Movement Patterns and Winter Habitat Use of Narwhal (*Monodon monoceros*) in the Eastern Canadian Arctic

by

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Abstract

Climate change is reducing the Arctic sea ice concentration and extent and it has been thought that narwhal will be poorly able to adjust. The goal of this thesis was to (a) analyzing narwhal year-round movement, and to (b) examine winter habitat selection in relation to sea ice and bathymetry. Narwhal from Admiralty Inlet and Eclipse Sound were equipped with satellite transmitters between 2009 and 2012. Narwhal conducted multiple late-summer movement patterns with three stocks overlapping, had a delayed fall migration compared to a tagging studies a decade earlier, and had decreased summer site fidelity. During the winter narwhal selected 1500 to 2000m depths, which likely have higher prey densities, regardless of the mobile pack ice structure. They also conducted extensive movements coinciding with a delayed growth in sea ice extent. These results indicate that narwhal may be more able to adjust to habitat changes than previously believed.

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Thesis Format and Manuscript Claims

This thesis is presented in a manuscript format. Chapter 1 Introduces the theme of the thesis and the overall research objectives. Chapter 2 provides a relevant literature review. Chapter 3 and Chapter 4 are structured with an abstract, introduction, methods, results, and discussion. Chapter 5 presents the major conclusions of the thesis and recommends what future research directions would be beneficial in advancing current understanding of narwhal spatial usage.

Chapter 3 examines Admiralty Inlet and Eclipse Sound narwhal year round movement patterns and seasonal home-range. Winter movement is only briefly described because Chapter 4 focuses on that season. The manuscript is currently in revision for submission to a peer-reviewed journal (to be determined):

Kenyon, K.A., D.Y. Yurkowski, J. Orr,D. Barber, S.H. Ferguson. Movement and Overlap between the Admiralty Inlet and Eclipse Sound Narwhal (*Monodon monoceros*) Stocks. (*in prep*)

The narwhal satellite transmitter data were collected by the Department of Fisheries and Oceans as well as hunters from Arctic Bay, NU and Pond Inlet, NU. The data collection was led by Jack Orr. I processed the data, analyzed the timings of narwhal year-round movement, conducted all statistical analysis, and wrote the chapter. Dr. David Barber and Dr. Steve Ferguson assisted me with designing the project. Dr. David Yurkowski assisted me with constructing the statistical analysis.

Chapter 4 examines narwhal habitat selection in relation to sea ice and bathymetry during the winter season. It has been submitted to Polar Biology where I am the corresponding author:

Kenyon, K.A., D.Y. Yurkowski DY, J. Orr, D. Barber, S.H. Ferguson. Baffin Bay narwhal (*Monodon monoceros*) select bathymetry over sea ice during winter. Polar Biology (*submitted*).

The Department of Fisheries and Oceans and hunters from Arctic Bay, NU and Pond Inlet, NU collected the narwhal satellite transmitter data. This field effort was led by Jack Orr. I acquired the sea ice and bathymetric data from the Canadian Ice Service and the International Bathymetric Chart of the Arctic Ocean respectively. I processed the data, conducted all statistical analysis, and wrote the chapter. Dr. David Barber assisted with designing the project. Dr. Steve Ferguson assisted with designing the project and editing of the paper. Dr. Dave Yurkowski assisted me with constructing the statistical analysis and editing of the paper.

Chapter 1

Research Objectives

The goal of this thesis is to increase our understanding of narwhal (*Monodon monoceros*) year-round spatial usage and important habitat features within the eastern Canadian Arctic. Satellite transmitters were equipped to narwhal within Admiralty Inlet (2009) and Eclipse Sound ($2010 - 2012$) which recorded the horizontal movement of narwhal for over one year. Previous tracking studies have indicated that these two narwhal stocks are isolated with no immigration or emigration, and have little spatial overlap outside the winter season (Dietz et al. 2001, 2008, Heide-Jørgensen et al. 2002, 2013). However a preliminary review of this dataset indicated that narwhal conducted more variable movement patterns than were previously recorded, with multiple narwhal traveling through other isolated stocks' summer grounds. Immigration and emigration rates impact management decisions including establishing accurate sustainable quotas for traditional subsistence harvests (Hixon et al. 2002). Additionally plasticity in site fidelity and migration routes and timings allow species to adjust to rapidly changing habitats and increased anthropogenic activities which are occurring, or will likely occur with climate change

(Faille et al. 2010, Monteith et al. 2011, Laidre et al. 2008, Cherry et al. 2013). Plasticity within this thesis was defined as the adaptability of individual narwhal to changes within its environment. Therefore the objectives of Chapter 3 are to examine (a) the timing and location of narwhal late summer movement, (b) the overlap between Admiralty Inlet and Eclipse Sound stocks, (c) the timing of the fall migration in comparison to what was concluded from previous tagging studies, and (d) summer ground and winter ground site fidelity. These results will improve our knowledge regarding how connected or isolated the Admiralty Inlet and Eclipse Sound stocks are, as well as how flexible narwhal may be in adjusting movement patterns, migration routes, and summer ground location with a changing climate.

The Arctic is rapidly changing due to climate change with decreasing sea ice concentrations and extents as well as warming ocean temperatures (Barber et al. 2012, Laidre et al. 2015, Park et al. 2015). This is projected to continue and will likely result in range shifts both as arctic species try to remain within their tolerable thermal range and as subarctic species capitalize on increased areas with seasonally or permanently open water (Moore and Huntington 2008, Wang and Overland 2012, Laidre et al. 2015, Descamps et al. 2017). Winter is thought to be a critical season for narwhal as they overwinter within dense pack ice and are heavily foraging (Heide-Jørgensen et al. 2002, Laidre and Heide-Jørgensen 2005a,b, Watt et al. 2015). However little is known about important winter habitat components because few satellite tags have lasted throughout the entire winter season (Dietz et al. 2001, 2008, Heide-Jørgensen et al. 2002, 2003, 2013). Understanding important habitat features allows managers to predict how changing habitat or anthropogenic activities may impact the target species, as well as allowing potential impacts to be mitigated (Basille et al. 2008). The objective of Chapter 4 is to analyse narwhal habitat selection in relation to sea ice structure and bathymetry during the winter season. Bathymetry was used as a proxy for foraging behaviour because both prey density and dive behaviour are related to bathymetry (Laidre et al. 2004, Jørgensen 2011, Treble 2015). This will improve our understanding on how physical changes within the pack ice structure itself may impact narwhal fitness as they use leads to access the atmosphere to breathe during the winter season. It will also provide insights on how narwhal may respond to a decreasing sea ice extent.

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Chapter 2

Relevant Literature Review

2.1 Spatial Utilization

When managers understand how a population moves through and utilizes its environment they are able to implement knowledgeable management decisions and plans that mitigate the impact of anthropogenic activities and changing habitats. This involves studying the location and timing of important migration routes(Dietz et al. 2008), how inter-connected different populations are (Heide-Jørgensen et al. 2006), which areas are year-round or seasonal critical habitat (Nielsen et al. 2015), and what features within habitat are most important for survival (Furgal et al. 1996). Understanding this allows managers to preserve or conserve important seasonal habitat regions (Augé et al. 2014), establish accurate sustainable harvest quotas (Bethke et al. 1996), manage habitat to improve species fitness (Faille et al. 2010), and create recommendations or guidelines for how to mitigate impacts of changing environments or anthropogenic activities (Reeves et al. 2014).

2.1.1 Migration and Site Fidelity

Migration is defined as “a relocation of the animal that is on a much greater scale, and involves movement of much longer duration, than those arising in its normal daily activities” (Dingle and Drake 2007). Species conduct migrations to leave an area prior to seasonal habitat changes or to take advantage of seasonally available resources (Dingle and Drake 2007, Monteith et al. 2011). Changes in abiotic conditions (e.g. temperature), seasonal changes of habitat quality, and other cues like photo-period are factors that can trigger migration for different species (Gwinner 1996, McCormick et al. 1998, Dingle and Drake 2007, Cherry et al. 2013). Juveniles often learn migration routes from their mothers. Populations with this style of learning often have little ability to adjust migration routes (Laidre et al. 2008, Colbeck et al. 2012). As migrations are energetically expensive it is important for species to occupy high quality habitat on either end, or during the migration route to build up and restore energy reserves (Lindström et al. 2000). Migratory species are vulnerable to habitat changes that shift the spatiotemporal coupling between migration and prey or forage availability so that these two aspects are mismatched. When this occurs species may not be able to recover the energy spent migrating (Laidre et al. 2008, Monteith et al. 2011, Cherry et al. 2013).

Migratory species often have high site fidelity, which is when individuals annually return to the same area (Faille et al. 2010). Ecological benefits to site fidelity include familiarity within an area that has resulted in reproductive success in the past, including locations of high quality foraging opportunities and refuge areas to assist in predator avoidance (Greenwood 1980). However populations with high site fidelity are vulnerable to habitat changes or anthropogenic development within the area they annually occupy, as they may continue to return to the same area even if it has become degraded (Laidre et al. 2008, Faille et al. 2010). High site fidelity can also be an indicator of a closed population, where no immigration or emigration occurs. However it is possible for immigration or emigration to occur at different seasons or with different sections of the population if only one sex or age class exhibit site fidelity (Hixon et al. 2002, Faille et al. 2010). Studying whether a population exhibits site fidelity, immigration, or emigration usually involves tracking individuals for over a year or unique identification through photographs (Whitehead 2001, Hixon et al. 2002, Heide-Jørgensen et al. 2003). Understanding whether a population has high site fidelity and whether it is open or closed are important when estimating sustainable harvest quotas, when predicting impacts from anthropogenic development or activities, and when creating or managing protected areas (Bethke et al. 1996, Augé et al. 2014, Reeves et al. 2014).

2.1.2 Habitat Selection

Examining habitat selection focuses on identifying habitat that is important for the focal species to complete their life cycle. This occurs on different scales (Vandermeer 1972, Rettie, W. James and cois Messier 2000, Basille et al. 2008). Home-range analysis examines habitat selection on a broad scale by estimating the area that an individual or population are likely to occur a particular percentage (often 95% and 50%) of the time. This reveals the extent of the seasonal range (95% home-range), and also reveals core areas within the seasonal range that are likely relatively important for survival (50% home-range;Worton (1989), Basille et al. (2008), Walter et al. (2015)). A more fine-scaled habitat selection identifies which habitat features within a home-range are important for a life-season or activity (Johnson 1980, Basille et al. 2008). An example would be identifying the snow depth on landfast ice that ring-seal prefer to create their natal dens (Furgal et al. 1996). Habitat features important for survival are inferred by examining what habitat features a particular wildlife species uses disproportionate to their availability. This theory assumes that wildlife select the habitat features that will best maximize their fitness (Johnson 1980, Rettie, W. James and cois Messier 2000, Basille et al. 2008). Understanding important habitat features allows for the protection or management of habitat to increase the fitness of the focal species.

