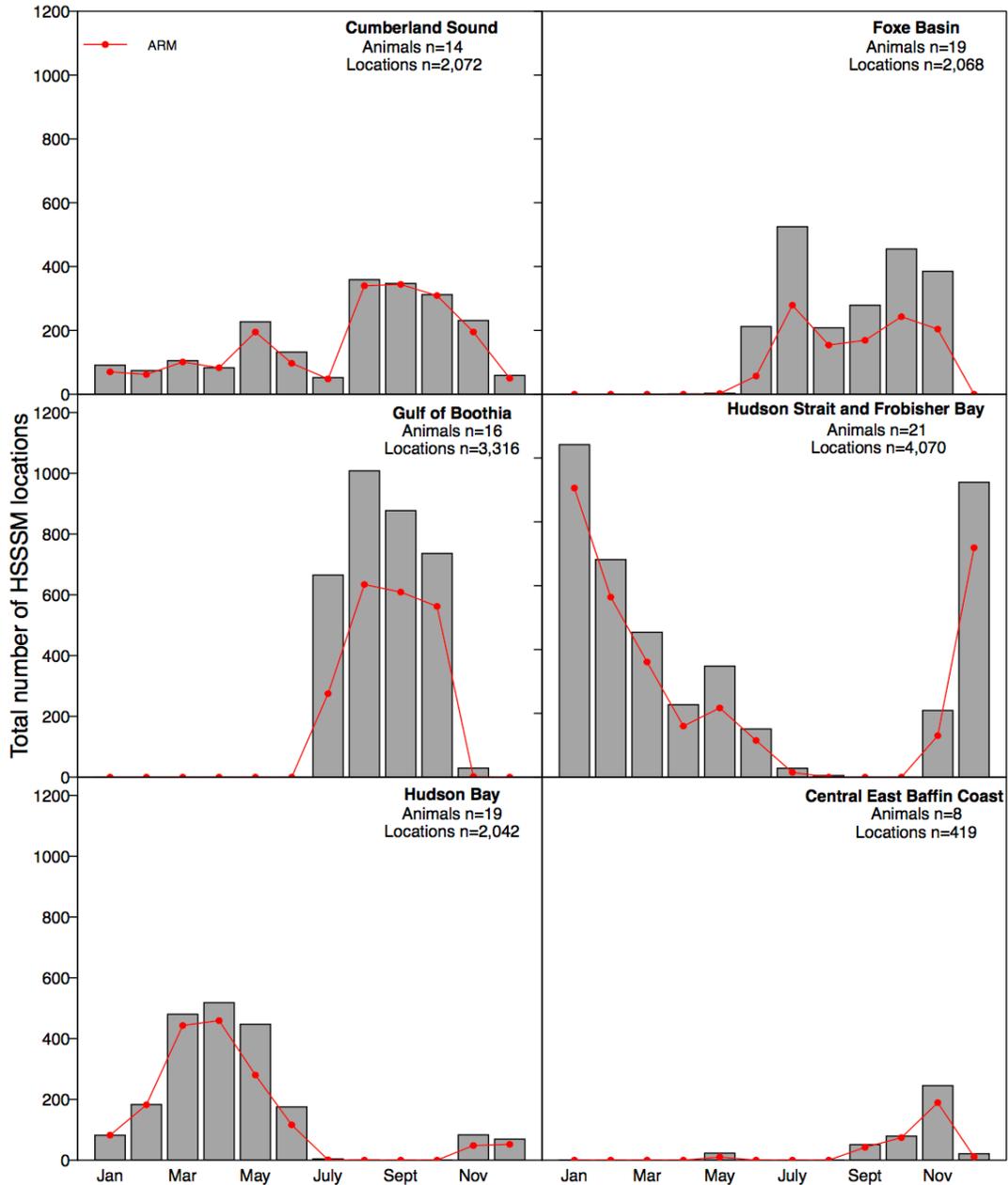


Figure 4.4: Total number of HSSSM predicted locations (gray bars) for 25 SPLASH tagged bowhead whales in 6 Eastern Canadian Arctic habitats and the total number of locations associated with ARM behaviour in red circles.

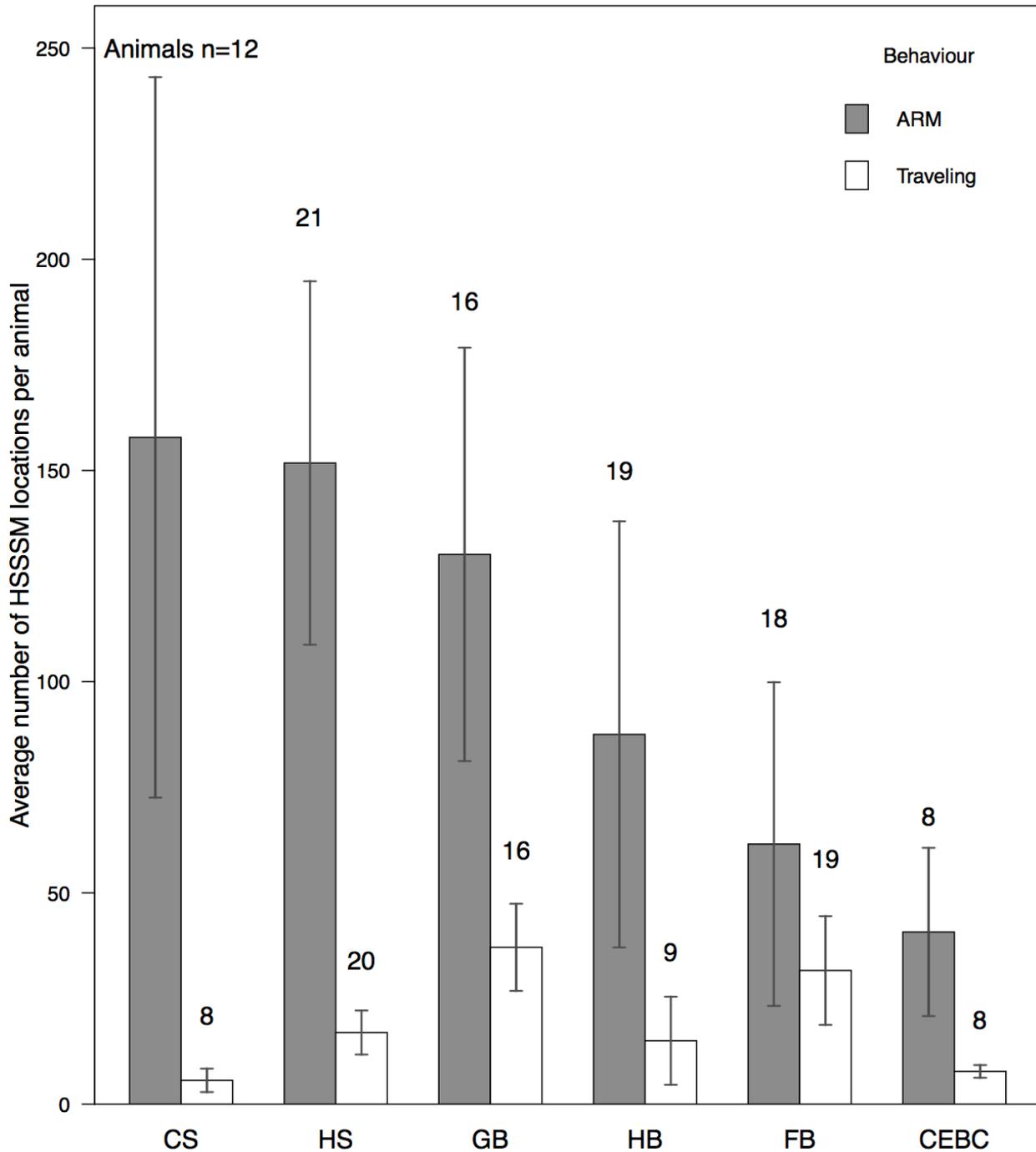


Figure 4.5: The average number of ARM and transiting Argos locations per animal as predicted by the HSSSM with gaps (>4 consecutive days) removed and standard error bars. Data were pooled across seasons and years, whereby CS=Cumberland Sound, HS=Hudson Strait, GB=Gulf of Boothia, HB=Hudson Bay, FB=Foxe Basin and CEBC=Central East Baffin Coast.

Table 4.2: Linear mixed-effects models for the impacts of dive shape, habitat and month on minimum dive duration and maximum depth. The change in AIC (Δ AIC) and likelihood ratio tests (LRT) are relative to the model earlier in the list for dive depth and duration. These indicate that there are interactions between dive shape, habitat and month for both dive duration and maximum depth.

Model	Fixed	df	AIC	LR test	Δ AIC
Maximum depth (m)					
null	~1	170963	1976519	~	~
1	~Shape	170960	1974981	1544.408 (p<.0001)	1538.0
2	~Shape+Habitat	170960, 5811	1974765	225.7019 (p<.0001)	216.0
3	~Shape*Habitat	170945, 5811	1971843	3254.952 (p<.0001)	2922.0
4	~Shape*Habitat*Month	170927, 5806, 263	1969927	1661.426 (p<.0001)	1916.0
Minimum dive duration (mins)					
null	~1	170963	2631777	~	~
5	~Shape	170960	2618064	13719.61 (p<.0001)	13713
6	~Shape+Habitat	170960, 5811	2618012	61.397 (p<.0001)	52
7	~Shape*Habitat	170945, 5811	2615549	2493.545 (p<.0001)	2463
8	~Shape*Habitat*Month	170927, 5806, 263	2614711	885.577 (p<.0001)	838

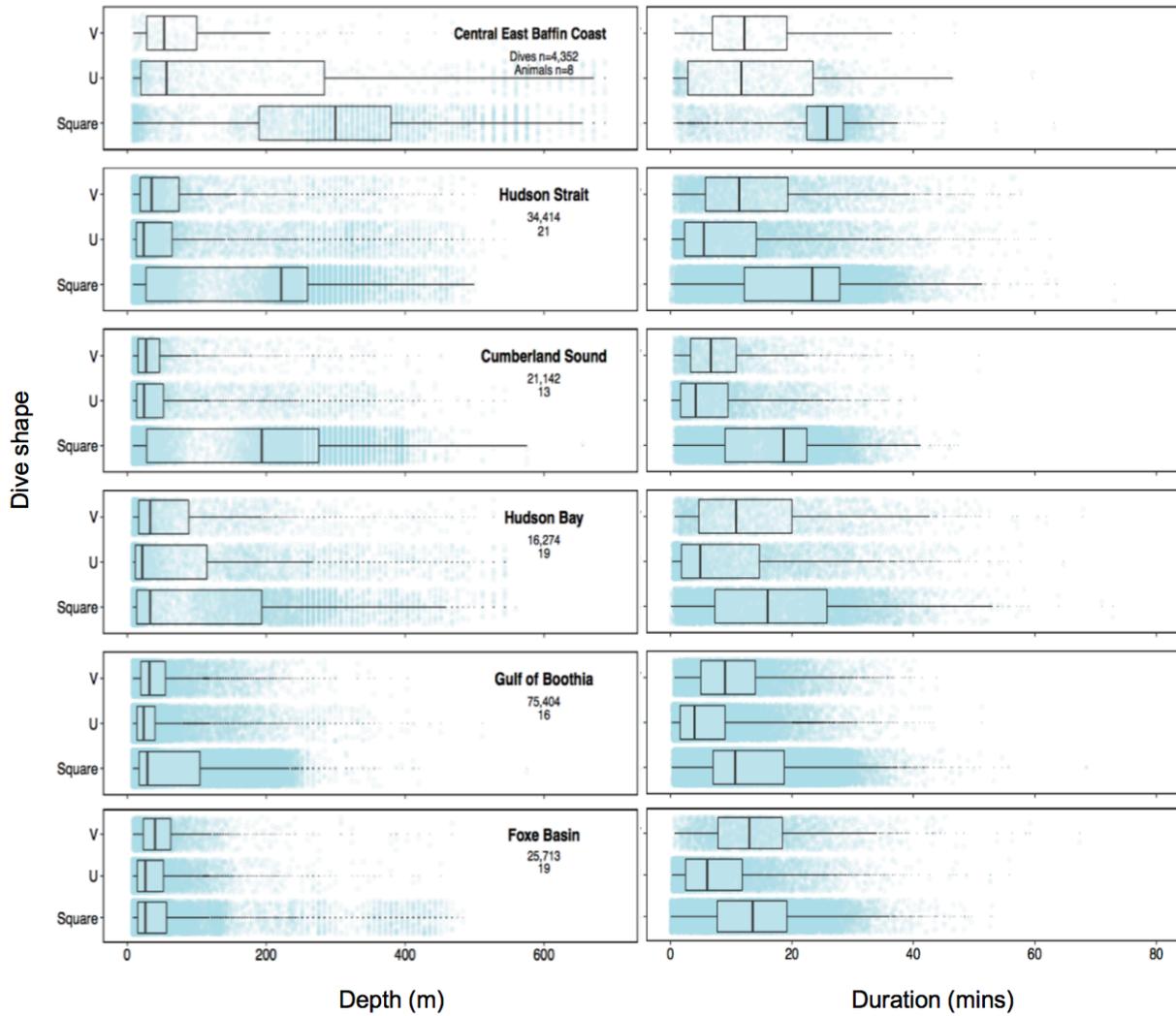


Figure 4.6: Maximum depth (meters) (left) and minimum dive duration (minutes) (right) of V, U and Square-shaped dives for n=25 bowhead whales by habitat with the total number of dives and total number of animals reported. Raw data are plotted (•) for each dive type.

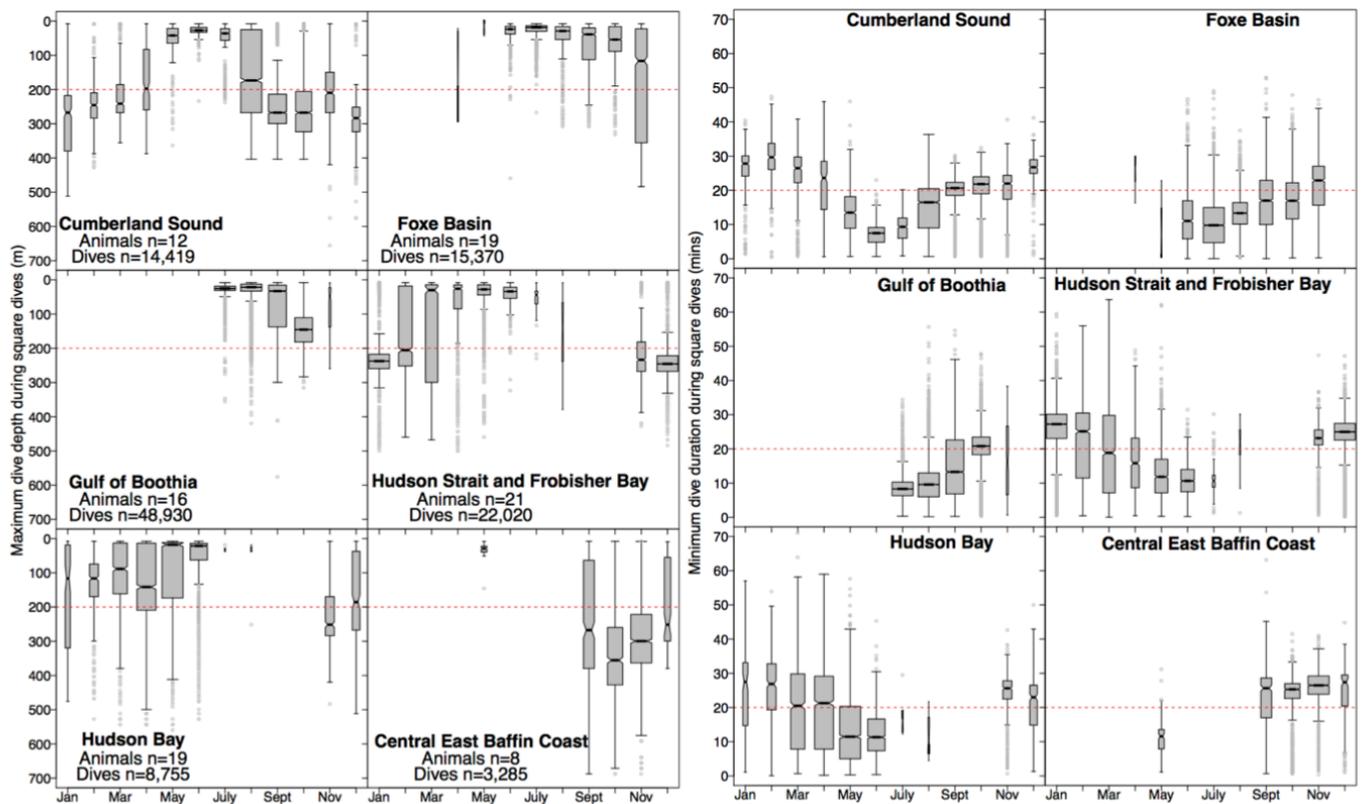


Figure 4.7: Left: Maximum dive depth (meters) of Square-shaped dives for 25 bowhead whales separated by habitat. Data were pooled across all years for all individuals. Box width is proportional to the Square-root of the number of dives per month. There is 'strong evidence' that the medians (black bar) differ significantly when the notches of two boxes do not overlap. The interquartile range is represented by the box, non-extreme maximum and minimum values are indicated by the whiskers and the gray dots indicate outliers. The red dotted line at 200 meters is used to aid in the identification of months where deep dives occurred (i.e., >200 meters). Right: Minimum dive duration (minutes) of Square-shaped dives for 25 bowhead whales separated by habitat, where data were pooled across all years for all individuals. The red dotted line at 20 minutes is used to help identify months with long dive durations (i.e., >20 minutes).

4.4.3 Cumberland Sound

Of all the Argos locations, 12.4% (n=2,072) occurred inside Cumberland Sound where 14 of the tagged bowhead whales resided seasonally. The majority (71%, n=1,471) of locations belonged to male bowhead whales compared to females (29%, n=601). Furthermore, the males were smaller on average in body length (1001 cm \pm 71 SD) compared to the females (1068 cm \pm 77 SD) based on visual estimates of body length. Occupancy by bowhead whales of Cumberland Sound was highest during August (17.3%, n=359), September (16.7%, n=347) and October (15.1%, n=312). Almost all Argos locations were associated with ARM behaviour (91.4%, n=1,894). Probable foraging behaviour (i.e., the percentage of all ARM locations that occurred within Cumberland Sound) was greatest during August (16.4%, n=340), September (16.6%, n=344) and October (14.9%, n=309). Conversely, transiting behaviour seldom occurred and represented 2.2% (n=45) of all Argos locations. However, 6.4% (n=133) of all locations were of unknown behavioural state. Dive information was available for 13 animals that conducted 21,142 dives (two were removed as outliers from a total of n=21,144) where 68.2% (n=14,419) were Squared-shaped, 22.2% (n=4,692) were U-shaped, 8.5% (n=1,803) were V-shaped and 1.1% (n=228) were of unknown shape.

4.4.4 Foxe Basin

Thirteen percent (n=2,068) of all bowhead whale locations occurred in Foxe Basin where 62% of locations were from female whales (n=1286) and only 32% (n=666) belonged to males. Of the 25 tagged whales, 18 spent 54% (n=1,108) of their time conducting ARM behaviour, 18 animals allocated 29% (n=601) of their time to transiting and 17% (n=359) in an unknown behavioural state. The greatest occupancy occurred during July (25%; n=525), October (22%; n=455) and November (19%; n=385) while the lowest occupancy occurred between December and March (n=0). While residing in Foxe Basin the whales conducted a total of 25,713 dives with 60% (n=15,370) Square-shaped, 28% (n=7,096) U-shaped, 12% (n=3,148) V-shaped and 0.4% (n=99) of unclassified shape.

4.4.5 Gulf of Boothia

Sixteen of the tagged bowhead whales occupied the Gulf of Boothia and their Argos locations comprised 20% (n=3,316) of the total in the Eastern Canadian Arctic. Bowhead whale residency occurred between July and November and was greatest during August (30%, n=1,008). ARM was the dominant behavioural state and represented 63% (n=2,082) of all locations, whereas transiting behaviour was less frequent (18%, n=594) as were unclassified behavioural states (19%, n=640). While in the Gulf of Boothia the whales conducted a total of 75,404 dives, 65% (n=48,930) of which were Square-shaped, 23% (n=17,129) were U-shaped, 12% (n=8,829) were V-shaped and 0.68% (n=516) were of unclassified shape.

4.4.6 Hudson Bay

Twelve percent of all locations occurred within Hudson Bay (n=2,042) where 19 of the tagged bowhead whales resided. The number of predicted locations were marginally greater for females (54%, n=1,107) compared to males (45%, n=922). Less than 1% of HSSSM locations were from animals of unknown sex (0.6%; n=13). Overall, 81% (n=1663) of all locations were associated with ARM behaviour, 7% (n=135) transiting and 13% (n=246) of an unknown behavioural state. Residency was greatest during March (24%; n=480), April (25%; n=518) and May (22%; n=447). A total of 16,274 dives (three dives were removed as outliers) occurred within Hudson Bay where 54% (n=8,755) were Square-shaped, 32% (n=5,157) U-shaped, 14% (n=2,244) V-shaped and 0.7% (n=118) of unknown shape.

4.4.7 Hudson Strait and Frobisher Bay

A quarter (25%, n=4,070) of all locations were from Hudson Strait and Frobisher Bay where 21 of the tagged animals resided. The sex ratio was comparable for males and females (53:46). ARM was the dominant behaviour with 78% (n=3,187) of all locations associated with probable foraging behaviour and only 8% (n=339) related with transiting behaviour. However, 13% (n=544) of all locations were of unknown behaviour. Occupancy was greatest during the winter with 23% (n=924) of all Hudson Strait and Frobisher Bay locations occurring during December, 26% (n=1042) during January and 17% (n=682) in February and lowest during late summer (August n=5) and fall (September n=0 and October n=0). A total of 34,414 dives were conducted in Hudson Strait and Frobisher Bay (two dives were removed as outliers; n=34,416 with

outliers included), of which, 64% (n=22,020) were Square-shaped, 24% (n=8,387) were U-shaped, 11% (n=3,865) were V-shaped, and 0.4% (n=142) were of unknown shape.

4.4.8 Central East Baffin Coast

Only 2.5% (n=419) of all Argos locations occurred off the Central East Baffin Coast near Qikiqtarjuaq. The HSSSM-predicted Argos locations consisted of 69% female (n=290) and 31% (n=129) male locations. Occupancy was greatest during September (12%; n=51), October (19%; n=79) and November (n=245). Feeding behaviour was associated with 77.8% (n=326) of all locations, 14.8% (n=62) were traveling behaviour and 7.4% (n=31) were of unknown behaviour. A total of 8 bowhead whales conducted 4,352 dives (10 dives were removed as outliers) and over three-quarters of all dives were Square-shaped (75.5%, n=3,285), 20% (n=871) were U-shaped, 4.3% (n=186) were V-shaped and 0.1% (n=10) were of unknown shape.

4.5 Discussion

Modeling the long-term (>365 days) horizontal and vertical movements of individual bowhead whales provided a perspective on seasonal and annual habitat-use patterns and feeding behaviour that previous analyses of smaller datasets (<365 days) could not capture. Most remarkably, I found that bowhead whales displayed dive behaviours consistent with feeding throughout the year, with most Square-shaped dives (70%) occurring during summer and fall and reduced probable foraging (i.e., Square dives ≥ 8 m) occurring over the spring and winter (30%). Furthermore, I found that Square-shaped dives were associated with slow swimming speed and high turning angle (i.e., ARM behavior), suggesting that hierarchical switching-state-space models (HSSSM) can be used to identify balaenid foraging behaviour. These findings provide new insight into the biology of bowhead whales and have management implications in terms of designating critical habitat.

The seasonal patterns in bowhead habitat use and foraging behaviour found in my study follow observed patterns of ice breakup and biological production. Previous studies have found that the distribution of Eastern Canada-West Greenland bowhead whales expands north in the spring and summer (Reeves and Heide-Jørgensen 1996, Cosens and Innes 2000, Cosens and Blouw 2003, Ferguson et al. 2010, Nielsen et al. 2015) and contracts south in the winter (e.g., Heide-

Jørgensen et al. 2003, Laidre et al. 2007, Ferguson et al. 2010, Pomerleau et al. 2011a). Spring migrations coincide with the timing of ice break-up (Ferguson et al. 2010) and the ascension of overwintering calanoid copepods (Falk-Petersen et al. 2009) following the phytoplankton bloom between April and June (Reeves and Mitchell 1990, Madsen et al. 2001, Swalethorp et al. 2011, Fujiwara et al. 2016). My findings are consistent with this understanding of bowhead whale movements, in that animals resided in low latitudes, such as Hudson Strait ($\sim 62^\circ$ North) and Frobisher Bay ($\sim 63^\circ$ North) during winter months (December-February) and then moved north to Hudson Bay ($\sim 64^\circ$ North) in spring (March-May), followed by further northern movements to Foxe Basin ($\sim 67.5^\circ$ North) in early summer (June – July), and either Cumberland Sound (August – November) ($\sim 65.5^\circ$ North) or Gulf of Boothia ($\sim 72^\circ$ North) (including Prince Regent Inlet and Admiralty Inlet) (July-October) during late summer and southbound movements along the Central East Baffin Coast ($\sim 68^\circ$ North) during fall (September-November).

4.5.1 Summertime feeding in the Canadian high Arctic

Unlike adult females belonging to the Eastern Canadian-West Greenland population tagged off the western coast of Greenland in Disko Bay during late winter that occupied the East Coast Baffin Island regularly (Heide-Jørgensen et al. 2003, Heide-Jørgensen et al. 2006, Heide-Jørgensen et al. 2012, Nielsen et al. 2015), I found that juvenile and adult animals of both sexes frequently occupied the Gulf of Boothia and adjacent waters (i.e., Prince Regent Inlet and Admiralty Inlet) during late summer. For example, I found that 20% ($n=3,316$) of all the Argos locations predicted by the state-space models occurred within the Gulf of Boothia and surrounding waters mostly between July and November with peak residency occurring in August. During this time, tagged animals ($n=16$) displayed predominately ARM behaviour (63% all locations) and conducted mostly Square-shaped dives (65% of all dives) to 61.6 m (± 16.7 SD). The agreement between horizontal (i.e., low swim speed, high turning angle) and vertical (i.e., optimized time spent a maximum dive depth) movement data suggests that the Gulf of Boothia is a summer bowhead feeding habitat.