2.2 Climate Change in the Eastern Canadian Arctic

Baffin Bay is a unique Arctic region in that it has relatively large oceanographic connections to southern water systems via Davis Strait. This results in a relatively high amount of exchange of water masses despite the Davis Strait sill (Parkinson et al. 1999). Baffin Bay is covered with pack ice during the winter and is primarily ice free during the summer (Parkinson et al. 1999, Stern and Heide-Jørgensen 2003). Pack ice is not one stable molded platform, but consists of different sized floes pushed and joined together. Between floes are leads, or stretches of temporary open water (Richter-Menge et al. 2002, Hopkins and Thorndike 2006). Leads can be important biologically as a location for marine mammals to access the atmosphere (Smith et al. 1990, Heide-Jørgensen et al. 2013).Historically multi-year ice from the Arctic Ocean moves south through Nares Strait into Baffin Bay early in winter until ice bridges form across Nares Strait, blocking any southward ice movement(Stern and Heide-Jørgensen 2003). The ice bridges also result in the formation of the North Water polynya, where new ice is consistently formed and forced south by winds. First year sea ice also grows and thickens throughout the region (Parkinson et al. 1999, Stern and Heide-Jørgensen 2003, Heide-Jørgensen et al. 2013).

Sea Ice formation and decay within Baffin Bay follows a relatively predictable pattern compared to other Arctic regions. From the September minimum extent sea ice grows moderately until October when the rate of growth increases through November (Parkinson et al. 1999). During this time sea ice begins developing in the north-west section of Baffin Bay and grows south into Davis Strait (Stern and Heide-Jørgensen 2003). From November until the March maximum sea ice will continue to grow slowly east towards West Greenland. Baffin Bay has a relatively high interannual variability in winter ice extent compared to other Arctic regions; however most years the pack ice reaches north of $68°$N at the West Greenland coast (Parkinson et al. 1999, Stern and Heide-Jørgensen 2003). Typically the sea ice extent does not cover the entire Baffin Bay/Davis Strait region as the warm West Greenland current causes decay or slows growth. The spring melt follows the opposite pattern, melting from the east towards the north-western side of Baffin Bay. Ice begins decaying in March and April, and the rate of decay slowly increases until between June and August when it reaches peak decay (Parkinson et al. 1999).

2.2.1 Changing Sea Ice within Baffin Bay

Sea ice concentrations within Baffin Bay decreased an average of $0 - 1.2\%$/year from 1979 to 2011 (Park et al. 2015). Most sea ice loss occurred along the pack ice edge near West Greenland or in the south-eastern portion of Baffin Bay (Barber et al. 2012, Park et al. 2015). There is a sea ice loss gradient between West Greenland and Baffin Island, with areas along the warm West Greenland current experiencing sea ice concentrations decreases of $0.8 - 1.2\%$/year with reduction in sea ice slowly declining towards Baffin Island where sea ice concentration decreases were $0 - 0.2\%$/year (Park et al. 2015).

Wang and Overland (2012) examined multiple models at different emission level scenarios to obtain a time estimate of when the future summer sea ice extent within the Arctic will be less than 1.0 million km^2. The time range in their top models suggest that this will occur within $14 - 36$ years after 2007, the final year of the model. The median value centers the time range within the 2030s. Their projections suggest that remaining summer sea ice will occur within the Canadian Arctic Archipelago and north of Greenland.

2.2.2 Anticipated Ecological Changes

Warming ocean temperatures, reduced sea ice extent, and an increased length in the open water season are anticipated to result in cascading ecological changes, particularly in terms of species distribution and abundance (Moore and Huntington 2008, Laidre et al. 2008, 2015, Descamps et al. 2017). In other Arctic regions where warming has been more intense, observed impacts on Arctic fish and wildlife have overall been negative (Descamps et al. 2017).

Some distribution and abundance shifts are already occurring for Arctic cod, capelin and killer whale within the eastern Canadian Arctic (Gaston and Elliott 2014, Yurkowski et al. 2016, Higdon et al. 2014). Long-term studies on marine mammals and seabirds diet in Hudson Bay and Cumberland Sound have noticed that the amount of capelin (*Mallotus villosus*) has increased in diets and the amount of Arctic cod (*Arctogadus glacialis*) has decreased since the 2000s (Marcoux et al. 2012, Provencher et al. 2012, Chambellant et al. 2013, Gaston and Elliott 2014, Yurkowski et al. 2016). Killer whales (*Orcinus orca*) are now spotted annually during the open water season in Hudson Bay as well as within the major sounds and inlets of Baffin Island including the Lancaster Sound region. Historically killer whales had infrequently visited, or extremely rarely visited these regions (Higdon et al. 2014). These top predators have been observed hunting marine mammals including narwhal (*Monodon monoceros*), beluga(*Delphinapterus leucas*), and bowhead whales (*Balaena mysticetus*) (Higdon and Ferguson 2009, Higdon et al. 2014, Ferguson et al. 2010). Narwhal exhibit avoidance behaviour of killer whales by hiding in shallow water along the shoreline (Higdon and Ferguson 2009, Breed et al. 2017). It is anticipated that fish and wildlife distribution and abundances will continue shifting, which could lead to increased interspecific competition as subarctic marine mammal and fish species shift their ranges northward (Moore and Huntington 2008, Laidre et al. 2008, Descamps et al. 2017).

2.3 Narwhal Ecology

Narwhal are difficult and logistically challenging to study because they remain along coastal areas for only three to four months, overwinter in the middle of dense pack ice north of the Arctic circle in complete darkness, and as cetaceans most of their activity occurs underwater (Dietz et al. 2001, 2008, Heide-Jørgensen et al. 2002, Laidre and Heide-Jørgensen 2005a). Satellite transmitters have been used for the past two decades to study migration routes and timings, winter ground locations, site fidelity, diving capabilities, and foraging behaviour (Heide-Jørgensen and Dietz 1995, Heide-Jørgensen et al.

2013, Laidre et al. 004c, Dietz et al. 2008, Watt et al. 015a). This data can reveal how interconnected or isolated different summer grounds are, which is critical information to sustainably manage the traditional harvest by Inuit communities. It also highlights areas of critical habitat which will be increasingly important as sea ice continues to decrease and anthropogenic interests increase.

Narwhal have successfully been equipped with satellite transmitters from six summering grounds (Dietz and Heide-Jørgensen 1995, Dietz et al. 2001, 2008, Heide-Jørgensen et al. 2002, 2003, 2013, 2015, Westdal et al. 2010). These researchers have concluded that there are three separate narwhal populations where no mixing occurs: Baffin Bay, Northern Hudson Bay, and East Greenland. The Baffin Bay population, which is the focus of this study, has had four summering grounds equipped with satellite transmitters and analysis to date have indicated that there is little mixing between summer ground locations. Each summering ground is therefore managed as an individual subpopulation, or stock (Heide-Jørgensen et al. 2013).These four summering grounds are located within Melville Bay, Admiralty Inlet, Eclipse Sound, and near Somerset Island (Fig. 2.1). This study focuses on the Admiralty Inlet and Eclipse Sound stocks, with some brief description of Somerset Island stock during the late summer season. The remainder of this chapter will focus on these three stocks during seasons relevant to the study.

2.3.1 Narwhal Summer and Fall Movement

During the open water summer season narwhal conduct localized movements in the deep waters within their summer grounds (Dietz et al. 2001, Heide-Jørgensen et al. 2002). The exception to this behaviour occurs when killer whales are in the region. Then narwhal hug

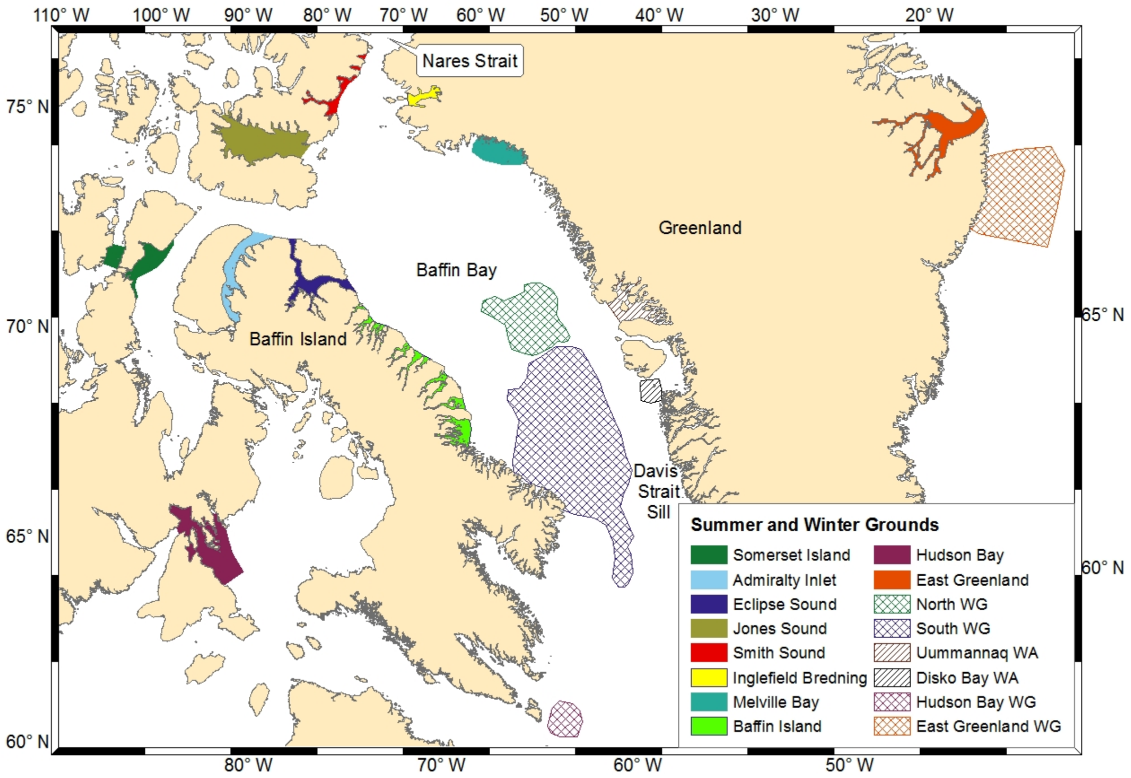

Figure 2.1: Approximate narwhal summer ground, winter ground (WG), and winter aggregation (WA) locations. Stocks outside of the Baffin Bay population are labeled after their appropriate population. Approximate summer and winter ground locations were created from tracklines recorded in (Heide-Jørgensen et al. 2002, 2003, 2015, Dietz et al. 2008, Westdal et al. 2010)

the shoreline in the shallow waters (Breed et al. 2017). During summer they frequently dive to the seafloor, which could indicate foraging or scraping molting skin on rocks (Dietz et al. 2001, Heide-Jørgensen et al. 2002, Watt et al. 015a, 2017). However while some foraging likely occurs, it is not thought to be as dominant an activity as the rest of the year (Finley and Gibb 1982, Laidre and Heide-Jørgensen 2005b, Watt et al. 2017). Stomach content and stable isotope analysis has shown that main prey species during the spring and summer are Arctic cod, armhook squid (*Gonatus fabricii*), Greenland halibut

(*Reinhardtius hippoglossoides*, shrimp (*Pandalus spp.*), and capelin (Finley and Gibb 1982, Laidre and Heide-Jørgensen 2005b, Watt and Ferguson 2015). The reason why narwhal consistently return to their summer grounds is unknown. One hypothesis is that summer ground location is related to calving requirements, however this remains only a hypothesis (Finley and Gibb 1982, Laidre et al. 004a).

Prior to landfast ice formation in September and early October, narwhal leave their summer ground and travel through Lancaster Sound to their winter ground within Baffin Bay. This migration is over 1000 km (Dietz et al. 2008). Young and immature narwhal appear to migrate with their mothers or other closely related individuals (Watt et al. 015b). Early tagging efforts found that narwhal from the same stock and year had highly coordinated movements during migration, with similar timing and type of movement. There was also incredible similarity between stocks and across years, with different stocks traveling offshore < 2 days apart and individual narwhal remaining within $15 - 100$ km apart between years (Dietz et al. 2001, Heide-Jørgensen et al. 2003, Laidre et al. 004a). While this reported observation has overall remained true, a few narwhal have been tracked traveling west upon leaving their summer ground prior to traveling east to Baffin Bay (Dietz et al. 2001, Heide-Jørgensen et al. 2013). Upon entering Baffin Bay narwhal typically travel along the shoreline or along the continental slope to their winter ground in southern Baffin Bay (Dietz et al. 2001). Narwhal conduct rapid directed movements, averaging 85 km/day (Heide-Jørgensen et al. 2002) and likely conduct little foraging or searching for resources during this time-period (Laidre et al. 004a).

2.3.2 Narwhal Behaviour on the Winter Ground

There are two main wintering grounds and two winter aggregations for the Baffin Bay stock (Fig. 2.1). Melville Bay, Admiralty Inlet, and Eclipse Sound stocks winter in an overlapping area called the south winter ground, while the Somerset Island narwhal overwinter in what is called the north winter ground (Dietz and Heide-Jørgensen 1995, Dietz et al. 2008, Heide-Jørgensen et al. 2003, 2013, Laidre et al. 004b). It appears that Somerset Island narwhal may also overwinter in the Uummannaq winter aggregation, as narwhal tagged in the Uumannaq winter aggregation completed a spring migration to the summer ground of the Somerset Island stock (Heide-Jørgensen et al. 2013). Both winter grounds are along the continental shelf, where bathymetric depths rapidly change from $500 - 2300$ m (Heide-Jørgensen et al. 2003, 2015).

Narwhal typically arrive at their winter ground in early November prior to extensive pack ice growth (Dietz and Heide-Jørgensen 1995, Dietz et al. 2001, 2008, Heide-Jørgensen et al. 2002, 2003, Laidre and Heide-Jørgensen 2005a). This observation means that narwhal chose their winter ground for other reasons than simply being barricaded by sea ice (Laidre and Heide-Jørgensen 2005a). Satellite images from $1978 - 2001$ indicated that sea ice grows most rapidly on the winter grounds between November and December, and that after mid-January the mean sea ice concentration is $95 - 98\%$. Overall ice conditions within the winter ground matched those of Baffin Bay (Laidre and Heide-Jørgensen 2005a). Narwhal are unable to break through pack ice and rely on leads to breath during this period of dense ice cover (Heide-Jørgensen et al. 2002).

Habitat selection within the pack ice has been poorly studied because historically few transmitters last throughout the entire season, making statistical analysis challenging (Dietz and Heide-Jørgensen 1995, Dietz et al. 2001, 2008, Heide-Jørgensen et al. 2002, 2003). An aerial survey over the Baffin Bay winter ground was conducted in early April prior to the pack ice break up, concluded that narwhal were more likely to be found in areas with $> 90\%$ sea ice than in areas with $< 50\%$ sea ice, even though there were regions with large leads providing areas with open water. Since narwhal were not found as often in areas of open water, it was concluded to be likely that they are primarily targeting something else such as quality foraging areas (Laidre and Heide-Jørgensen 2011).

Diving behaviour during the winter season has been more thoroughly studied and indicates that narwhal are foraging extensively at deep depths (Heide-Jørgensen et al. 2002, Laidre et al. 2003, Watt et al. 015a). Around 50% of the time that narwhal spend diving occurs at depths > 800 m but they frequently dive to depths > 1500 m (Laidre et al. 2003, Watt et al. 015a). Such deep dives are energetically expensive, and narwhal spend most of time in vertical transit, leaving little time for foraging (Laidre et al. 2003, Williams et al. 2011). This indicates that narwhal probably target high densities of benthic prey during these deep foraging-shaped dives (Laidre et al. 2003). Narwhal also frequently conduct surface dives, likely to recover from the energetically expensive deep dives (Watt et al. 015a). Both the frequency of dives > 900 m and the duration of dives increase with increasing depth and distance from shore (Laidre et al. 004b).

Dive behaviour and stomach analysis have indicated that narwhal forage on Greenland halibut, armhook squid, and potentially capelin during the winter season (Laidre and Heide-Jørgensen 2005b, Watt and Ferguson 2015). Greenland halibut are the most abundant benthic fish species and occur throughout Baffin Bay and Davis Strait (Orr and Bowering 1997, Jørgensen et al. 2005). Young fish occur in fjords and all along the coastal area of Greenland (Gundersen et al. 2013). Disko Bank is considered a nursery, with high densities of one year old fish at $300 - 500$ m depths (Jørgensen et al. 2005, Jørgensen 2013). As halibut grow larger and older they move to deeper waters within Baffin Bay where they are most abundant at > 800 m depths (Jørgensen 2011, Treble 2015) and are found to depths of at least 2000 m (Orr and Bowering 1997, Jørgensen et al. 2005, Jørgensen 2013). While armhook squid are the most abundant cephalopd species in the eastern Canadian Arctic it has primarily been studied as bycatch from other trawl surveys, likely resulting in a low catch rate, particularly of mobile adults (Frandsen et al. 2004, Zumholz and Frandsen 2006, Gardiner and Dick 2010). Juvenile squid appear to be most abundant at depths < 600 m and descend to deeper waters as they mature (Kristensen 1984, Frandsen et al. 2004, Zumholz and Frandsen 2006). Adults are primarily found in depths ranging from 400-1100m, but have been caught down to depths of 2000 m. They occur along the continental slopes and rarely travel to the surface waters (Piatkowski and Wieland 1993, Frandsen et al. 2004).

2.3.3 Narwhal Spring Migration and Site Fidelity

Few transmitters have lasted through the winter season such that the spring migration the subsequent summer site fidelity is relatively poorly understood. The beginning of spring migration is variable but typically occurs sometime in April prior to the pack ice breaking up (Laidre and Heide-Jørgensen 2005a, Dietz et al. 2008). In spring narwhal travel slower and take a less direct route than during the fall migration (Dietz et al. 2008). They often periodically remain stationary at different locations, likely waiting for leads to open up within the landfast or pack ice in front of them. While narwhal wait for leads to develop within the landfast ice, they frequently forage under the ice edge on Arctic cod, squid, and capelin (Bradstreet 1982, Finley and Gibb 1982, Crawford and Jorgensen 1990, Watt and Ferguson 2015). Narwhal enter Lancaster Sound between June and July, depending on when leads form and ice breaks up (Heide-Jørgensen et al. 2003, 2013, Dietz et al. 2008).

Only eight transmitters across all narwhal stocks have lasted long enough to track narwhal approaching, or residing within a summer ground after the spring migration (Heide-Jørgensen et al. 2003, 2013, 2015, Dietz et al. 2008, Westdal et al. 2010). When transmitters failed, six narwhal had either returned to the mouth of their previous summering ground but were still blocked by landfast ice, or they were residing within their previous summer ground (Heide-Jørgensen et al. 2003, 2015, Dietz et al. 2008, Westdal et al. 2010). Two narwhal were harvested or photographed within or near their original summer ground (Heide-Jørgensen et al. 2008, 2015). As narwhal have never been recorded traveling to a different summer ground, either after the spring migration or during the summer it has been assumed to date that they have high site fidelity and are isolated stocks with little or no immigration or emigration.

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Chapter 3

Movement and Overlap Between the Admiralty Inlet and Eclipse Sound Narwhal (*Monodon monoceros*) Stocks

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3.1 Abstract

Narwhal (*Monodon monoceros*) are thought to be relatively sensitive to the impacts of climate change due to their consistent migration routes and high site fidelity. The goal of this component of my thesis was to increase the understanding of the movement patterns and interconnectivity between Admiralty Inlet and Eclipse Sound narwhal. Twenty-four narwhal were equipped with satellite tags in Admiralty Inlet and Eclipse Sound from $2009 - 2012$. Eight tags recorded part of the spring migration with two tags transmitting long enough to record narwhal approaching or residing within a summer ground location the subsequent year. The 95%, 75%, and 50% yearly summer and winter home-range areas were estimated and generalized least squares models were conducted to examine the relationship between individual home-range area with narwhal size and sex. Admiralty Inlet and Eclipse Sound narwhal conducted multiple movement patterns in the late summer and early fall. This resulted in the $2010 - 2012$ Eclipse Sound 95% summer home-range overlapping 50% of the 2009 Admiralty Inlet 95% summer home-range. One narwhal tagged in Eclipse Sound summered in Admiralty Inlet the subsequent year even though both areas were ice-free. Therefore it appears that Admiralty Inlet and Eclipse Sound stocks are connected in September and October, and potentially have an exchange of individuals between years. Additionally, the larger flexibility in late summer movement patterns and summer site fidelity indicates that that narwhal may be more able to adjust the timings and patterns of fall migration and possibly summer ground location in the face of changing environmental conditions than previously believed.

3.2 Introduction

Understanding wildlife spatial use throughout their range is essential to both estimate the potential impacts of anthropogenic activities and climate change, as well as to establish sustainable harvest levels (Bethke et al. 1996, Williams et al. 2008, Faille et al. 2010). Foundational aspects of population spatial use include delineating population boundaries (Bethke et al. 1996), estimating rates of immigration and emigration (Hixon et al. 2002), examining the existence of site fidelity (Faille et al. 2010), examining whether the population is resident or migratory, and the types of migrations conducted if applicable (Hixon et al. 2002, Dingle and Drake 2007). Species that occur within a small geographic area, have low rates of immigration or emigration, have high site fidelity, or which conduct lengthy and directed migrations with consistent interannual timings and routes are thought to have low plasticity and be less resilient to rapid environmental changes (Dingle and Drake 2007, Laidre et al. 2008, Williams et al. 2008, Faille et al. 2010, Descamps et al. 2017). Additionally understanding a population's natural boundaries and the rates of immigration and emigration are essential to calculate harvest quotas that allow for sustainable harvests (Bethke et al. 1996).

Narwhal (*Monodon monoceros*) are a small Arctic cetacean with a relatively narrow geographical range from the eastern Canadian Arctic to the east Greenland Arctic (Heide-Jørgensen et al. 2013, 2015, Garde et al. 2015). They are hunted by Inuit communities throughout their range as part of a traditional subsistence harvest and are an important source of vitamin A, D, and E (Kuhnlein et al. 2006). In the Canadian Arctic Archipelago narwhal from three different summer grounds (Somerset Island, Admiralty

Inlet, and Eclipse Sound) have been tracked with satellite transmitters to delineate population boundaries, estimate immigration and emigration rates, learn migration patterns, and assess site fidelity (Dietz et al. 2001, 2008, Heide-Jørgensen et al. 2002, 2003, 2013). These studies conclude that narwhal remain relatively stationary within their summer ground, conduct directed migrations > 1000 km to overwinter within Baffin Bay, and return to the same summer ground the subsequent year. Their fall migration was concluded to follow consistent interannual timing and routes with all tagged narwhal having similar departure dates. A few exceptions to this pattern were observed, with narwhal traveling through other summer grounds during the early fall or having a delayed migration (Heide-Jørgensen et al. 2002, 2013). These three summer grounds were therefore considered separate, isolated stocks for management purposes. Due to these long rigid migrations and high site fidelity narwhal are thought to be relatively sensitive to climate change (Laidre et al. 2008).