My results are consistent with earlier tagging and diet studies conducted in the Eastern Canadian Arctic. For example, a telemetry study of 4 bowhead whales concluded that the Gulf of Boothia was a likely summertime feeding area (Pomerleau et al. 2011b) and had high abundances of Arctic calanoid copepods such as *Calanus hyperboreus* between depths of 75 and 100 m during

September 2009 (Pomerleau et al. 2011c). I also found that twelve tagged animals dove to comparable depths of 72.1 m on average (± 37.7 SD) during September (2012-2014) based on weighted-averages. Additional support for this being a feeding area comes from stable isotope studies that found similarities in the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of the skin samples of biopsied EC-WG bowhead whales and the zooplankton prey species collected from the Gulf of Boothia, suggesting that bowhead whales originating from the Eastern Canadian Arctic use this habitat for foraging purposes (Pomerleau et al. 2012). These findings collectively provide strong support for bowhead whales using high-Arctic habitats such as the Gulf of Boothia to exploit energy rich-Arctic copepods.

4.5.2 Evidence of winter feeding in southern habitats

Although it was well established that bowhead whales overwinter in southern latitude areas such as Hudson Strait (Reeves and Heide-Jørgensen 1996, Heide-Jørgensen et al. 2006, Koski et al. 2006), the biological significance of these locations have been relatively unknown. Previous studies suggested that bowhead whales foraged principally during the open water season during summer and fall (Finley 2001, Pomerleau et al. 2011b, Pomerleau et al. 2011c, Pomerleau et al. 2012) and that fasting was likely occurring during the winter (Finley et al. 1993, Lowry 1993) while they overwintered in the unconsolidated pack ice in Hudson Strait and Davis Strait (Reeves et al. 1983, Finley 1990, Reeves and Mitchell 1990, Nielsen et al. 2015). However, I found that the 21 whales (49:49 sex ratio; sex information was not available for one animal) that seasonally occupied Hudson Strait and Frobisher Bay were likely foraging. Most notably, the whales ($n=18$) spent the greatest amount of time conducting ARM behaviour (78%) and deep Square-shaped dives (72%; $n=5,504$) to 210.7 m (± 35.1 SD) during January when peak residency occurred. The bathymetry in Hudson Strait ranges between relatively shallow (100-200 m) and deep (200-1000 m) regions (Canada 2015) and bowhead whales appeared to occupy mostly the deeper areas of the Strait.

The prevalence of ARM behaviour in Hudson Strait and Frobisher Bay during winter may reflect, in part, reduced mobility due to increased ice cover whereby animals reside within smaller geographic areas and have slower swimming speeds and higher turning angles. However, the dominance of deep (maximum depth 499.5 m during January) Square-shaped dives suggests that the whales were investing considerable time and energy into foraging activities. It is possible that

the overwintering whales were exploiting energy-rich, diapausing copepods (*Calanus* spp.) (Falk-Petersen et al. 2009, Swalethorp et al. 2011, McMeans et al. 2012) given that their maximum dive depths may have approached the sea bottom (~100-1000 m) at times during winter where overwintering copepods likely concentrate (Madsen et al. 2001). However, corroboration of this hypothesis requires the collection of co-located zooplankton and bowhead whale dive behaviour during winter months. Detailed bathymetry data is also required for Hudson Strait and Frobisher Bay to determine proximity to the sea bottom during probable foraging dives.

Winter foraging has also been inferred indirectly from stable isotope analysis and examination of diving frequency for Eastern Canada-West Greenland bowhead whales. Bowheads were presumed to feed year-round, with a potential reduction in feeding rate, during the winter from isotope cycles measured in baleen from harvested whales (Matthews and Ferguson 2015). Further evidence of winter feeding in Hudson Strait can be ascertained from diving records (n=7 animals) collected from predominately adult females originating from Disko Bay (Nielsen et al. 2015). Foraging was believed to occur in Hudson Strait because the tagged animals conducted fewer than 3 dives h⁻¹ while occupying the habitat between July and March (a threshold diving rate based on previous studies that quantified the characteristics and frequency of foraging dives in Disko Bay; Heide-Jørgensen et al. 2010). A limitation of this study, however, is that dive shape was not distinguished and thus exploratory V-shaped dives were likely included in the analysis, which may in part explain the shallower dive depths (42.6 m) reported by (Nielsen et al. 2015) compared with my study (163.21 m ± 53.14 SD for Square dives). Nevertheless, there is increasing evidence that EC-WG bowhead whales feed while occupying southern habitats during winter.

4.5.3 Infrequent feeding along eastern coast of Baffin Island

Although bowheads appear to feed throughout their range in the Eastern Canadian Arctic, little foraging occurred along the eastern coast of Baffin Island. Previous studies have found that bowhead whales aggregate near Clyde River, Nunavut (Central East Baffin Coast) during the summer to forage and engage in social activity (Finley 1990, Richardson et al. 1995, Nielsen et al. 2015). Consequently, the Ninginganiq National Wildlife Area was designated by Environment and Climate Change Canada in 2010 off the northeast coast of Baffin Island (69°37' North / 67°00' West), Nunavut (just south of Clyde River) to protect and conserve bowhead whales and their habitat. The Ninginganiq National Wildlife Area represents the only designated and managed

bowhead whale habitat in the Eastern Canadian Arctic. However, few of the whales tagged in Foxe Basin and Cumberland Sound went to the eastern coast of Baffin Island (n=8, 69:31 sex ratio). Overall, only 2.5% of all the locations predicted by the state-space models occurred along the eastern coast of Baffin Island near Qikiqtarjuaq where the predominate behaviour was ARM (77.8%) (Fig. 4.1) below the Ninginganiq National Wildlife Area where animals conducted deep foraging dives. However, transiting behaviours were observed from central to northern east coast Baffin Island (Fig. 4.1) for animals traveling two and from the Gulf of Boothia.

The eastern coast of Baffin Island may serve as a southbound migratory route rather than an important foraging area for a segment of the ECWG bowhead population (i.e., 17.8% of all predicted state-space model locations in the eastern Canadian Arctic were associated with transiting behaviour along the Baffin coast when including locations outside the eastern coast of Baffin Island region and 14.8% of HSSSM locations were consistent with transiting within the Central East Baffin Coast habitat alone) (Fig. 4.1). It appears from my data that some animals (mostly females) occupying high-Arctic habitats (e.g., Gulf of Boothia) during late summer traveled south along the eastern coast of Baffin Island to return to southern habitats (e.g., Cumberland Sound and Hudson Strait) for the winter. The prevalence of transiting Argos locations occurring along the eastern coast of Baffin Island (outside the Central East Baffin Coast habitat) suggests that this area may not be a significant foraging habitat for whales originating in Foxe Basin and Cumberland Sound during early summer. However, it is also possible these results reflect tagging biases as bowhead whales appear to show habitat preferences based on age and sex (Cosens and Blouw 2003) as mostly females occupied this area in my study. Furthermore, predominately adult females originating from western Greenland (Disko Bay) regularly occupy the Central East Baffin Coast (e.g., Nielsen et al. 2015) and Isabella Bay (located further north in Baffin Bay) (e.g., Chambault et al. 2018). Given the wide foraging range of bowhead whales, managers may consider expanding their conservation efforts to include the designation of additional seasonal high-use foraging habitats such as the Gulf of Boothia as critical habitat (DFO 2015).

4.6 Conclusions

My findings provide new insight into the seasonal movements, habitat use patterns and year-round foraging behaviour of bowhead whales in the Eastern Canadian Arctic. Furthermore, I identified important foraging areas throughout their range by accounting for the time spent

conducting horizontal and vertical movements indicative of feeding (e.g., slow swimming speed, high turning angle and Square shaped dives) in specific habitats. Given that bowhead whales appear to display a flexible foraging strategy such that they feed throughout their range during all times of year, I anticipate that whales will adjust their seasonal movements in response to environmental change. For example, animals may expand their northern range into the Arctic Archipelago as the extent of summer ice decreases, creating new foraging opportunities in response to a potential reduction in feeding opportunities in more southern habitats. Furthermore, as sea ice retreat continues to occur earlier in the season, bowheads may take advantage of secondary phytoplankton blooms that act to concentrate zooplankton in near surface waters at lower latitudes (Fujiwara et al. 2016) and forage later into the open water season. However, assessing how bowhead whales will ultimately respond to climate change on a population level will require assessing the quality and quantity of prey available to foraging whales and the energetic gains made throughout the year. This will entail monitoring changes in habitat use patterns, collecting co-located prey data near feeding whales, modeling the nutritional requirements of different demographic groups and quantifying prey consumption.

Chapter 5: Evidence of moulting and the function of “rock-nosing” behaviour in bowhead whales in the eastern Canadian Arctic

5.1 Summary

Bowhead whales (*Balaena mysticetus*) have a nearly circumpolar distribution, and occasionally occupy warmer shallow coastal areas during summertime that may facilitate moulting. However, relatively little is known about the occurrence of moulting and associated behaviours in bowhead whales. I opportunistically observed whales in Cumberland Sound, Nunavut, Canada with skin irregularities consistent with moulting during August 2014, and collected a skin sample from a biopsied whale that revealed loose epidermis and sloughing. During August 2016, I flew a small unmanned aerial system (UAS) over whales to take video and still images to: 1) determine unique individuals; 2) estimate the proportion of the body of unique individuals that exhibited sloughing skin; 3) determine the presence or absence of superficial lines representative of rock-rubbing behaviour; and 4) measure body lengths to infer age-class. The still images revealed that all individuals (n=81 whales) were sloughing skin, and that nearly 40% of them had mottled skin over more than two-thirds of their bodies. The video images captured bowhead whales rubbing on large rocks in shallow, coastal areas—likely to facilitate moulting. Moulting and rock rubbing appears to be pervasive during late summer for whales in the eastern Canadian Arctic.

5.2 Introduction

The skin (epidermis) and hair (keratinized epidermal cells) of marine mammals are specially adapted for life in an aquatic environment. The periodic shedding of part or all of their outer layer of epidermal covering, which is then replaced by new growth (Reeb et al. 2007) has been well studied for seals and sea lions—which moult annually to repair and renew their skin and pelt (e.g., Scheffer 1962, Ling 1970, 1978, Smith & Hammill 1981, Boily 1995, Kovacs et al. 1996, McConkey et al. 2002). In contrast, whales, dolphins and porpoises are generally thought to continuously shed and replace their epidermis (Ling 1974, 1984). However, this may not be the case for Arctic species that experience pronounced changes in environmental conditions by seasonally occupying uncharacteristically warmer areas such as estuaries and fiords (Aubin *et al.* 1990).

Beluga whales (*Delphinapterus leucas*) and most likely narwhal (*Monodon monoceros*) (e.g., Inuit hunter observations; Wagemann & Kozłowska 2005) undergo a seasonal epidermal moult during summer. The beluga whale moult appears to be facilitated in part by the warm and low salinity environmental conditions found in seasonally occupied estuaries (Aubin et al. 1990, Frost et al. 1993). The elevated water temperatures are postulated to influence the growth and turnover of epidermis by increasing metabolic activities (Aubin et al. 1990) or provide an evolved physiological cue (e.g., daylight; Martinet et al. 1983). Furthermore, physical features of estuaries such as gravel bottoms provide an abrasive surface to rub against and expedite exfoliation (Finley 1982).

In contrast to what is known about moulting for beluga whales, little is known about this phenomenon in bowhead whales (*Balaena mysticetus*). It is known, for example, that the structure of epidermal, dermal and hypodermal layers of balaenid whales (bowhead and right whale, *Eubalaena* sp.), closely resembles that of odontocete species that are known to slough skin (e.g., beluga whales) and differs from the more closely related balaenopterids (e.g., fin, blue, and sei whale) (Reeb et al. 2007). Furthermore, southern right whale (*Eubalaena australis*) calves are known to shed multiple layers of their epidermis (Reeb et al. 2005), which is similar to beluga calves that conduct a multilayered moult to remove fetal epidermis (Yablokov et al. 1974). Histological analysis has revealed that bowhead whales belonging to the Okhotsk Sea population moult during summer months while occupying a warm, shallow bay in the Shantar Archipelago (Chernova et al. 2016). However, it is not known whether other populations of bowhead whales, such as the Eastern Canada-West Greenland (EC-WG) population, undergo a seasonal moult or whether they moult continuously and whether the moulting process is similar for all age classes of whales.

5.3 Methods

I opportunistically made boat-based sightings of EC-WG bowhead whales in Cumberland Sound, Nunavut, Canada—specifically in Kingnait Fiord (located on the northeast side of Cumberland Sound; Fig. 5.1)—on five days from 13–21 August, 2014. As a result of these preliminary observations, a directed study to test the hypothesis that bowhead whales use Cumberland Sound in part for moulting during summer months was carried out in August 2016.