While narwhal movement patterns have been studied previously, few transmitters have been attached compared to the estimated population size for Admiralty Inlet ($35,000$), Eclipse Sound ($10,500$), and Somerset Island ($50,000$;Dietz et al. (2001), Heide-Jørgensen et al. (2002, 2003, 2013), Dietz et al. (2008), Doniol-Valcroze et al. (2015). Of the transmitters that have been successfully attached, it is rare to have one last a full year to show summer site fidelity ((Dietz et al. 2001, Heide-Jørgensen et al. 2002, 2003, 2013, Dietz et al. 2008)). Additionally other methods of analyzing movement, immigration, and site fidelity are challenging as narwhal predominantly occur below visual depth and are cryptically coloured, making unique identification on colour alone rare with such large populations, though unique identification through scaring is promising (Auger-Méthé et al. 2010).

Therefore the goal of this component of my thesis was to increase the understanding of the interconnectivity between the narwhal stocks in the Canadian Arctic Archipelago by (a) examining narwhal summer, fall, and spring movement patterns and residency, (b) assess overlap in summer home-range between different stocks, and (c) examine summer site fidelity. My building upon the previous tracking data has revealed new information about narwhal spatial behaviour and increased confidence in applying movements patterns from tagged individuals to the larger population.

3.3 Methods

3.3.1 Capturing and Handling of Narwhal

Tagging occurred in Admiralty Inlet at Kakiak Point (72°41′00”N, 86°41′20”W) in August 2009 and in Eclipse Sound at Tremblay Sound (72°21′23”, 81°6′23”W) in August 2010, 2011, and 2012 (Fig. 3.1). Black or dark green nets that were $3.5 - 5$ m deep with a 40x40 cm mesh size were set up perpendicular to the shoreline. The bottom of the nets were anchored while the tops of the nets were attached to white buoys. Nets were constantly monitored by field crew along the shoreline. When narwhal were caught in the net the floats were forced underwater and crew in two zodiac boats brought the captured narwhal to the surface. The nets were released from the anchors and the narwhal was brought to shallow water where it was physically restrained. Body length, fluke length, and tusk length when appropriate were measured. Sex was determined through testing a biopsy sample. A veterinarian measured heart rate and body condition throughout the handling procedure. Capturing and handling procedures took thirty minutes maximum to complete. Captured narwhal were equipped with satellite transmitters (SPLASH tags) through the dorsal ridge (Wildlife Computers, Redmond, WA, USA). Additional details regarding capturing and handling of narwhal, satellite transmitter details, and the process of attaching transmitters are described in Orr et al. (2001), Dietz et al. (2008).

Transmissions were received through the Argos system (CLS) which used least squares analysis to assign accuracy codes of B, A, $0 - 3$ in increasing order of accuracy. Tags were programmed to transmit daily until September 31, after which they were duty cycled at 4 (2009) and 3 (2010; 2011; 2012) days with multiple transmissions occurring each transmission day. Transmissions that appeared on land were located tightly to the shoreline and were therefore retained. Locations on land primarily occurred from August to late October when narwhal were within inlets, fjords, or otherwise traveling close to shore. Daily positions were obtained by choosing the coordinate locations with the most accurate error structure (LC value) on each transmission day. When multiple coordinate locations had the same LC value, the first location was selected similar to Witt et al. (2010). Daily positions were used to calculate tracklines within ArcGIS (10.2, ESRI, Redlands, California, USA).

Figure 3.1: Study area in the Canadian Arctic Archipelago with major place names relevant to the study

3.3.2 Seasonal Home-Range Analysis

Summer and winter seasons for home-range analysis were defined by comparing the date and latitude similar to the approach of Dietz et al. (2008). Narwhal summered either in Admiralty Inlet or Eclipse Sound in northern Baffin Island. The mouth(s) of these inlets occur at 73°6N (Admiralty Inlet), and 72°9 and 73°7N (Eclipse Sound). Narwhal were considered to have started their fall migration when they made directed movements north or south from the corresponding latitude of the mouth of the inlet where they had been tagged. Therefore, the summer season was defined as occuring between the tagging date and September 15, which was the earliest date a narwhal began its fall migration. The winter season was defined when narwhal stopped their rapid southward migration and conducted relatively localized movements, therefore remaining within a consistent latitude until they began moving northward during the spring migration. For home-range analysis the winter season was considered to occur between November 7 and March 31. Daily positions were used to estimate the summer and winter 95^{th}, 75^{th}, 50^{th} and fixed-kernel density with a $h_{plug-in}$ bandwidth using the Geospatial Modelling Environment (Beyer 2012) extension for ArcGIS (10.2, ESRI, Redlands, California, USA).

A generalized least squares (GLS) model was conducted using the gls function within the nlme package in R (Pinherio et al. 2017) to analyze the relationship between the sex and age of narwhal and individual home-range area. GLS models allow the incorporation of different variance structures, allowing for variance to fluctuate with independent variables. This accommodates for heterogeneity within residuals (Zuur et al. 2009). The dependent variable was home-range area and the independent variables were sex, body length, and year. Body length was used as an approximation for narwhal age, as narwhal do not have extra teeth available for extraction to calculate age (Garde et al. 2015). All home-range areas were log-transformed because the raw data had a positive skewed distribution. All statistical analyses were conducted using this transformed data. Multiple models with different variance structures were run to determine which variance structure best explained the heterogeneity within the residuals. The best model was selected using the Akaike information criterion (AIC) as well as the log likelihood ratio when models were nested. When AIC values and the log likelihood ratio between models were similar, the model with the most simple variance structure was retained (Zuur et al. 2009). Standardized residuals were examined. A Tukey Post Hock analysis was conducted to examine the relationship between years using the lsmeans package in R (Lenth 2016). Narwhal $2011 - 39315$ was removed from the winter individual home-range models. It primarily conducted linear movements south until the tag failed on December $22(16$ data days during winter season), resulting in a poorly fitted individual home-range and a large outlier within both 95% and 50% winter home-range area datasets.

3.4 Results

A total of twenty-four total narwhal were captured and equipped with satellite transmitters. Seven narwhal (4M; 3F) were tagged between August 15 and $19, 2009$, five narwhal (2M; 3F) were tagged between August 21 and $24, 2010$, seven narwhal (1M; 6F) were tagged between August 6 and 20, 2011, and five narwhal (2M; 3F) were tagged between August 14 and $19, 2012$. Transmitters lasted between 30 and 413 days, with all but one tag lasting at least 117 days as shown in Table 3.1. Three transmitters per year in $2009, 2010$ and 2011 lasted throughout the winter season. Five tags transmitted for over 300 days, providing data about spring migration routes and summer site fidelity. All 2012 tags stopped transmitting by December 22, 2012, therefore winter home-range was not calculated for the 2012 tag year.

3.4.1 Summer and Fall Movement

Movement analysis for the Admiralty Inlet stock is based off narwhal tagged at Kakiak Point in 2009. Narwhal tagged in Admiralty Inlet moved predominantly along the western shoreline of the inlet, traveling at least as far south as Yeoman Island (Fig. 3.2). Only narwhal 39287 visited connecting inlets or sounds, briefly visiting Adams Sound. Six of the seven narwhal left between September 17 and 18 and travelled west along the Brodeur Peninsula. Two narwhal (39256; 39287) continued west across the mouth of Prince Regent Inlet and turned north, crossing Lancaster Sound and conducting localized movements between Maxwell Bay and Croker Bay. The other four narwhal (39313; 39249; 39290; 39309) entered Prince Regent Inlet between September 18 and 19, traveling south along the eastern shoreline before crossing over towards Brenford Bay. One narwhal visited Bellot Strait, but did not cross through it, while the other three moved through or resided within the Creswell Bay area. Three narwhal left the Creswell Bay area, traveling north along the west shoreline of Prince Regent Inlet until reaching Lancaster Sound between September 29 and October 10. The two earliest to return to Lancaster Sound crossed north and briefly remained between Maxwell Bay and Burnett Inlet before all three headed east towards Baffin Bay. The fourth narwhal (39290) did not return to Lancaster Sound, but instead travelled south through the Gulf of Boothia as well as Fury and Hecla Strait before entering Foxe Basin on November 3. This narwhal appeared to over-

Table 3.1: Narwhal stock (ES = Eclipse Sound; AI = Admiralty Inlet), deployment date (yyyy-mm-dd), date of last transmission (yyyy-mm-dd), sex, and length data

Narwhal Stock	ID	Sex	Deployment Date	Tag Duration (days)	Last Transmission	Length (cm)
AI	39249	F	2009 − 08 − 18	127	2010 − 01 − 10	386
AI	39256	M	2009 − 08 − 17	310	2010 − 07 − 05	450
AI	39287	M	2009 − 08 − 17	289	2010 − 06 − 11	439
AI	39290	F	2009 − 08 − 15	200	2010 − 02 − 23	373
AI	39309	M	2009 − 08 − 15	259	2010 − 01 − 06	376
AI	39311	M	2009 − 08 − 17	230	2010 − 05 − 02	307
AI	39313	F	2009 − 08 − 16	171	2010 − 02 − 11	391
ES	51871	M	2010 − 08 − 21	250	2011 − 04 − 28	444
ES	51872	M	2010 − 08 − 21	320	2011 − 06 − 08	461
ES	51873	F	2010 − 08 − 22	413	2011 − 10 − 04	400
ES	51874	F	2010 − 08 − 22	187	2010 − 12 − 19	390
ES	51875	F	2010 − 08 − 24	153	2011 − 01 − 25	380
ES	39270	F	2011 − 08 − 18	202	2012 − 03 − 07	394
ES	39314	F	2011 − 08 − 18	233	2011 − 03 − 31	406
ES	39315	F	2011 − 08 − 06	137	2011 − 12 − 22	389
ES	51876	F	2011 − 08 − 16	191	2012 − 02 − 13	391
ES	51878	M	2011 − 08 − 16	128	2011 − 12 − 22	310
ES	51879	F	2011 − 08 − 16	314	2012 − 06 − 26	401
ES	57590	F	2011 − 08 − 19	302	2012 − 06 − 16	404
ES	115956	F	2012 − 08 − 14	31	2012 − 09 − 13	396
ES	115957	M	2012 − 08 − 14	128	2012 − 12 − 19	348
ES	115958	F	2012 − 08 − 17	128	2012 − 12 − 22	390
ES	115959	M	2012 − 08 − 18	124	2012 − 12 − 19	440
ES	115960	F	2012 − 08 − 19	120	2012 − 12 − 16	261

winter in Foxe Basin as it remained in this area until the transmitter failed on February 23, 2010. The seventh narwhal (39311) left Admiralty Inlet between October 6 and 10 and immediately conducted rapid movements east through Lancaster Sound. All narwhal entered Baffin Bay between Oct 10 and 18 and travelled to southern Baffin Bay primarily along the continental slope.

Movement analysis for Eclipse Sound narwhal is based on tags equipped to narwhal in Tremblay Sound in $2010, 2011$, and 2012. All narwhal tagged in Eclipse Sound during

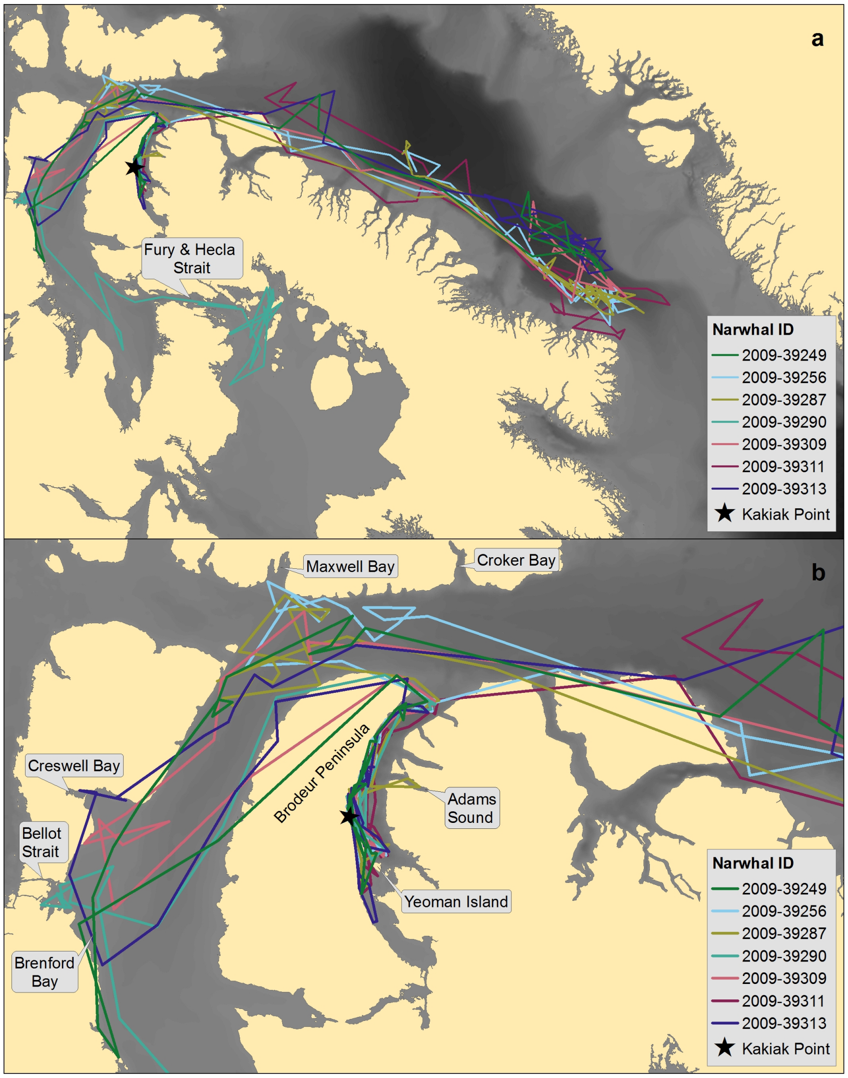

Figure 3.2: 2009 Admiraly Inlet narwhal tracklines from when narwhal were tagged until (a) the transmitter failed, and (b) until narwhal entered Baffin Bay. General bathymetry ranges from light gray (shallow waters) to black (> 2000 m)

2010 travelled initially within Tremblay Sound and Milne Inlet, but were primarily located within Eclipse Sound and Pond Inlet (Fig. 3.3). During the summer three narwhal (51871;51872;51873) went to Eskimo Inlet, one narwhal (51873) visited Koluktoo Bay, and one narwhal (51875) travelled within Navy Board Inlet.

Upon leaving Admiralty Inlet all five narwhal immediately began their fall migration and travelled directly to the Baffin Bay winter ground. Four narwhal left Eclipse Sound through Pond Inlet, while it is unclear whether the fifth narwhal (51875) left through Navy Board Inlet or Pond Inlet. Two narwhal (51871; 51872) entered Baffin Bay on September 20 and travelled south along the coastline of Baffin Island, spending $13 - 18$ days visiting Paterson Inlet, Royal Society Fiord, Isbjorn Strait, and Sam Ford Fiord during their migration. They both continued traveling south and resided within or near Cumberland Sound for $26-44$ days from mid-October to late-November. Narwhal 51871 entered Baffin Bay on December 1 over the Davis Strait sill and remained there until January when it moved north for the rest of the winter. Narwhal 51872 entered Baffin Bay on November 19 and continued moving towards Disko Bay where it remained from December 4, 2010 to January 4, 2011. Afterwards it moved to the Davis Strait sill where it remained until late March. The other three narwhal left Eclipse Sound between Oct $4 - 16$. One narwhal travelled along the Baffin Island coastline except between Clyde River and Qikiqtarjuaq where it travelled along the continental shelf. This narwhal was not recorded visiting any inlets or fjords. The other two narwhal travelled south along the continental ridge to their winter ground.

Three different movement patterns were observed in narwhal tagged in 2011 before they entered Baffin Bay (Fig. 3.4). Narwhal 39270, 51879 and 57590 remained briefly within

Eclipse Sound before conducting directed movements out of Navy Board Inlet and entering Admiralty Inlet between August 31 and September 1. All three narwhal travelled past Kakiak Point, where Admiralty Inlet narwhal had been tagged in August. They then travelled along the west shoreline, the center of the inlet, and the east shoreline between

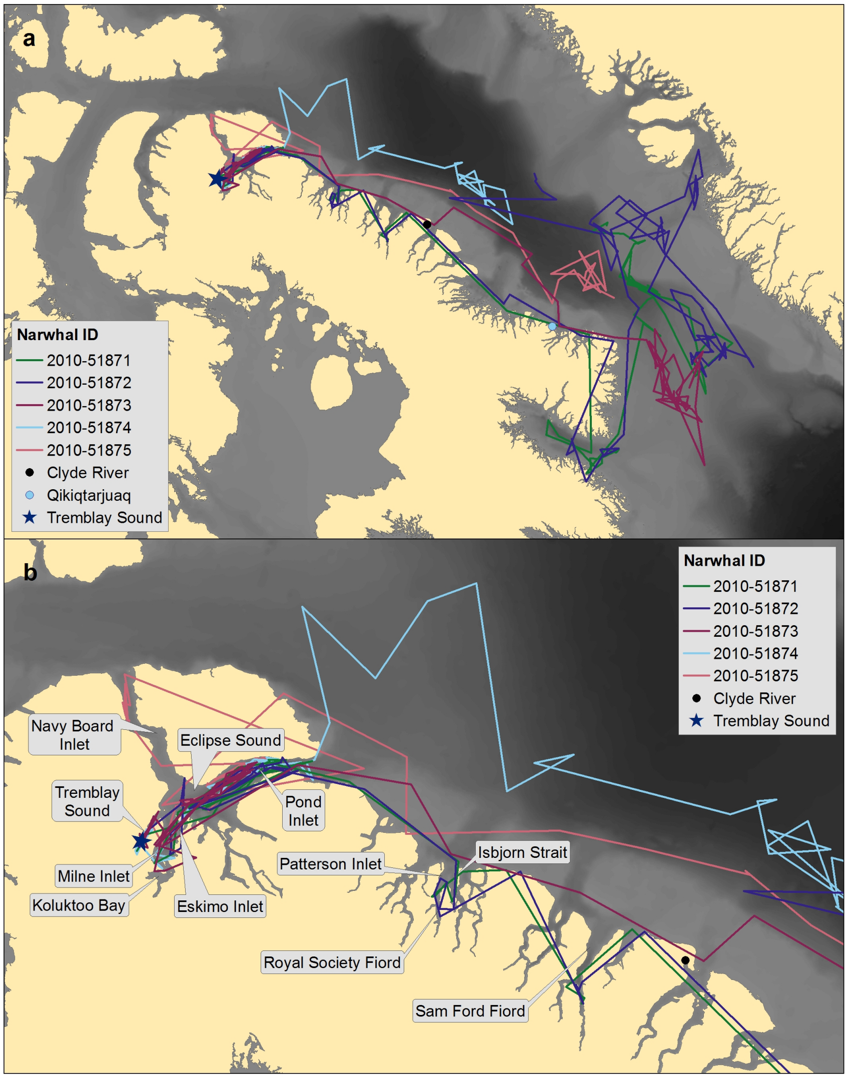

Figure 3.3: 2010 Eclipse Sound narwhal tracklines from when narwhal were tagged until (a) the transmitter failed, and (b) until narwhal entered Baffin Bay. General bathymetry ranges from light gray (shallow waters) to black (> 2000 m)

Yeoman Island and the mouth of Admiralty Inlet, with only 39270 briefly visiting Elwin Ilnet. Narwhal 51879 re-entered Lancaster Sound between October 16 and 19 and headed east towards Baffin Bay. Narwhal 39270 and 57590 re-entered Lancaster Sound earlier on Sept 29 and continued west, entering Prince Regent Inlet between September 30 and October 4. They briefly travelled south along the east shoreline or central part of the inlet before returning to Lancaster Sound between October 7 and 10 and rapidly travelled east towards Baffin Bay.

The other four narwhal travelled through Milne Inlet but were primarily within Eclipse Sound and Pond Inlet. Two narwhal (39315; 51878) visited Koluktoo Bay, one (51878) visited Eskimo Bay, and one (51876) visited Tay Sound. Three narwhal (39314; 39315; 51878) conducted directed movements through Navy Board Inlet entering Lancaster Sound between October 1 and 13. They travelled west where 51878 briefly entered Admiralty Inlet white the other two narwhal crossed the mouth of Lancaster Sound before all three travelled east towards Baffin Bay. The seventh narwhal (51876) left Eclipse Sound through Pond Inlet and headed directly to the winter ground. While there were three different movement patters, all narwhal entered Baffin Bay between October 10 and 19. The two main migration routes within Baffin Bay were along the continental slope, and along the Baffin Island coastline until narwhal reached Home Bay, where they switched to the continental slope.