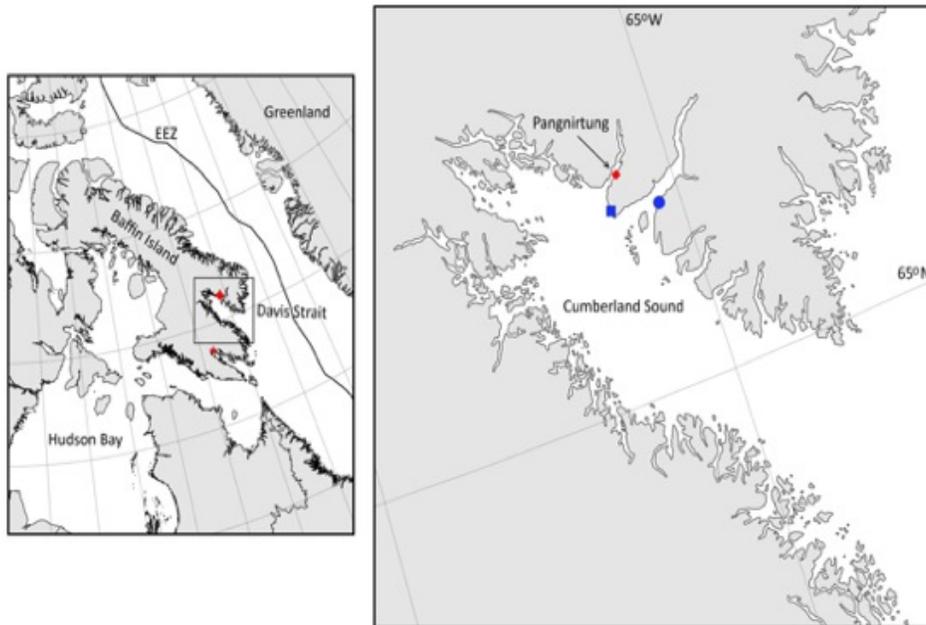


Figure 5.1: Locations of fieldwork conducted in the eastern Canadian Arctic showing Baffin Island, Canada (left panel), and Iqaluit (★, the capitol of Nunavut) and Pangnirtung (◆, a community located in Cumberland Sound). The inset map of Cumberland Sound shows where bowhead whale (*Balaena mysticetus*) observations were made in a small bay in Kingnait Fiord (●) in 2014 from a vessel and from UAS in Brown Harbour (■), Pangnirtung Fiord and Kingnait Fiord in 2016.

Zooplankton samples were opportunistically collected during August 2014 from surface waters (0.5 m) near bowhead whales, and also following an unusual observation of bowhead whales in shallow, coastal waters in Kingnait Fiord. All samples were collected using 333-micrometer (μm) conical mesh net (30 cm in diameter) fitted with a General Oceanics helical flow meter. The zooplankton net was sprayed down with a hose using seawater to collect the sampled organisms in an attached cod-end bucket once it was brought onboard the boat. Once organisms were no longer visible in the zooplankton net, the cod-end bucket samples were filtered through a 333 μm mesh sieve and transferred to a 250 mL sample jar and preserved in 5% buffered formalin solution for identification.

Boat-based and aerial sightings of bowhead whales were made in Pangnirtung Fiord, Brown Harbour (located between Pangnirtung Fiord and Kingnait Fiord; Fig. 5.1) and Kingnait Fiord from 7–31 August 2016. High-resolution aerial images ($n=1143$) and video were obtained of encountered whales using a small unmanned aerial system (UAS), the DJI Phantom 3 Professional. The UAS was equipped with a global positioning system (GPS) and altimeter that

allowed for the whale's position and the UAS altitude to be automatically recorded when each image was captured. The UAS was flown at an average altitude of 12.9 m (\pm 5.4 SD) with a maximum distance of 1000 m from the survey vessel, and was hand-deployed and hand-retrieved from the ~8 m aluminum vessel. Flight times lasted ~8-12 min.

Still UAS images of bowhead whales were used to determine unique animals during August 2016 as well as their body lengths and skin conditions. Individual animals were identified using well-established permanent black and white dorsal patterns (Rugh et al. 1992). The markings used to identify unique individuals included: 1) white scars on their body attributed to breaking sea ice, encounters with fishing gear or from interactions with killer whales (*Orcinus orca*) (i.e., killer whale rake marks; Reinhart et al. 2013); and 2) white pigmentation found on the dorsal flukes, caudal peduncle and lower jaw. Body length measurements (distance between snout and fluke notch) were made for animals that were photographed with the vessel (an object of known size used for calibration) in the same frame or another animal of known size (i.e., previously photographed with the vessel). The measuring tool in Adobe Photoshop CS6 extended was used to measure body length. Skin condition was also assessed from still images to determine: 1) proportion of the body that contained sloughing skin (0=none, 1=<33%, 2=33–66%, 3=>66% and <100% and 4=100%; Fig. 5.2); and 2) the type of sloughing (0=none, 1=light gray lines across the body likely caused by rock rubbing, 2=irregular patches of gray sloughed skin, 3=smooth gray body attributed to complete or near complete sloughing; Fig. 5.3). The presence of gray tissue is indicative of new skin growth—based on my observations and those of bowheads moulting in the Okhotsk Sea (Chernova et al. 2016). Three people independently scored each animal, and agreement between at least two people was required to obtain a final score.

I opportunistically collected oceanographic data during August 2016 to evaluate the physical properties of Kingnait Fiord. Vertical profiles of the water column were made using a seabird SBE19Plus conductivity, temperature, and depth (CTD) profiler. CTD data were corrected using Seabird software and temperature and salinity plots were generated using the downcast data for each cast (n=86).

5.4 Results and Discussion

5.4.1 2014 Observations

Unusual behaviours of bowhead whales in shallow coastal-waters were first noted on 21 August 2014 in Kingnait Fiord when 8-10 bowhead whales were observed frequently rolling onto their sides and backs and lifting their pectoral flippers out of the water (Fig. 5.4). The small, shallow bay was marked with large boulders ($65^{\circ} 55'15.2''$ N and $65^{\circ} 17'50.8''$ W, Fig 5.4 & 5.5) and the whales were in ~ 8 m of water. The animals did not appear to be associated with one another as they were widely distributed throughout the bay and exhibited individually specific behaviours. Several audible vocalizations were heard without a hydrophone from the vessel over the course of the sighting. Net sampling revealed very low zooplankton biomass, particularly for species that are known bowhead whale prey (e.g., calanoid copepods, euphausiids, amphipods), indicating that the whales were not feeding in the bay. There was little likelihood that the whales were feeding because subsequent zooplankton sampling failed to capture bowhead whale prey.

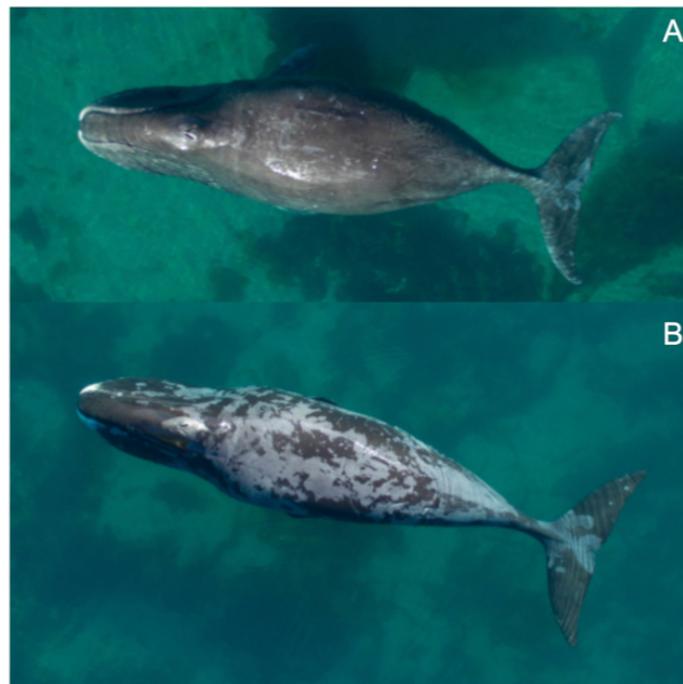


Figure 5.2: Example of an animal with nearly no sloughing skin (i.e., proportion of body with sloughing skin = $<33\%$) (A) and another bowhead whale with a high degree of sloughing ($>66\%$ of body) and a blotchy skin type (B).



Figure 5.3: Example of (A) a bowhead whale with thin and sharp light gray lines and (B) of a whale with shorter and wider gray lines, that both likely reflect prior rock-rubbing behaviour.

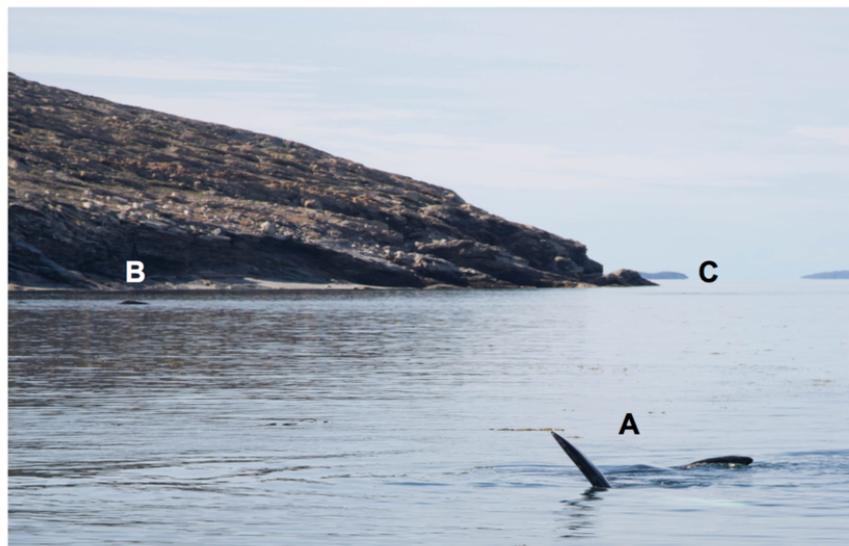


Figure 5.4: Example of observed behaviour and relative distribution of three individual bowhead whales (A-C) inside the bay in Kingnait Fiord (2014). Whale (A) is resting close to shore with its head out of the water, (B) is on its back with pectoral flippers extended, and (C) is breaking the surface of the water in the distance.



Figure 5.5: Large boulders located in the shallow bay where the bowhead whales (*Balaena mysticetus*) aggregated in Kingnait Fiord, Nunavut, during 2014 and where prey samples were subsequently collected.

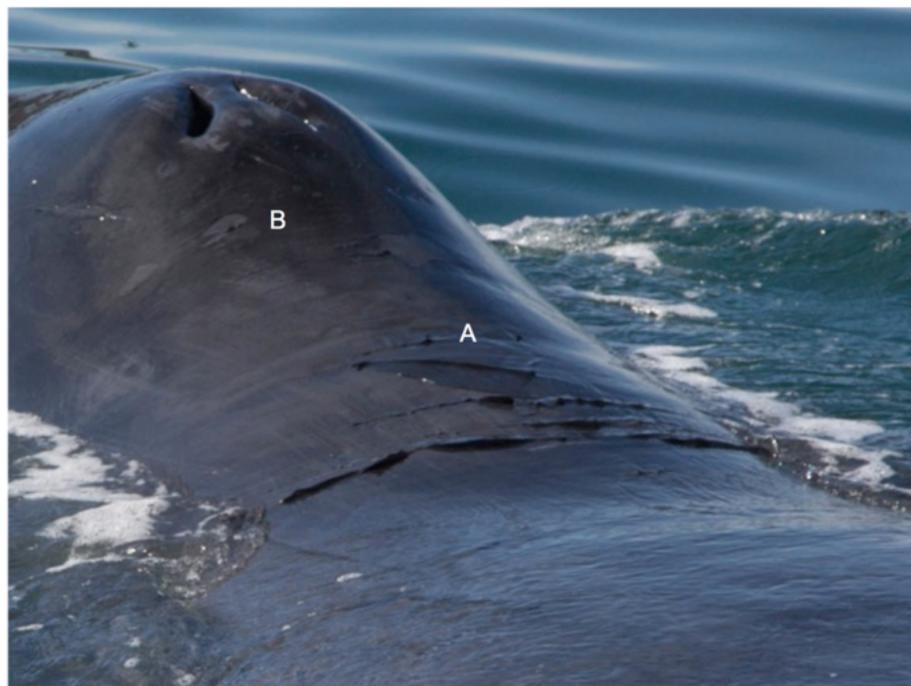


Figure 5.6. Example of sloughing epidermis (A) located behind the blowholes of a bowhead whale (*Balaena mysticetus*) and mottled skin (B) found near the blowholes.

Irregularities in bowhead whale skin condition were observed from animals visiting the bay. Photographs taken of two whales before they reached the bay revealed large pieces of loose epidermis. The sloughing epidermis was predominately located posterior to the whale's blowholes (Fig. 5.6). Animals also presented mottled skin consisting of light gray irregular patches on their heads near the blowholes and on their backs (Fig. 5.6). Furthermore, histological analysis of a sample of loose epidermis from one whale obtained using a crossbow and biopsy dart was consistent with moulting. These documented skin irregularities were similar to the histology of biopsy and opportunistic skin collected from bowhead whales in the Okhotsk Sea (Chernova et al. 2016), and provide support that moulting occurs during summer based on the timing of collection and histological properties of my bowhead samples (Braham 1984).

5.4.2 2016 Observations

5.4.2.1 Rock rubbing

Following my initial observations in 2014, I used the UAS to document four bowhead whales rubbing on large boulders in shallow coastal waters on 7 August 2016 in Brown Harbour (65° 58'31.0" N and 65° 57'19.0" W, Fig. 5.1). While simultaneously filming this rubbing behaviour, I made boat-based observations of whales rolling onto their sides with pectoral flippers extended out of the water similar to my prior observations (during summer 2014). The aerial video and high-resolution still images of the animals displaying surface behaviours confirmed that they were rubbing their bodies against rocks (Fig 5.7 & A.1). The whales were seen rubbing their chins, head, back and sides on a cluster of boulders and had mottled skin with what appeared to be long superficial scratches that ran lengthwise and widthwise along their bodies (e.g., Fig 5.7 animal C). This rubbing behaviour was consistent with previous observations and supported my hypothesis that bowhead whales engage in exfoliation activities during the summer in Cumberland Sound. I presume that rubbing activities caused the linear markings. One animal was observed rock rubbing for a minimum of 8 minutes based on aerial imagery (A.1).