In 2012 one of the five transmitters failed prior to the narwhal leaving Eclipse Sound. Only one narwhal (115959) in 2012 displayed the westward movement pattern recorded in 2011 (Fig. 3.5). It briefly visited Milne inlet before leaving through Navy board Inlet on September 1 and entered Admiralty Inlet on September 2. Over nine days it visited

Elwin Inlet, Baillarge Bay, and Strathcona Sound before traveling throughout Admiralty Inlet past Kakiak Point on the west shoreline, the center of the inlet, and the eastern shoreline. Narwhal 115959 then left Admiralty Inlet between October 1 and 4, and briefly re-entered Navy Board Inlet before heading to Baffin Bay. The other three narwhal visited

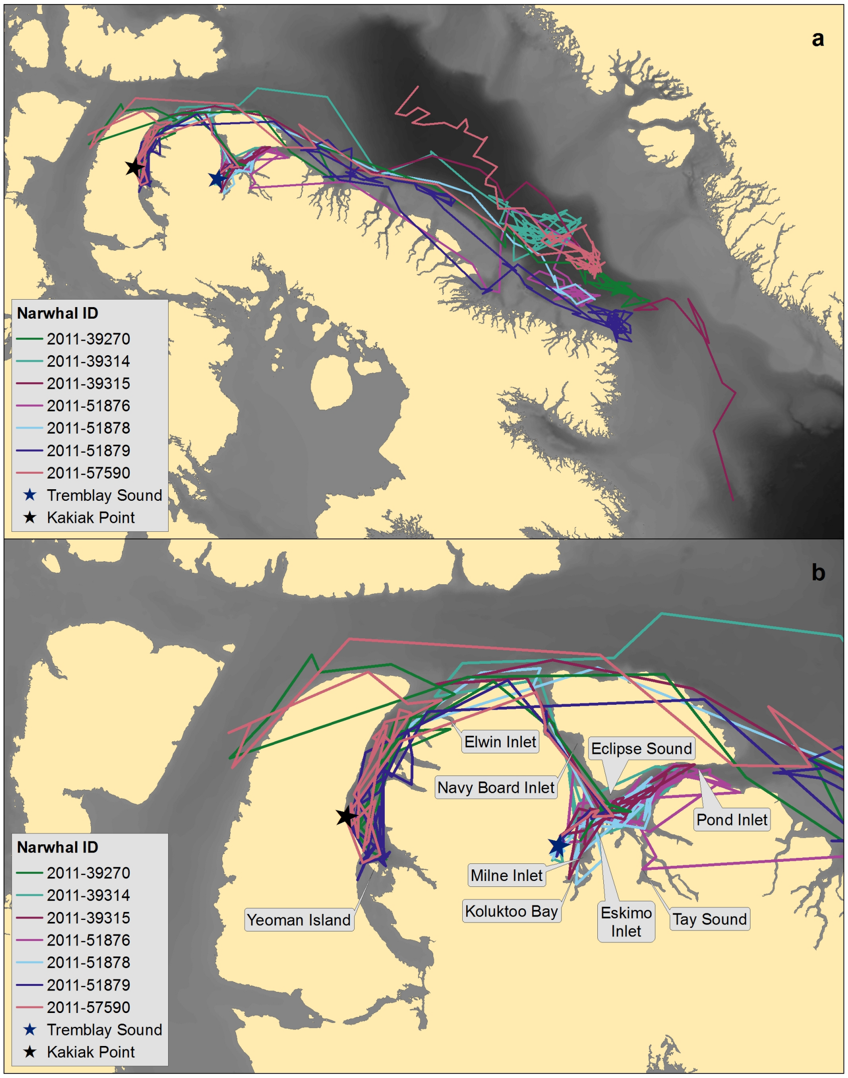

Figure 3.4: 2011 Eclipse Sound narwhal tracklines from when narwhal were tagged until (a) the transmitter failed, and (b) until narwhal entered Baffin Bay. General bathymetry ranges from light gray (shallow waters) to black (> 2000 m)

Milne Inlet but were primarily located within Eclipse Sound and Pond Inlet. One narwhal (115958) visited Navy Board Inlet and another narwhal (115960) visited Koluktoo Bay before the three narwhal left through Pond Inlet. All four narwhal entered Baffin Bay between Oct 1 and 19 and then migrated south either along the Baffin Island coastline until Home Bay where they switched to the continental slope, or over the shelf parallel to the continental slope. Two of these narwhal were still traveling south with no indication of settling within a typical localized winter ground location when their transmitters failed. The other two appeared to have begun localized winter movements before their transmitters failed. It should be noted that all narwhal in the previous four years began localized movements by November 7, while these two began between Nov 16 and 22.

3.4.2 Spring Migration

A total of nine tags lasted throughout the winter season in 2009, 2010, and 2011 (3/year), however only eight continued transmitting long enough to record the spring migration (Fig. 3.6. In 2009 three narwhal (39256; 39287; 39311) were tracked during their spring migration. Narwhal 39256 and 39287 began directed movements northward between April 16 and 28, 2010 and travelled along the continental slope. Once north of Clyde River they remained in a localized area from May 10, 2010 to June 15, 2010. During this time 39287 stopped transmitting. Narwhal 39256 reached the mouth of Lancaster Sound on June 28, 2010 and entered the mouth of Admiralty Inlet, where it had been tagged the previous summer. The tag failed on July 5, 2010 as it entered the mouth of Admiralty Inlet (Fig. 3.7). Narwhal 39311 began directed northward movements on March 31, 2010 along the continental slope until it reached the area where the other two narwhal conducted localized movements. After which it travelled directly to the mouth of Lancaster Sound where it conducted localized movements from April 20 to $28, 2010$. Between April $28, 2010$ and May $2, 2010$ it turned around and was traveling south when the transmitter failed.

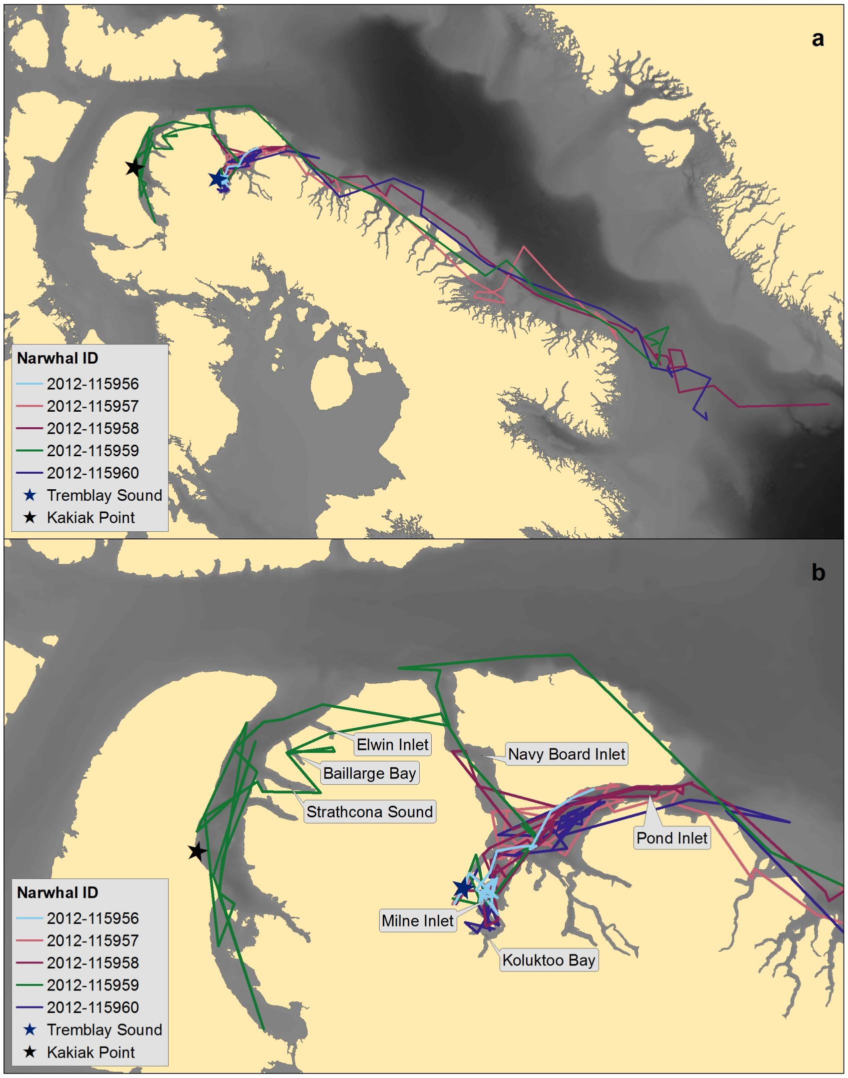

Figure 3.5: 2012 Eclipse Sound narwhal tracklines from when narwhal were tagged until (a) the transmitter failed, and (b) until narwhal entered Baffin Bay. General bathymetry ranges from light gray (shallow waters) to black (> 2000 m)

Three tags from the 2010 tagging in Eclipse Sound recorded at least some of the spring migration. Narwhal 51871 began to move north after April 4, 2011 over the east shelf. It moved slowly, traveling just over a 100 km distance when the tag failed on April 28, 2011. Narwhal 51872 began to make northward movements after May 25 and travelled predominantly along the east continental slope. It was still over 650 km away from the mouth of Lancaster Sound when it's transmitter failed on June 8, 2011. Narwhal 51873 was tracked for over one year and therefore where it summered in 2011 was recorded. It began moving north after April 16, 2011 along the continental slope. It conducted localized movements north of Cape Dyer from April 19, 2011 to May 1, 2011 and offshore of

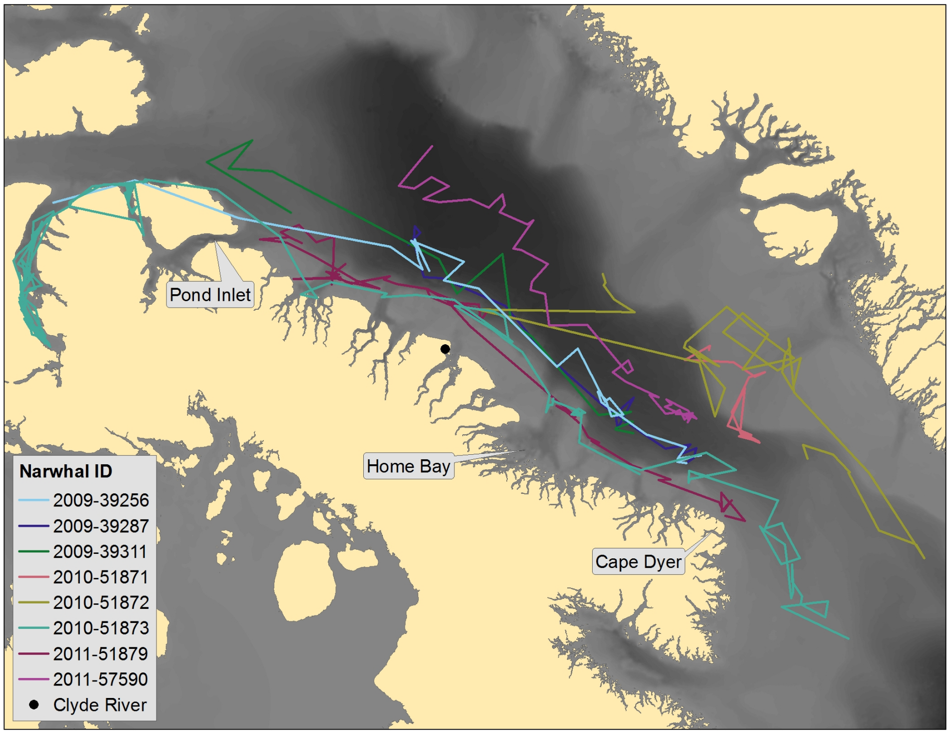

Figure 3.6: Narwhal spring migration routes. Tracklines begin with one month of the winter season remaining (March 1) and end when the satellite tag failed. General bathymetry ranges from light gray (shallow waters) to black (> 2000 m)