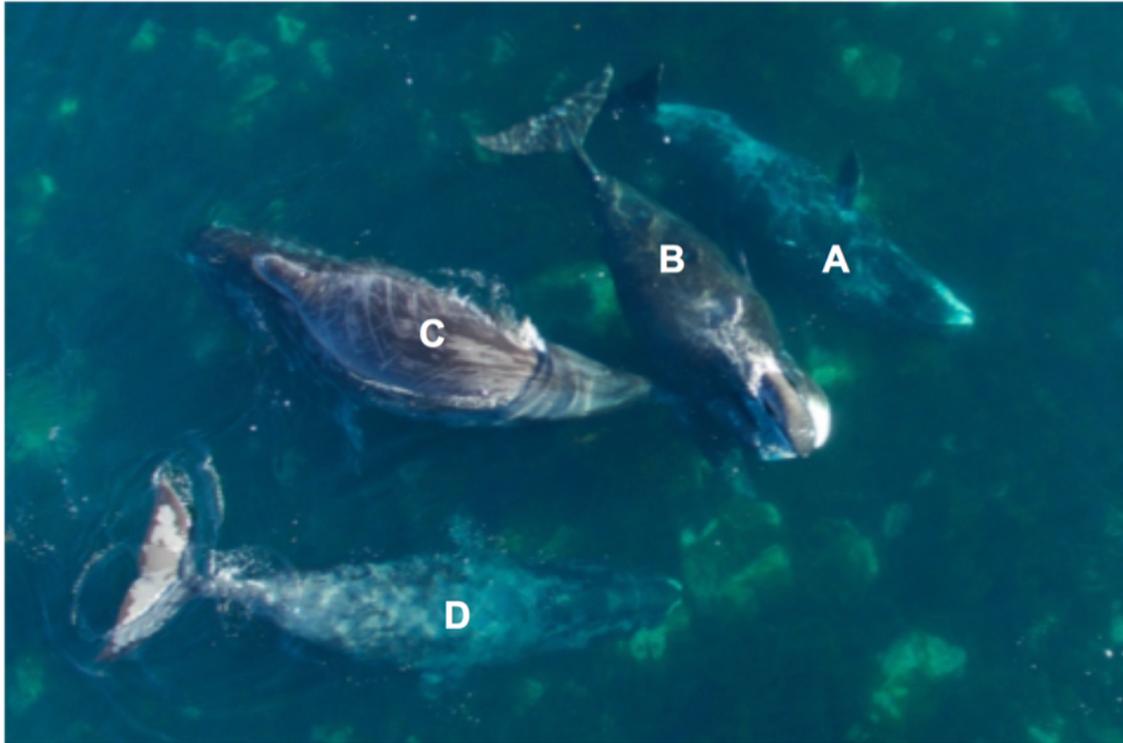


Figure 5.7: Example of four bowhead whales (*Balaena mysticetus*) with mottled skin rubbing their bodies against boulders in Brown Harbour on 7 August 2016. Animal (A) pictured rubbing the right side of its head on a boulder (A.1) and animal (D) is using the rocks to exfoliate its chin. Evidence of prior rock-rubbing is apparent for animal (C) with long, thin lines running length and width-wise across the body.

Previous observations of bowhead rock-rubbing behaviour have been documented during late summer and early fall in Isabella Bay (Baffin Bay), whereby bowhead whales engaged in “grooming” activities by rubbing on the bottom (Koski & Davis 1980, Finley 1990). Similarly, whaling records (Guerin 1845) provide historical support for bowhead rubbing behaviour dating back to ~1845, whereby whales found in the bays and inlets of Davis Strait (such as Cape Searl) were referred to as “rock-nose” whales because they would place their head or “nose” close to the shore on a rock (Reeves et al. 1983). More recently, similar “rock-nose” behaviour was observed during an aerial survey of Isabella Bay on 13 September 1979 (Koski & Davis 1980).

Recent Inuit observations of bowhead whales with moulting skin during summer were made near Clyde River (nearest community to Isabella Bay) (NWMB 2000). Whales were also observed circling around a large rock off the coast of Clyde River (NWMB 2000), and were hypothesized to use the rocks for resting purposes (Guerin 1845). However, the association between EC-WG bowhead whales with moulting skin and their physical environment suggests

otherwise. The whaling data provide further evidence that they have engaged in rock-rubbing behaviour off the coast of Baffin Island for at least hundreds of years.

5.4.2.2 Aerial image analysis

My analysis of high-resolution images from the UAS indicates pervasive moulting for individuals occupying Cumberland Sound during summer. Overall, image quality was sufficient to assess moulting extent and type for 97.6% (n=81) of the uniquely identified individuals (n=83), and revealed that 100% of the individuals had skin irregularities consistent with moulting (Fig. 5.8A). I found that moulting was extensive for 37.4% of the identified whales, whereby sloughing skin represented >66% of their body. I also found that 37.04% of animals had sloughing skin over 33 to 66% of their body and 25.93% had moulting skin on <33% of their body. Over half (58.02%) of the photographed animals had the mottled skin pattern without evidence of rubbing, while 40.74% showed signs of rock-rubbing behaviour (Fig. 5.8B).

My estimated occurrence of rock rubbing from my photographs is likely underestimated due to: 1) limited image quality, particularly when whales were photographed below ~10 m depth; and 2) limited perspective of individual's body whereby evidence of rock rubbing (i.e., light gray lines) may be on the ventral side of the animal and thus excluded from my analysis. As a consequence, my estimate of the proportion (40.74%) of unique individuals bearing marks from probable rock-rubbing behaviour is a minimum estimate.

Overall, I measured body lengths for 16 unique whales ranging from 6.3–14.2 m, with a mean length of 10.60 m (± 2.01 SD) (Fig 5.9). Age-class was broadly inferred based on previous studies (Koski et al. 1993, George, Zeh, et al. 2004, Higdon & Ferguson 2010) that found calves (i.e., young-of-the year) are ~4–7.5 m in August and September, young juveniles (1 to 8-10 y) are 5.8–10 m (Koski et al. 2010), sexually immature sub-adults (8-10 to ~25 y) are 10–13 m, and sexually mature adult (25+ y) males exceed 12.5 m (O'Hara 2002) and females exceed 13 m (George et al. 2011). I used the threshold of 13 m for assigning individuals adult status. Of the animals measured, none were calves based on the morphological differences between calves and yearlings (Koski et al. 2010). However, I did observe one small yearling measuring 6.26 m. Consequently, I concluded that 38% (n=6) of the measured animals were young juveniles (8.59 m, ± 1.33 SD), 56% (n=9) were sub-adults (11.54 m, ± 0.91 SD), and only one animal was an adult (6%) with a body length of 14.22 m. Overall, my measurements of total body length demonstrated

that both juvenile and adult animals occupied Cumberland Sound, and that all animals had sloughing skin.

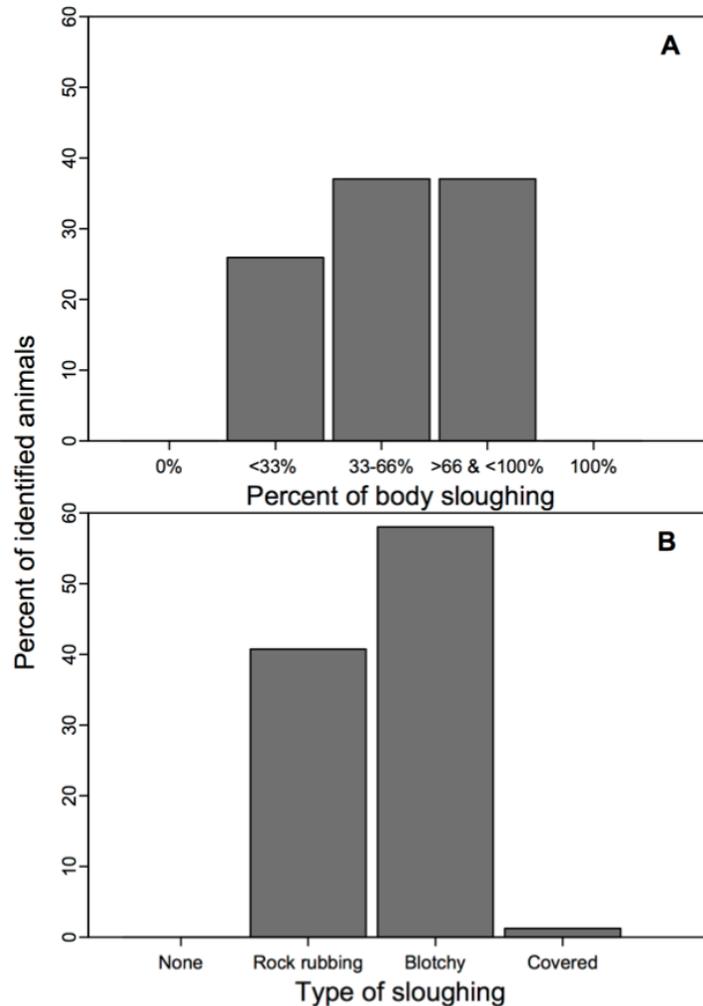


Figure 5.8: Percentage of photographically identified bowhead whales with sufficient image quality to quantify the amount of the body containing sloughing skin (n=81) (A). Overall, all animals showed signs of moulting in late August, and no animals had bodies with 100% new skin cover. Also shown is type of sloughing skin (B) whereby ‘none’ represents animals with no skin irregularities, ‘rock rubbing’ is indicated by animals with both sharp, thin light gray lines and/or wider, less pronounced light gray lines which are likely a result of prior rock rubbing, ‘blotchy’ comprises animals with irregular patches of new epidermis and ‘covered’ includes animals with extensive new skin growth.

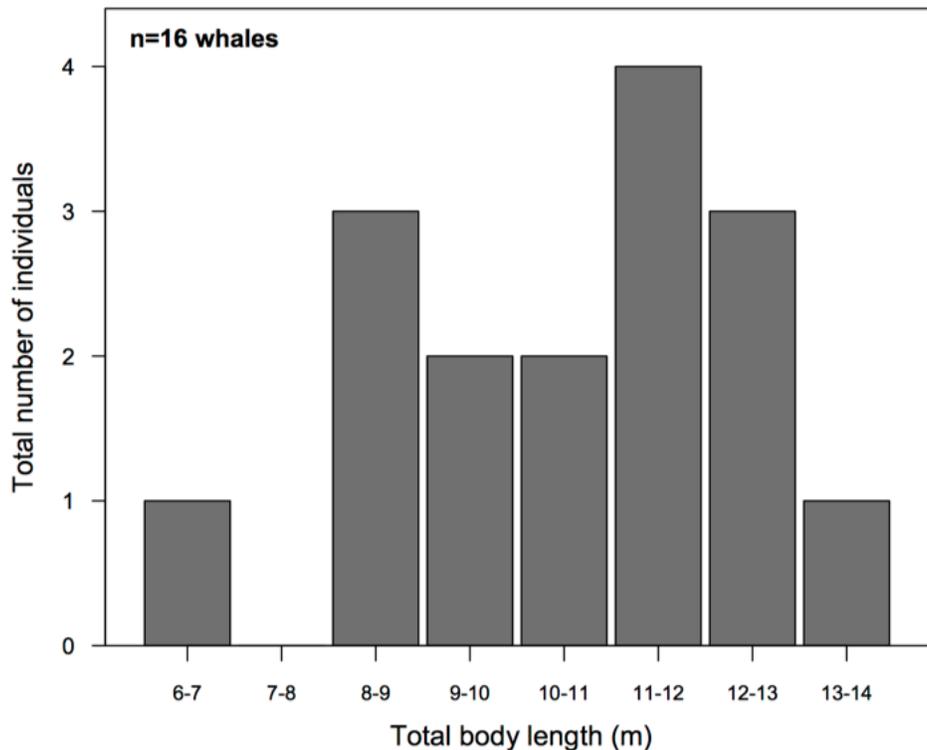


Figure 5.9: The measured body lengths of 16 unique bowhead whales separated into 8 bins where ~6 m was the minimum size and ~14 m was the maximum. The total body length represents the straight-line distance calculated between the tip of the snout to the fluke notch.

5.4.3 Energetic implications of moulting

Although I was unable to quantify the proportion of time allocated to moulting activities, whales were routinely observed, during daylight hours, resting in addition to actively rubbing against the rocks suggesting that individuals allocate considerable time to these two activities. On numerous occasions, my UAS deployments documented moulting individuals resting in nearshore waters where rock rubbing was previously observed.

Moulting is energetically costly for pinniped species that elevate their resting metabolism while increasing blood flow to the epidermis and generating new hair (e.g., Boyd et al. 1993, Boily 1996, Williams et al. 2007, Paterson et al. 2012). Seals and sea lions have behavioural adaptations to partially offset the metabolic costs associated with moulting, such as increasing the time spent on land (i.e., reduced energy expenditure due to thermoregulation and activity costs associated with swimming). Similarly, bowhead whales may adjust their daily activity costs by increasing the proportion of time spent resting. This may be simultaneously beneficial as warmer water may

expedite the moulting process (Boily 1995) and taking refuge in shallow, protected bays may mitigate predation from killer whales.