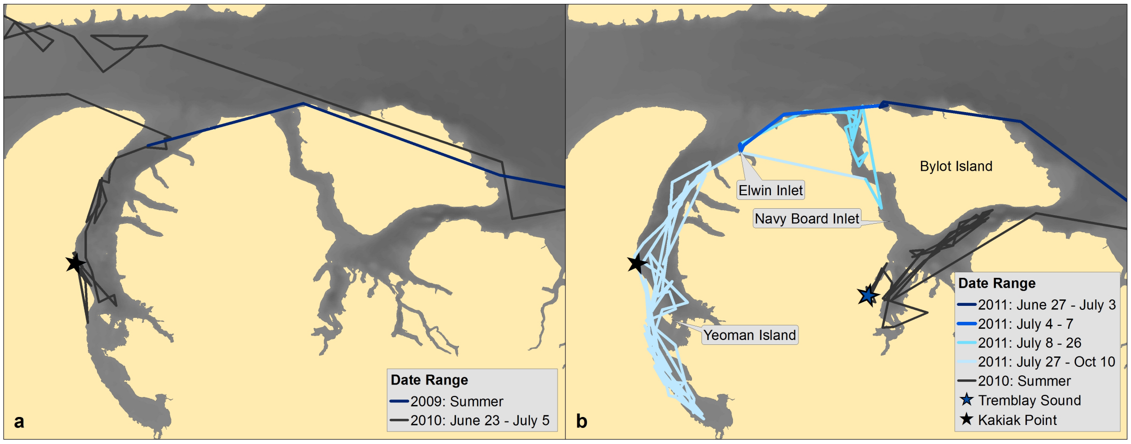

Figure 3.7: Summer ground fidelity of two narwhal. (a) Narwhal 39256 was tagged within Admiralty Inlet in 2009 and entered the mouth of Admiralty Inlet on July 5, 2010 when the transmitter failed (b) Narwhal 51873 was tagged within Eclipse Sound in 2010 and summered in Admiralty Inlet in 2011. Prior to selecting a summer ground it switched between Navy Board Inlet and Admiralty Inlet, which is shown in different coloured tracklines

Home Bay from May 16, 2011 to June 10, 2011 before entering Lancaster Sound on June 29, 2011. It remained relatively stationary near the north shore of Bylot Island just east of the mouth of Navy Board Inlet from June 29, 2011 to July 3, 2011 before traveling to the mouth of Admiralty Inlet. It remained stationary at the mouth of Elwin Inlet from July 5, 2011 to 8, 2011 before returning to and entering Navy Board Inlet. However it only remained within Navy Board Inlet until July 27, 2011, with the most southern location being 72°59’17”N, −80°32’46”W. It then immediately entered Admiralty Inlet where it remained until the transmitter failed on October 4, 2011 (Fig. 3.7). Narwhal 51873 travelled throughout Admiralty Inlet, including past Kakiak point and south of Yeoman Island. This narwhal travelled the furthest south into Admiralty Inlet of any narwhal within this study.

While three tags from the 2011 tagging in Eclipse Sound lasted through the winter season, only two recorded part of the spring migration. One narwhal (51879) remained near Home Bay from March 29, 2012 to April 7, 2012 before slowly moving north along the continental slope. It remained in a localized area between April 7, 2012 and May 4, 2012 near Clyde River before reaching the shelf close to the mouth of Pond Inlet on June 14, 2012. It remained there until the transmitter failed on June 26, 2012. Narwhal 57590 began moving north after May 1, 2012 and travelled through the middle of Baffin Bay, reaching a latitude of 73°15'22"N on June 16 and had not yet turned west towards Lancaster Sound.

3.4.3 Seasonal Home-Range Area

The 95%, 75%, and 50% summer home-range areas across years are presented within Table 3.2. The Admiralty Inlet and Eclipse Sound yearly and average 95% summer home-ranges overlapped as shown on Fig. 3.8). The 95% summer home-range for narwhal tagged in Eclipse Sound overlapped 0% (2010), 68.0% (2011), 19.03% (2012), and 50.28% (2010 – 2012) of the 95% summer home-range of narwhal tagged in Admiralty Inlet. On the other hand, the Admiralty Inlet 95% summer home-range overlapped 0% (2010), 32% (2011), 11.52% (2012), and 26.12% (2010 – 2012) of the Eclipse Sound 95% summer home-range.

Summer home-range area and location were fairly consistent between years for narwhal tagged in Eclipse Sound. The 2011 and 2012 Eclipse Sound summer home-range overlapped 99.20% and 93.28% of the 2010 summer home-range respectively. The 2010 summer home-range was smaller than the other years and only overlapped 23.58% (2011) and 37.96% (2012). The 2011 Eclipse Sound 95% summer home-range overlapped 84.30%

Table 3.2: Narwhal stock (ES = Eclipse Sound; AI = Admiralty Inlet) summer (SHR) and winter (WHR) home-range area (km^2)

Narwhal Stock	Year	50% SHR	75% SHR	95% SHR	50% WHR	75% WHR	95% WHR
AI	2009	2 095	4 584	11 336	14 836	33 040	72 533
ES	2010	2 101	3 997	7 585	55 101	116 293	259 763
ES	2011	5 350	12 978	31 970	20 767	40 775	84 369
ES	2012	2 700	6 047	18 497			
ES	$2010-12$	3 247	7 556	21 737			
ES	$2010-11$				42 159	92 935	203 399

of the 2012 Eclipse Sound home-range, and 2012 home-range overlapped 49.24% of the 2011 home-range.

Results for the 95%, 75%, and 50% winter home-range areas are presented within Table 3.2. Despite having the fewest narwhal tagged across years, the 2010 Eclipse Sound 95% winter home-range was over 2x larger than for narwhal tagged either in Admiralty Inlet in 2009 or in Eclipse Sound in 2011. The 2010 Eclipse Sound winter home-range overlapped 82.46% of the Admiralty Inlet winter home-range and 77.35% of the 2011 Eclipse Sound winter home-range (Fig. 3.9). In contrast the Admiralty Inlet and 2011 Eclipse Sound winter home-ranges only overlapped 23.04% and 25.14% of the 2010 Eclipse Sound home-range respectively. The winter home-range for narwhal tagged in Admiralty Inlet and those tagged in Eclipse Sound in 2011 were very similar. The 2011 Eclipse Sound 95% winter home-range overlapped 91.90% of the Admiralty Inlet home-range, while the Admiralty Inlet home-range overlapped 79.012% of the 2011 Eclipse Sound 95% winter home-range.

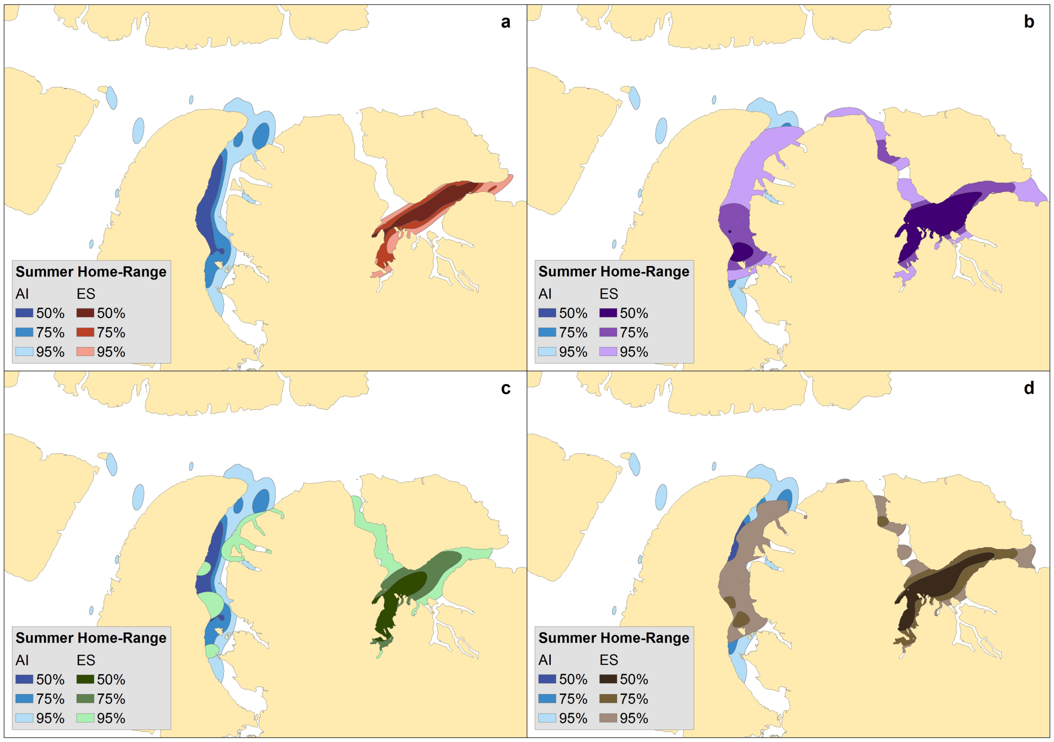

Figure 3.8: Summer home-range from the tagging date to September 15. (a) 2009 Admiralty Inlet (AI) and 2010 Eclipse Sound (ES) home-range (b) 2011 ES and 2009 AI home-range (c) 2012 ES and 2009 AI home-range (d) Combined (2010 – 2012) ES and 2009 AI home-range. Of note is the ES home-range overlap with AI home-range

3.4.4 Individual Home-Range Model Selection

The two best fit models for both the 95% and the 50% summer individual home-range GLS models had variance covariates of year, or year and sex combined. They both had similarly low AIC values and had no difference between their log-likelihood ratios. Therefore the most simple variance covariate structure of year was retained, allowing the variance to fluctuate with year (Table 3.3). A high amount of variability was explained within the 95% summer home-range model, which had a pseudo-R^2 of 0.746 and a resid-