Unlike seals and sea lions that reportedly experience thermoregulatory benefits by hauling out while moulting, bowhead whales may overheat while moulting in warmer water because they are too well-insulated (bowheads have the thickest blubber of any marine mammal, ranging from 20-35 cm) (Haldiman et al. 1981, Fetter & Everitt 1982, Haldiman & Tarpley 1993, George 2009, Ford et al. 2013) and have small surface area to volume ratios that favor retention of metabolic heat. Maximum daily surface water temperatures ranged from ~4 to 9.5° C in Kingnait Fiord based on the CTD data collected during August 2016, and appeared to be highest near the rock-rubbing habitat with surface temperatures ranging from ~8 to 9.5° C. However, maximum water temperatures encountered by bowhead whales may be even warmer in shallower (~8 m) areas compared with my measurements, which were made in comparatively deep (~100 m) areas of the bay just outside of where rock rubbing occurred. Consequently, bowheads may have to use vascular adaptations to dissipate excess heat while rock rubbing in the warmer, coastal waters.

One way for bowhead whales to dump excess heat may be to use their intraoral thermoregulatory organ located in the root of the tongue (i.e., counter current retial vessels) (Werth 2007) and at the center of the hard palate stretching to the tip of the rostral palate (i.e., palate rete or corpus cavernosum maxillaris) (Ford et al. 2013). They could effectively use this organ by slightly opening their mouths to permit cooling seawater to enter their mouth and flow over the retial vessels in the tongue and the palate rete. I observed several bowhead whales in the aerial images with their mouths slightly agape (A.2) near rock rubbing areas (i.e., Brown Harbour). While it is possible that they were feeding, prior prey sampling in similar shallow habitats in Kingnait Fiord found very few zooplankton and their baleen was not visibly extended. It therefore seems more plausible that the whales opened their mouths to cool themselves because they were thermally stressed in the warmer, shallow rock-rubbing habitat while actively swimming during exfoliation activities. They may have thus regulated their body temperature by exchanging heat from enlarged blood vessels in their tongues and palates with the comparatively cooler seawater (Werth 2007, Ford et al. 2013).

5.4.4 Biological significance of moulting

There are biological factors affecting skin condition that may explain why bowhead whales moult. One is that they may slough their skin to shed ectoparasites such as cyamids (i.e., whale lice) (Haldiman *et al.* 1985; Von Duyke *et al.* 2016) and accumulated diatoms (i.e., phytoplankton) (Heckmann *et al.* 1987) that may damage their epidermis and potentially impede thermoregulation. Another possibility is that bowhead whales are shedding solar damaged skin (Martinez-Levasseur *et al.* 2011). Annual replacement of skin may reduce the risk of extended exposure to ultraviolet radiation during summer in high-latitude habitats (de Gruijl *et al.* 2003), and may be particularly important for long-lived species such as bowhead whales because skin damage accumulates with age (Martinez-Levasseur *et al.* 2013). Regularly sloughing skin damaged by the accumulation of parasites, diatoms and solar radiation may thus allow bowhead whales to maintain epidermal function and integrity over time.

5.5 Conclusions

Overall, my observation of skin irregularities (e.g., mottled skin pattern, sharp light gray lines, loose epidermis) of various age-classes (juveniles, sub-adults and adults) provides strong evidence that moulting is pervasive for bowhead whales during summer in Cumberland Sound. In Cumberland Sound, moulting occurred in shallow, warm coastal areas that had low-salinity surface waters (characteristic of sub-Arctic fiords), and appeared to be facilitated by rubbing on large rocks. The elevated water temperature in rock-rubbing habitat may stimulate epidermal growth (Aubin *et al.* 1990; Watts *et al.* 1991), whereby increased water temperature elevates skin temperature and enhances the rate of cutaneous metabolic processes (Aubin *et al.* 1990). Furthermore, increased ambient temperatures promotes cutaneous blood flow, bringing nutrients and hormones (e.g., thyroid hormone) known to stimulate epidermal proliferation (Aubin *et al.* 1990). Such habitat is comparable to areas where beluga whales rub on rocky substrate in estuaries (Finley 1982; Aubin *et al.* 1990; Watts *et al.* 1991), and where bowheads belonging to the Okhotsk Sea population were observed moulting (Chernova *et al.* 2016).

My findings lend support to previous hypotheses that moulting is facilitated by pronounced changes in oceanographic conditions such as water temperature (Aubin *et al.* 1990; Watts *et al.* 1991), and suggest that rock-rubbing behaviour is used to facilitate the moulting process through exfoliation. Additional research needs to address questions regarding the seasonality of the moult

(i.e., is moulting more pronounced during summer months or does it occur uniformly and continuously throughout the year?) by collecting year-round aerial imagery (excluding winter months with 24 hour darkness), and monitoring the skin condition of bowhead whales over time. Finally, my observations provide evidence that the function of “rock-nosing” observed by whalers, scientists, and northern community members is related to exfoliation to facilitate moulting.

Chapter 6: Conclusions

The primary objective of my thesis was to examine the present environmental conditions and feeding strategies that are contributing to the recovery of the eastern Canada-West Greenland bowhead whale population. It is my hope that the results of my research will permit future evaluation of the energetic consequences of climate-induced shifts in prey quality and quantity. I sought to determine where key foraging areas occurred throughout their range, how foraging activities changed temporally (seasonally and diurnally) and what the composition of their primary prey was under present climate conditions. I also sought to test a long-standing hypothesis that Cumberland Sound, Nunavut was an important feeding habitat for eastern Canada-West Greenland bowhead whale population.

There are considerable logistical challenges associated with studying the diet and feeding behaviour of large whales in the Arctic Ocean, where environmental conditions are highly variable leaving only a brief window of time available for field collection. I therefore combined horizontal and vertical bowhead whale movement data with the vertical distribution and abundance of their prey in a summer habitat (Cumberland Sound) to demonstrate that bowhead feeding could be inferred based on the characteristics of their vertical (e.g., dive shape and depth) and horizontal movement (e.g., swimming speed and turning angle). Doing so allowed me to use long-term bio-logging data to determine when and where the whales fed over the course of a year and also speculate about what prey the whales were targeting.

My research approach included a multi-scale foraging ecology study where I equipped whales with fine-scale (hours) archival tags and coarser-scale, but longer-term (days) time-depth telemetry tags to examine their habitat-use and diving behaviour. I collected information about the vertical distribution, abundance and species composition of prey to determine what depths the whales were diving to for feeding purposes and what their primary prey was. To determine where bowhead whales were likely feeding throughout their expansive range and when peak feeding occurred, I examined long-term (months to years) time-depth telemetry tag data and used state-space models to differentiate area-restricted movement from traveling behaviour. I also analysed the dive characteristics of the whales in areas where area-restricted movement was dominant to make inferences about where the whales were feeding in the water column. Additionally, I collected behavioural, morphometric and skin condition data aerially using an unmanned aerial

system (UAS) to test a hypothesis about whether Cumberland Sound served as an important area of skin exfoliation in addition to being used as a foraging ground.

Despite the inherent limitations and caveats associated with marine mammal field studies such as mine, the large sample size and long time-series of movement data permitted a new and robust examination of the habitat-use patterns and probable feeding behaviour for an understudied segment of the ECWG population. The quantitative state-space modeling approach showed that bowheads have a temporally flexible feeding strategy whereby individuals forage during all times of year and do not fast during winter contrary to previous beliefs. The fine-scale foraging ecology study advanced understanding of the environmental conditions necessary to support bowhead feeding and provided important insight into the diet of a poorly studied portion of the ECWG population—adult males and juveniles of both sexes. I was also able to corroborate that historical observations of bowhead whales associated with large rocks along the Baffin Island coast were indeed engaging in rock-rubbing behaviour, and that the biological significance of this behaviour was to facilitate the moulting process. This result sheds new light on not only the biology of the species, but also on the importance of the physical characteristics of bowhead whale habitat.

6.1 Summary of research hypothesis and findings

6.1.1 Chapter 2

The objective of Chapter 2 was to determine whether Cumberland Sound was an important summertime feeding area by correlating bowhead whale diving behaviour with the vertical distribution of their prey. This is the most comprehensive foraging ecology study conducted on bowhead whales in the eastern Canadian Arctic and involved collecting physical (e.g., temperature and salinity) and biological (e.g., zooplankton species composition and particle abundance) oceanographic data near tagged and untagged whales. I used an Optical Plankton Counter (OPC) to count and size particles in the water column to determine the depth of maximum particle abundance and biomass (i.e., the depth where I anticipate whales diving to if they were feeding). Integrated water column tows using a mesh net were conducted to identify the species and life-stages of zooplankton present. One bowhead whale stomach was collected from a harvested animal to corroborate that the zooplankton samples obtained were representative of actual bowhead whale prey. I simultaneously determined the depths to which the whales were diving during probable foraging dives using multi-scale biologgers. I modified the existing design for the fine-scale

dermal tag to accommodate a satellite transmitter for tag retrieval, which allowed for longer tag attachment times than previously obtained (Baumgartner et al. 2015). Perhaps most important, however, was that the modified tag allowed me to leave the whale after tagging and record undisturbed diving behaviour.

My hypotheses for Chapter 2 were that: 1) Square-shaped dives were reflective of feeding behaviour; and 2) bowheads were exploiting diapausing Arctic copepods (*Calanus glacialis* and *C. hyperboreus*) at depth (>100 m) in Kingnait Fiord during August. I anticipated recording repetitive Square-shaped dives to a consistent depth during daytime and then correlating the maximum depth of these probable foraging dives with the depth of maximum zooplankton biomass in Kingnait Fiord. I also expected to find that the net collected zooplankton samples were dominated by diapausing life-stages (e.g., CIII-CV) of Arctic taxa. Consequently, I predicted that there would be a single prey layer that was sufficient to meet the feeding requirements of juvenile and adult bowhead whales and that it would be located near the sea bottom. My expectation was based on what is known about the life-history characteristics of *Calanus* spp. and the timing at which diapause is initiated in Arctic and sub-Arctic habitats and from preliminary investigations of summary dive data for bowhead whales in the region.

Counter to my expectation, I found that there were two discrete prey layers—a shallow layer that contained occasionally high abundances of smaller particles and a deeper layer that although less dense, contained proportionally larger particles based on the OPC data. When particle measurements were converted into biomass, I found that biomass was greater at depth compared with near the surface. Interestingly, the tag data demonstrated that the whales employed a flexible foraging strategy whereby individuals alternated between shallow and deep probable foraging dives, but appeared to preferentially target lower abundances and deeper aggregations of prey (presumably composed of higher energy Arctic taxa such as *Calanus glacialis* and *C. hyperboreus* based on species identifications from net samples and OPC equivalent circular diameter measurements). Consequently, it appears as though bowheads may offset the potentially increased energy required to conduct prolonged deep foraging dives by opportunistically exploiting shallowly aggregated prey when they occur in high abundances.

The findings from my predator-prey study provide strong support for my first hypothesis that Square-shaped (and even shallow U-shaped dives) indeed reflect feeding and thus dive shape can be used as a metric to make inferences about feeding activity. Zooplankton species

identification and enumeration from net collected samples showed a combination of diapausing and non-diapausing life-stages of *Calanus* spp. I thus speculated that the smaller and earlier life-stage organisms represented the smaller particles recorded by the OPC in the near surface waters and that these organisms were actively feeding *Calanus* spp. Conversely, the larger and later life-stages of *Calanus* spp. were likely the comparatively larger particles found at depth by the OPC that are undergoing diapause. Overall, it appears as though predator-prey interactions in Kingnait Fiord are more complex than originally thought such that bowhead whales opportunistically exploit prey layers at multiple depth strata, but that ultimately, they prefer depths with the greatest biomass (providing support for my second hypothesis).

6.1.2 Chapter 3

In Chapter 3, I examined seasonal and diel patterns in bowhead whale foraging behaviour in Cumberland Sound using long-term time-depth telemetry tags and by collecting zooplankton net samples (August 2013) for species identification and enumeration and stomach contents from one harvested animal (July 2013) for diet confirmation. My primary hypotheses for Chapter 3 were that: 1) although occupied during all seasons, feeding activities are greatest during the summer; and 2) the maximum depth of probable foraging dives change seasonally; and 3) bowheads display diel patterns in their diving behaviour that follow expected day and night patterns in zooplankton vertical distribution during August.

To demonstrate the seasonal importance of Cumberland Sound as a feeding ground, I anticipated finding that whales allocated the most time to horizontal (i.e., area restricted movement) and vertical movements (i.e., Square dives) consistent with feeding behaviour during summer. I then anticipated finding differences in the depth of probable feeding dives during the day and night in the summer, whereby the whales would conduct shallow Square-shaped dives during night (when zooplankton are thought to migrate to the surface waters to forage on phytoplankton while minimizing predation from visual predators) and comparatively deeper Square dives during the day (when migrating zooplankton typically descend to the poorly lit near bottom waters where they can avoid being eaten). Furthermore, I expected to find that the maximum depth of probable foraging dives was shallowest during late spring and early summer while zooplankton exploit surface aggregations of phytoplankton and deepest during late summer and early fall when *Calanus* spp. are thought to commence diapause at depth.

Through analysis of the time bowhead whales spent conducting area-restricted search and Square-shaped dives, I found evidence that juvenile and adult females and juvenile and sub-adult males feed during all months—making Cumberland Sound the only known area that supports bowhead whale foraging year-round. Furthermore, I found support for my first hypothesis whereby late summer and early fall are particularly important feeding times when whales likely target Arctic calanoid copepods such as *Calanus glacialis*. I also found distinct seasonal and diel patterns in bowhead whale dive behaviours that appear to correspond to temporal changes in the vertical distribution of their prey that are related to well-studied life-history characteristics (providing support for my second and third hypotheses). However, I also found evidence of asynchronous diapause whereby bowheads may alternate between deep-water aggregations of diapausing copepods during the day and night, and shallowly aggregated actively feeding prey after dusk (consisting of smaller bodied and earlier life-stage *Calanus* spp.).

Perhaps the most surprising finding of my study was that bowheads appeared to allocate only a fraction of their time to feeding activities on a daily basis compared with the closely related North Atlantic right whale during summer. Such discrepancies in foraging effort may reflect: 1) availability of higher quality prey and thus greater energetic consumption on a daily basis; 2) lower daily energy needs (e.g., reduced metabolic rate compared with North Atlantic right whales); or 3) more opportunities for foraging annually (e.g., foraging year-round). Overall, I found that bowheads are able to exploit seasonally available prey in Cumberland Sound and that this apparent flexibility in their foraging strategy may allow them the behavioural ability to adapt to climate induced changes in their habitat. However, it remains to be seen how climate change will affect the quality and quantity of their prey, and how bowhead whales will ultimately fare energetically.

6.1.3 Chapter 4

In Chapter 4, I expanded the breadth of my study by conducting a large-scale movement analysis of bowhead whale satellite telemetry and dive data. My objective was to identify seasonally important habitats for bowhead whales in the eastern Canadian Arctic and determine when and where they likely feed throughout their range. Of all my data chapters, this one was the most exploratory in nature due to the questions asked. The main hypothesis I sought to test was that bowhead whales indeed fasted (or displayed considerably reduced foraging effort) while overwintering in Hudson Strait during winter. I expected to see a higher proportion of transiting

locations during winter compared with other seasons (particularly summer) and a lower proportion of probable foraging dives compared with exploratory V-shaped dives.

The greatest strength of this study was the new and comprehensive insight into the migratory and foraging behaviour of the species that I was able to glean from the long tag attachment times, whereby animal tracks were available for over a year (and on occasion for nearly two years for some individuals; max $n=737$ days) on average per individual. Counter to expectation, I found that bowheads employed a flexible foraging strategy whereby they appeared to feed throughout their range during all times of year—including during winter in Hudson Strait. Overall, the diving and Argos location data allowed me to identify 6 feeding areas (Cumberland Sound, Foxe Basin, Hudson Strait and Frobisher Bay, Hudson Bay, Gulf of Boothia, and Central East Baffin Coast).

Although the whales likely forage throughout the year in the eastern Canadian Arctic, peak foraging appears to occur between July and September suggesting that Cumberland Sound and the Gulf of Boothia are the most important feeding grounds for this segment of the ECWG population. Given these results, I anticipate that whales will be able to adjust their seasonal movements in response to environmental change and potential range shifts in their prey. It is plausible that new feeding opportunities will occur in response to decreases in summer ice extent, whereby whales may expand their northern range into the Arctic Archipelago and occupy habitats such as the Gulf of Boothia earlier in the year. Furthermore, bowheads may take advantage of secondary phytoplankton blooms that facilitate the concentration of zooplankton near the surface waters at lower latitudes and feed shallowly later into the open water season in response to earlier sea ice retreat.

6.1.4 Chapter 5

In response to the unusual bowhead behaviours that were uncharacteristic of feeding activities (observed while conducting the field component of Chapter 2), I sought to test the hypothesis that whales occasionally engaged in rock-rubbing behaviour to facilitate an epidermal moult in Cumberland Sound during summer. I anticipated recording visual observations of the whales physically interacting with the large boulders that marked the shallow bays in Kingnait Fiord where I initially observed the behaviour during August 2014. I also expected to find that a

high proportion of the encountered whales displayed mottled skin that was consistent with moulting.

Using an unmanned aerial system to record the underwater behaviour of the whales, I obtained video evidence that the whales were indeed engaging in rock-rubbing behaviour as individuals with visibly sloughing skin were actively rubbing their bodies against the boulders. Through analysis of the skin condition of the whales using still aerial images, I observed skin irregularities (e.g., mottled skin pattern, sharp light gray lines, loose epidermis) of various age-classes (juveniles, sub-adults and adults) that were consistent with moulting. I speculated that the warmer water temperatures measured near the shallow bays where rock-rubbing occurred may help expedite the sloughing process. Combined, these results suggest that Cumberland Sound is a multi-use habitat and that bowhead whales utilize this area for not only feeding but exfoliation purposes as well.

6.2 Research strengths and limitations

Despite the comprehensive nature of my study, there were several inherent constraints due to logistics, technology, and environmental and behavioural factors that limited the scope of the research and require discussion. A sampling bias undoubtedly exists for the long-term time-depth telemetry and fine-scale tagging component because animals were tagged from only two locations, and bowheads are known to segregate based on age-class and sex. For example, I found that predominately juvenile and sub-adult animals occupied Kingnait Fiord based on aerial measurements of body length (Chapter 6). Thus adult animals are poorly represented in my sample. Consequently, I was only able to model the movement of a segment of the eastern Canada-West Greenland population.

To avoid tagging a calf, I set a conservative minimum size limit that excluded calves (0-1 y and ~4–7.5 m) and young juveniles (1 to 8-10 y and 5.8–10 m) from my study. Thus the horizontal and vertical movement of sub-adult animals (8-10 to ~25 y and 10–13 m) was over-represented relative to younger age-classes. Additionally, to prevent any potential disruption of the energy transfer between lactating females and their offspring, I did not tag any lactating females and thus do not know how their habitat-use patterns and foraging behaviour may differ to other demographic groups. A strength of this study, however, is that nearly equal numbers of male and female whales were tagged, and that presumed immature and sexually mature animals were

included in the sample (based on visual observations of body length from the vessel). Furthermore, the tag attachment times were the longest of any recorded, providing important insight into the annual and seasonal migrations and feeding behaviour of individual animals that was not previously available.

Another limitation of my study involved low temporal resolution of Argos locations and uncertainty regarding the animals' true location. An unavoidable challenge associated with large-whale telemetry studies is that obtaining frequent Argos positions is difficult because it requires the whales to be regularly at the surface, which is inherently challenging for animals that are capable of conducting long dives (e.g., ≥ 60 mins). Consequently, I could not examine fine-scale horizontal movements of individual animals due to a low number of daily Argos positions. Furthermore, location quality depends upon the duration of the surface interval and the proximity of a satellite to the tagged animal. If whales conduct a series of short dives they may only require a few breaths before diving again, and this may be insufficient for the multiple satellite transmissions required to generate accurate location estimates. Consequently, obtaining some low quality positions was unavoidable and resulted in some locations appearing to occur on land.

Despite these challenges, I found that using a speed threshold to remove biologically improbable locations (i.e., those resulting from unrealistic swimming speeds) and a hierarchical state-space model to predict two locations per day per tagged animal from the filtered data removed many poor-quality locations and allowed for consistency when comparing the horizontal movement of individual animals. Overall, the temporal resolution of the location data was more than sufficient for analysing longer-term movements (e.g., weeks-months), but prevented examining daily movements.

The largest limitation for the fine-scale tagging and prey sampling component of the study was not being able to collect co-located prey data in locations where tagged whales dove as previously intended due to the apparent effect the research vessel had on tagged whale behaviour. I found that while conducting focal follows of tagged whales, individuals would reside in shallow, coastal waters where previous zooplankton sample collections revealed extremely low prey abundances.

The presence of killer whales (the only known predator to bowhead whales other than humans) in Cumberland Sound is believed to cause whales to remain close to the shoreline—perhaps to mitigate predation. Consequently, it appeared as though the presence of my research

vessel may be altering the behaviour of the whales. I attempt to reduce the potential impact of my boat on whale behaviour by increasing my distance to >500 m and <1,000 m (to remain within detection range of the acoustic transmitter) and used the unmanned aerial system to remotely monitor the whales' behaviour in real time. I conducted 1-9 hours of consecutive focal follows on individual animals and found that overall the tagged whales did not leave the shoreline and that they consistently conducted shallow dives (based on the time-depth recorder data). This contrasted with the behaviour of adjacent animals that were occupying deeper areas in Kingnait Fiord and conducting long, high-fluking dives (i.e., likely deep dives).

In response to the apparent effect the research vessel had on whale behaviour, I decided to revise my field strategy and immediately left whales after tagging them and collected prey data in adjacent waters. Although this meant sacrificing the collection of co-located bowhead whale dive and prey data, it did result in the recording of probable foraging dives including deep dives (>100 m) that previously were not obtained. I also decided to collect vertical prey data from high-quality locations where SPLASH tagged whales last transmitted in Kingnait Fiord to improve the spatio-temporal correlation between bowhead whale diving and zooplankton distribution and abundance data. Overall, I was able to relate bowhead dive behaviour to the vertical distribution of zooplankton in Kingnait Fiord despite a reduction the spatio-temporal co-location in data collection.

The other limitation I experienced involved challenges associated with differentiating *Calanus* species. My original intention was to convert OPC particle measurements (i.e., equivalent circular diameter) to specific species and life-stages of *Calanus* spp. based on prosome measurements to determine differences in the vertical distribution of these morphologically similar taxa in the water column. However, my net samples demonstrated that diversity was high whereby zooplankton composition was not dominated by a single species and life-stage of calanoid copepod. Consequently, overlap in equivalent circular diameter (ECD) occurred across species such that different species of the same life-stage are known to overlap in size (Parent et al. 2011) and different life-stages of different species also similarly overlap (Madsen et al. 2001).

Another factor leading to uncertainty when attempting to associate particle sizes with specific species and life-stages is that measures of ECD are known to be affected by the orientation and transparency of the organism as it passes the light beam (Herman 1992, Baumgartner 2003). Other studies have calibrated the OPC measurements for a specific size range based on prosome

measurements of a particular species and quantitatively determined the vertical structure of the target species in the water column because the system was largely dominated by a single species of a specific life-stage (e.g., *Calanus finmarchicus* CV in the Bay of Fundy and elsewhere in the Gulf of Maine; (Baumgartner 2003, Baumgartner & Mate 2003, Baumgartner et al. 2003, 2017). However, I was able to make qualitative inferences regarding the vertical distribution of specific species and life-stages of *Calanus* spp. based on the ECD measurements and species and life-stage specific prosome measurements I made from net collected samples.

6.3 Future research

My results demonstrate that Cumberland Sound is an important foraging and moulting habitat for different demographic groups of eastern Canada-West Greenland bowhead whales. However, diet composition is sparsely known in other areas that I identified as being probable foraging habitat such as the Gulf of Boothia. Based on my analysis of long-term movements and habitat-use patterns (Chapter 4), I found that some individuals alternated between feeding in Cumberland Sound and Gulf of Boothia, but that they only visited one of these habitats per year. Prey collection during late summer and early fall in high Arctic habitats such as the Gulf of Boothia would be informative for understanding how prey quality and quantity varies latitudinally across their range. Furthermore, if vertical prey collections were made in conjunction with fine-scale tagging studies, hypotheses could be tested about where the whales are feeding in the water column and about the life-history of their prey (e.g., shallow Square-dives targeting actively feeding Arctic copepods). I could also compare the quality of both habitats under current environmental conditions to determine whether whales are better able to meet their nutritional needs in one habitat over the other.

An understanding of how zooplankton are distributed throughout the water column based on species and life-stage is currently unknown. To test the hypothesis I proposed in Chapter 1 regarding smaller bodied earlier life-stage *Calanus* spp. occurring near the mixed layer for active feeding during daytime and the deep layer containing larger and later-stage *Calanus* spp. that are undergoing diapause, zooplankton should be collected at discrete depths in the water column (e.g., using a pump or multi-net close-open-close system). Depth stratified sampling (e.g., 4 m depth bins) such as this would enable species identification and enumeration. Furthermore, co-located OPC measurements could be made and converted into size specific abundances per 4 m depth bin

and compared with the abundance of similarly sized zooplankton species from the pump samples. The collection of co-located, depth-stratified OPC and pump samples should enable direct comparison between both data sets, thus allowing for more rapid and informative prey sampling using the OPC for future collections. One challenge associated with this study design is the laboratory time required to process the pump samples. Another alternative, would include using a lightframe on-sight key-species investigation (LOKI) system that provides rapid mapping of zooplankton abundance as well as taxonomic and size composition using an imaging device (Schulz et al. 2010) and an automated species identification model (Schmid et al. 2016).

Determining which species and life-stages of *Calanus* spp. undergo diel vertical migration in Cumberland Sound during August would test my hypothesis from Chapters 1 and 2 that bowhead whale foraging varies over diel time scales. I suggested that August is a transitional period for *Calanus* spp. whereby larger bodied organisms that had accumulated sufficient lipids would conduct diel vertical migration and descend to depth during the day, while smaller and less lipid rich organisms may continue feeding in the surface waters where predation risk is presumed to be greater (i.e., asynchronous diel vertical migration). I also suggest that during late August, some *Calanus* spp. may have terminated feeding altogether and remain at depth in diapause until the following spring. To determine whether zooplankton follow DVM and whether some organisms have initiated diapause, a day and night zooplankton study could be performed.

For this diel vertical migration study, the vertical movements of zooplankton would be monitored by conducting continuous vertical sampling with an OPC and depth-stratified net tows approximately every ~1 hour over a 24 hour period. Additionally, a moored multi-frequency echosounder could be used to study the fine-scale vertical movements of zooplankton. If the sampled organisms are in diapause it would be expected that they would not vertically migrate after dusk. However, non-diapausing copepods would likely exhibit DVM as a means to avoid predation from visual predators such as zooplanktivorous fish (Baumgartner et al. 2011). Diapausing copepods may be differentiated from non-diapausing animals by examining lipid sac volume (e.g., diapausing organisms will tend to have larger lipid sacs), guts (e.g., diapausing organisms will tend to have no food in their guts), RNA:DNA ratios (e.g., diapausing copepods have low RNA:DNA ratios) (Baumgartner & Tarrant 2017; Tarrant et al. 2008). If bowhead whale diving behaviour could be simultaneously recorded while 24-hour prey sampling occurs, I could determine the spatio-temporal variability in diel vertical migration and the relationship between zooplankton depth distribution and bowhead whale dive behaviour.

Additional research is required to confirm my hypothesis that the bowhead whale moult is seasonal as opposed to being continuous in the eastern Canadian Arctic. Consequently, it is important that questions regarding the seasonality of the moult (i.e., is moulting more pronounced during summer months or does it occur uniformly and continuously throughout the year?) are answerable by collecting aerial images of individual whales year-round and evaluating skin condition over time. Furthermore, it would be interesting to know whether rock-rubbing occurs exclusively in Cumberland Sound or whether there are similarly hospitable environments elsewhere along the coastline of Baffin Island. Consequently, similar studies using unmanned aerial systems should seek to observe bowhead whale behaviour in shallow coastal waters such as near Qikiqtarjuaq where bowheads display area-restricted movement behaviour during October and November based on my movement analysis in Chapter 4. Collaboration with northern community members to collect UAS data seasonally in Cumberland Sound and in other areas (e.g., near Qikiqtarjuaq) should be encouraged because accessibility and local knowledge regarding seasonal movements and habitat patterns of bowhead whales would be imperative for the success of such studies.

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Appendices

Table A.1: Summary zooplankton abundances (orgs per m⁻³) and weights (mg C m⁻³) calculated first by early (CI-CIV) and late life-stage (CV-Adult) per species and then combined for each species (*Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus* and *Pseudocalanus* spp.). The fished volume is the total water filtered during the *oblique* or vertical net tows. Total abundance is the number of all staged *Calanus* spp. and *Pseudocalanus* spp. per cubic meter and the total weight is the total biomass (mg C m⁻³) of these organisms. Data were separated between sampling locations—Pangnirtung Fiord and Kingnait Fiord and mean and standard deviations (SD) for each measurement is present per area.

Date	Fished volume (m ⁻³)	Total abund (orgs m ⁻³)	Total weight (mg C m ⁻³)	<i>C. hyp</i> abund (orgs m ⁻³)	<i>C. hyp</i> Weight (mg C m ⁻³)	<i>C. glac</i> abund (orgs m ⁻³)	<i>C. glac</i> weight (mg C m ⁻³)	<i>C. fin</i> abund (orgs m ⁻³)	<i>C. fin</i> weight (mg C m ⁻³)	<i>Pseudo</i> abund (orgs m ⁻³)	<i>Pseudo</i> weight (mg C m ⁻³)
Pangnirtung Fiord											
16-08-05	14.13	75.16	1.17	3.82	0.18	8.92	0.36	8.49	0.17	53.93	0.47
16-08-05	4.12	254.05	4.06	2.91	0.13	27.66	1.12	86.62	1.72	136.85	1.09
16-08-05	9.81	80.71	1.29	1.22	0.06	9.17	0.37	26.60	0.53	43.72	0.33
16-08-05	10.40	91.43	1.53	1.44	0.07	14.71	0.60	25.38	0.50	49.90	0.36
16-08-07	12.56	75.48	1.98	9.55	0.44	21.50	1.01	14.81	0.29	29.62	0.24
16-08-10	21.48	43.77	1.35	4.84	0.33	11.92	0.69	7.64	0.15	19.37	0.17
Mean	12.08	103.43	1.90	3.97	0.20	15.65	0.69	28.26	0.56	55.56	0.44
SD	5.73	75.48	1.10	3.07	0.15	7.49	0.32	29.71	0.59	41.87	0.33
Kingnait Fiord											
16-08-10	60.19	26.63	2.34	5.12	0.37	3.84	1.80	0.35	0.01	17.33	0.16
16-08-15	70.93	17.17	1.57	2.11	0.25	5.50	1.23	1.10	0.02	8.46	0.07
<i>16-08-15</i>	<i>94.95</i>	<i>15.50</i>	<i>2.04</i>	<i>3.12</i>	<i>0.54</i>	<i>2.44</i>	<i>1.39</i>	<i>0.42</i>	<i>0.02</i>	<i>9.52</i>	<i>0.09</i>
16-08-16	56.52	19.75	1.45	4.67	0.40	2.87	0.90	1.49	0.05	10.72	0.09
<i>16-08-16</i>	<i>28.18</i>	<i>28.11</i>	<i>0.80</i>	<i>6.81</i>	<i>0.31</i>	<i>7.52</i>	<i>0.31</i>	<i>4.97</i>	<i>0.10</i>	<i>8.80</i>	<i>0.08</i>
<i>16-08-16</i>	<i>27.58</i>	<i>53.08</i>	<i>2.44</i>	<i>14.36</i>	<i>0.75</i>	<i>14.50</i>	<i>1.41</i>	<i>5.66</i>	<i>0.11</i>	<i>18.56</i>	<i>0.17</i>
<i>16-08-16</i>	<i>28.26</i>	<i>21.16</i>	<i>1.12</i>	<i>6.65</i>	<i>0.31</i>	<i>5.38</i>	<i>0.70</i>	<i>2.55</i>	<i>0.05</i>	<i>6.58</i>	<i>0.06</i>
16-08-19	54.54	27.72	0.63	0.00	0.00	10.67	0.43	5.06	0.10	11.99	0.10

16-08-19	95.52	21.03	2.14	3.74	0.35	3.08	1.66	0.22	0.00	14.00	0.13
16-08-20	29.96	35.25	1.85	2.60	0.12	15.22	1.53	4.41	0.09	13.02	0.12
16-08-19	89.84	25.38	3.90	4.94	0.46	6.81	3.30	0.40	0.01	13.22	0.12
16-08-23	52.14	46.38	3.81	8.17	0.85	11.97	2.64	2.99	0.11	23.25	0.21
16-08-23	57.37	33.43	2.21	6.83	0.39	6.83	1.59	1.83	0.07	17.94	0.16
16-08-23	54.97	31.33	3.34	4.91	0.87	6.55	2.25	1.42	0.05	18.45	0.17
16-08-23	50.87	35.50	2.34	6.61	0.44	9.32	1.65	2.83	0.10	16.75	0.15
16-08-23	67.26	23.83	2.66	5.72	0.57	5.93	1.95	1.46	0.04	10.72	0.10
16-08-26	44.65	35.21	2.33	4.43	0.44	11.56	1.69	2.02	0.04	17.20	0.16
16-08-27	50.64	49.27	2.68	9.87	0.80	16.29	1.61	3.36	0.08	19.75	0.18
16-08-27	47.76	27.14	1.25	3.27	0.15	9.80	0.97	1.51	0.03	12.56	0.11
16-08-28	46.63	22.20	0.73	4.72	0.22	5.15	0.39	1.61	0.03	10.72	0.09
Mean	55.44	29.75	2.08	5.43	0.43	8.06	1.47	2.28	0.06	13.98	0.13
SD	20.49	10.40	0.94	3.06	0.24	4.19	0.75	1.66	0.04	4.45	0.04

Table A.2: Samples collected from oblique tows are in italics and the others were obtained from vertical hauls. Samples shaded in grey are from Pangnirting Fiord and the unshaded samples were collected in Kingnait Fiord. Total counted is the total number of organisms identified per aliquot per sample while the total sampled is the total number of zooplankton collected in each net tow. The total abundance is the number of organisms per cubic meter. Aliquot species counts are provided for the most numerous taxa (e.g., *Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus*, *Pseudocalanus* spp., *Metridia* spp., *Oithona* spp., *Acartia longiremis*, *Pareuchaeta* spp. and *Cyclops* spp.).

Date	Total counted	Total sampled	Total abundance	<i>C. hyp</i>	<i>C. glac</i>	<i>C. fin</i>	<i>Pseudo</i> spp.	<i>Metridia</i> spp.	<i>Oithona</i> spp.	<i>Acartia longiremis</i>	<i>Pareuchaeta</i> spp.	<i>Cyclops</i> spp.
16-08-05	209	1254	88.75	9	21	20	127	1	0	2	0	0
16-08-05	373	1119	271.52	4	38	119	188	0	0	0	0	0
16-08-05	387	1161	118.32	4	30	88	145	1	0	3	0	0
16-08-05	448	1344	129.22	5	51	88	175	0	0	1	0	0
16-08-07	347	1041	82.88	40	90	62	125	1	1	1	0	4
16-08-10	263	1052	48.98	26	64	41	105	0	0	1	0	1
16-08-10	280	1960	32.56	44	33	3	149	37	0	0	0	0
16-08-15	237	1422	20.05	25	65	13	102	26	0	0	0	0
<i>16-08-15</i>	<i>212</i>	<i>1696</i>	<i>17.86</i>	<i>37</i>	<i>29</i>	<i>5</i>	<i>113</i>	<i>23</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>0</i>
16-08-16	212	1272	22.51	44	27	14	101	12	0	0	0	0
<i>16-08-16</i>	<i>239</i>	<i>956</i>	<i>33.93</i>	<i>48</i>	<i>53</i>	<i>35</i>	<i>62</i>	<i>1</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>0</i>
<i>16-08-16</i>	<i>424</i>	<i>1696</i>	<i>61.49</i>	<i>99</i>	<i>100</i>	<i>39</i>	<i>128</i>	<i>1</i>	<i>0</i>	<i>1</i>	<i>0</i>	<i>1</i>
<i>16-08-16</i>	<i>462</i>	<i>924</i>	<i>32.70</i>	<i>94</i>	<i>76</i>	<i>36</i>	<i>94</i>	<i>3</i>	<i>0</i>	<i>0</i>	<i>1</i>	<i>0</i>
16-08-19	263	1578	28.93	0	97	46	109	0	0	0	0	0
16-08-19	323	2261	23.67	51	42	3	191	29	0	0	0	0
16-08-20	200	1200	40.06	13	76	22	65	2	0	0	0	0
16-08-19	440	2640	29.39	74	102	6	198	52	0	0	0	0
16-08-23	422	2532	48.56	71	104	26	202	6	0	1	0	0
16-08-23	328	2296	40.02	56	56	15	147	34	0	0	0	0
16-08-23	332	1992	36.24	45	60	13	170	33	0	0	0	0
16-08-23	327	1962	38.57	56	79	24	142	11	1	0	0	0
16-08-23	311	2177	32.37	55	57	14	104	71	0	0	1	0
16-08-26	284	1704	38.16	33	86	15	128	9	0	0	0	0
16-08-27	532	2660	52.53	100	165	34	200	1	0	0	0	0
16-08-27	228	1368	28.64	26	78	12	100	0	0	0	0	0
16-08-28	227	1135	24.34	44	48	15	100	4	0	0	0	0

Table A.3: Samples collected from vertical net tows in Kingnait Fiord during August 2013 in the fluke print of a diving bowhead whale. Total zooplankton abundances (orgs/m⁻³) were calculated for all enumerated organisms (Total abund) for each sample. Total weights (mg C m⁻³) and abundances (orgs/m⁻³) of specific taxa were additionally calculated for *Calanus* and *Pseudo* spp. as they were the most numerically dominant.

Sample ID	Total abund [†]	Total weight <i>Calanus</i> & <i>Pseudo</i> [‡]	Total abund <i>Calanus</i> & <i>Pseudo</i> [†]	Total abund <i>C hyp</i> [†]	Total weight <i>C hyp</i> [‡]	Total abund <i>C gla</i> [†]	Total weight <i>C gla</i> [‡]	Total abund <i>C fin</i> [†]	Total weight <i>C fin</i> [‡]	Total abund <i>Pseudo</i> [†]	Total weight <i>Pseudo</i> [‡]
Sb006	36.52	1.07	33.05	1.24	0.05	8.08	0.77	3.11	0.11	20.62	0.15
Sb007	27.63	1.03	22.73	0.88	0.04	5.40	0.82	2.26	0.06	14.19	0.11
Sb008	31.31	0.94	28.34	1.68	0.14	6.86	0.62	1.42	0.04	18.37	0.13
Sb009	31.75	1.25	25.98	1.68	0.07	7.12	1.02	2.41	0.04	14.77	0.12
Sb010	34.36	2.22	30.43	1.16	0.36	12.09	1.70	2.18	0.06	15.00	0.11
Sb011	30.10	0.67	25.36	0.64	0.10	5.89	0.41	1.79	0.03	17.04	0.13
Sb012	43.95	1.15	34.73	1.01	0.18	8.71	0.75	3.79	0.06	21.22	0.16

[†]orgs/m⁻³ [‡]mg C m⁻³

A.1: Aerial video collected from an unmanned aerial system of bowhead whales engaged in rock-rubbing behaviour in Cumberland Sound, Nunavut during August 2016 (Chapter 5).

<https://www.dropbox.com/s/35otd1pi6ysnw4f/A%205.1%20Movie.mov?dl=0>

A.2: Example of a bowhead whale mouth slightly agape near Brown Harbour during August 2016 (Chapter 5).