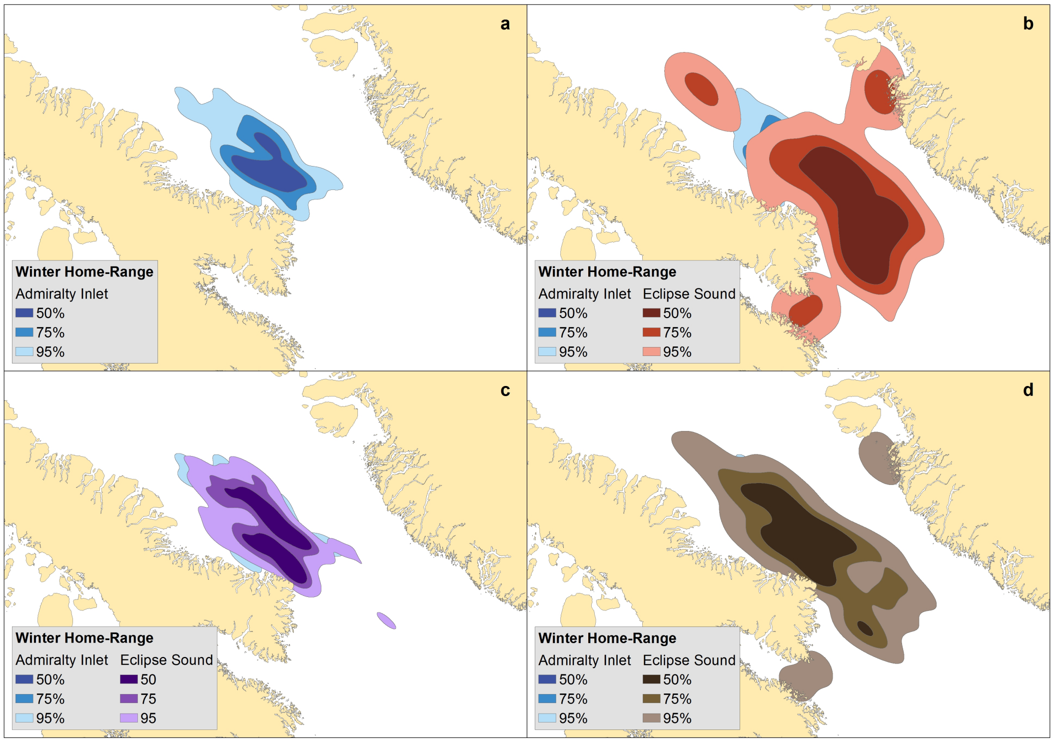

Figure 3.9: Winter home-range from November 7 to March 31. (a) 2009 Admiralty Inlet home-range. (b) 2010 Eclipse Sound and 2009 Admiralty Inlet home-range (c) 2011 Eclipse Sound and 2009 Admiralty Inlet home-range (d) Combined (2011 − 2012) Eclipse Sound and 2009 Admiralty Inlet home-range. Of note are the large home-range in 2010 and the similarity between 2009 and 2011

ual standard error of 0.198. The 95% individual summer home-range area was larger when narwhal had larger body lengths ($p =< 0.0001$) and was smaller in 2010 than in 2009 ($p = 0001$; Table 3.5). Sex was not significant ($p = 0.685$; Table 3.4). The 50% home-range model had a pseudo-R^2 of 0.401 and a residual standard error or 0.439. Year was significant in the GLS model ($p = 0.0209$; Table 3.4) however the Tukey Post Hock Analysis did not discern significance between years (Table 3.5. Narwhal length ($p = 0.2512$) and sex ($p = 0.8816$) were not significant in relation to individual 50%

Table 3.3: Generalized least squares model variance covariate selection. All models had home-range area (km^2) as the dependent variable and independent variables of sex, body length, and year. Final models are in bold

Model Name	Variance Covariate	AIC	LogLik	Test	L. Ratio	p-value
95% Summer Home-Range						
M.gls3	**year**	**20.40**	**-0.20**	–	–	–
M.gls1	null	34.24	−10.12	1 vs 3	19.53	0.0002
M.gls2	length	33.93	−9.96	2 vs 3	19.53	0.0002
M.gls4	sex	34.01	−9.00	4 vs 3	17.61	0.0002
M.gls5	year + sex	22.27	−0.14	5 vs 3	0.13	0.720
50% Summer Home-Range						
M.gls8	**year**	**40.18**	**-10.09**	–	–	–
M.gls6	null	42.50	−14.25	6 vs 8	8.31	0.040
M.gls7	length	42.30	−10.09	7 vs 8	8.12	0.044
M.gls9	sex	41.83	−12.91	9 vs 8	5.65	0.059
M.gls10	year + sex	39.62	−8.81	10 vs 8	2.57	0.109
95% Winter Home-Range						
M.gls14	**sex**	**18.56**	**-2.28**	–	–	–
M.gls11	null	22.21	−5.11	11 vs 14	5.65	0.0174
M.gls12	length	21.85	−4.92	12 vs 14	5.29	0.0215
M.gls13	year	22.82	−3.41	13 vs 14	2.26	0.133
M.gls15	year + sex	20.53	−1.27	15 vs 14	2.03	0.3627
50% Winter Home-Range						
M.gls19	**sex**	**18.83**	**-2.42**	–	–	–
M.gls16	null	21.19	−4.59	16 vs 19	4.36	0.0368
M.gls17	length	20.64	−4.32	17 vs 19	3.81	0.051
M.gls18	year	23.17	−3.59	18 vs 19	2.34	0.1262
M.gls20	year + sex	21.29	−1.65	20 vs 19	1.54	0.4629

home-range area (Table 3.4).

The 95% and 50% winter home-range GLS final models both had a variance covariate as sex, allowing the variance to fluctuate with sex (Table 3.3). The 95% winter home-range model accounted for high variation with a pseudo-R^2 of 0.534 and the residual

Table 3.4: Variables within the individual home-range generalized least squares models

Model Parameters	df	F-value	p-value
95% Summer Home-Range			
Intercept	1	552567.3	< 0.0001***
Length	1	216.9	< 0.0001***
Year	3	14.5	< 0.0001***
Sex	1	0.2	0.685
50% Summer Home-Range			
Intercept	1	12304.403	< 0.0001***
Length	1	1.614	0.2201
Year	3	4.169	0.0209*
Sex	1	0.023	0.8816
95% Winter Home-Range			
Intercept	1	11673.695	< 0.0001***
Length	1	0.020	0.8899
Year	3	6.941	0.0099**
Sex	1	0.339	0.5711
50% Winter Home-Range			
Intercept	1	7367.424	< 0.0001***
Length	1	0.001	0.9774
Year	3	7.984	0.0062**
Sex	1	0.296	0.5965

Note: '*' $p < 0.05$; '**' $p < 0.01$; '***' $p < 0.001$

standard error was 0.133. Individual home-range area was larger in 2009 than in 2011 ($p = 0.0001$; Table 3.5) while narwhal length and sex were not significant ($p = 0.426$; $p = 0.571$; Table 3.4).The 50% winter home-range model accounted for a similar amount of variability with a pseudo-R^2 of 0.574 and a residual standard error was 0.144. Both 2009 and 2010 individual home-ranges were larger than those in 2011 ($p = 0.0208$; $p = 0.0554$). Length and Sex were not significant ($p = 0.599$; $p = 0.758$; Table 3.4).

Table 3.5: Tukey Post Hock analysis on the significant categorical variable 'Year' within all final GLS models

Model Parameters	Value	SE	t-ratio	p-value
95% Summer Home-Range				
2009 − 2010	0.445	0.078	5.721	0.0001***
2009 − 2011	0.011	0.178	0.063	0.9999
2009 − 2012	0.142	0.194	0.731	0.8833
2010 − 2011	−0.433	0.161	−2.693	0.0649
2010 − 2012	−0.302	0.181	−1.667	0.3689
2011 − 2012	0.131	0.242	0.542	0.9475
50% Summer Home-Range				
2009 − 2010	0.477	0.180	2.646	0.0712
2009 − 2011	0.083	0.243	0.340	0.9860
2009 − 2012	0.248	0.263	0.944	0.7817
2010 − 2011	−0.394	0.177	−2.233	0.1522
2010 − 2012	−0.229	0.221	−1.035	0.7318
2011 − 2012	0.166	0.272	0.610	0.9276
95% Winter Home-Range				
2009 − 2010	0.097	0.116	0.838	0.6876
2009 − 2011	0.348	0.110	3.161	0.0208*
2010 − 2011	−0.251	0.096	2.610	0.0554
50% Winter Home-Range				
2009 − 2010	0.067	0.124	0.537	0.8546
2009 − 2011	0.377	0.117	3.221	0.0186*
2010 − 2011	0.310	0.102	3.017	0.0269*

Note: '*' $p < 0.05$; '**' $p < 0.01$; '***' $p < 0.001$

3.5 Discussion

There appear to be multiple fall migration patterns within the Eclipse Sound and the Admiralty Inlet stock. These different migration patterns connect Eclipse Sound, Admiralty Inlet, and Somerset Island stock during September and the beginning of October. Additionally there was a decrease in summer site fidelity with one narwhal that was tagged within Eclipse Sound returning to Admiralty Inlet the following summer. Therefore it appears that these three summering locations are not completely isolated, particularly in the fall and potentially between years.

3.5.1 Multiple Movements Patterns

Admiralty Inlet narwhal appear to conduct at least two different fall movement patterns. Narwhal tagged in 2009 either left Admiralty Inlet on September 17 or 18 and travelled west, or left in early October and immediately travelled east towards Baffin Bay (Fig. 3.10). While this westward movement upon leaving Admiralty Inlet was the predominant movement pattern in 2009, historically this has not been the case (Dietz et al. 2008, Heide-Jørgensen et al. 2013). However since this movement has been recorded previously (Heide-Jørgensen et al. 2013) and most narwhal tagged in 2009 conducted this westward movement, it is unlikely to be exploratory behaviour. Additionally when these narwhal moved west there was also a pod of killer whales (*Orcinus orca*) within Prince Regent Inlet. When this concurrently tagged killer whale pod was within Admiralty Inlet, the narwhal displayed strong avoidance behaviour (Breed et al. 2017). It therefore seems unlikely that the narwhal would then spend $11 - 19$ days exploring an area where the same killer whales were currently patrolling. Two narwhal even resided within Creswell Bay while a tagged killer whale was at the mouth of the bay (Breed et al. 2017). It is more likely that Prince Regent Inlet was part of a regular travel route or has historically supported a positive biological benefit during this season.

Whether the two westward patterns where narwhal either entered Prince Regent Inlet or remained near Maxwell Bay are two separate westward movement patterns is unclear. All narwhal traveling west left Admiralty Inlet at the same time regardless of their westward destination. The one narwhal previously observed to enter Prince Regent Inlet did so at least two weeks earlier than the ones tagged in 2009 (Heide-Jørgensen et al. 2013). The few narwhal in 2003 and 2004 that did travel west, remained over the Brodeur Peninsula and did not cross or enter Prince Regent Inlet or remain near Maxwell Bay (Dietz et al. 2008). This lack of consistency in pattern or timing of westward movement across years makes discerning between westward movement patterns out of Admiralty Inlet unclear at this time.

Narwhal from the Eclipse Sound stock conducted three movement patterns upon leaving Eclipse Sound itself (Fig. 3.10). Out of the sixteen narwhal tagged in Eclipse Sound, four narwhal over two years briefly remained in Eclipse Sound before conducting rapid, directed movements through Navy Board Inlet and into Admiralty Inlet by September 1. They then remained within Admiralty Inlet for over one month. Similar behaviour was previously recorded from two narwhal tagged in 1999 that left Navy Board Inlet on August 26 and Sept 11 and immediately entered Admiralty Inlet, where they remained for around two weeks (Heide-Jørgensen et al. 2002). As this movement pattern has now been recorded across three years which span over a decade apart it is likely to be a regular movement pattern rather than exploratory behaviour. The second notable movement pattern involved narwhal leaving Eclipse Sound through Navy Board Inlet just over a month after the first group and traveling west over the mouth of Admiralty Inlet prior to entering Baffin Bay. While this was documented for three narwhal, it only occurred in the 2011 tag year (Dietz et al. 2001, Heide-Jørgensen et al. 2002) and could be related to exploratory behaviour or a season specific event. Narwhal that exhibited the third movement pattern

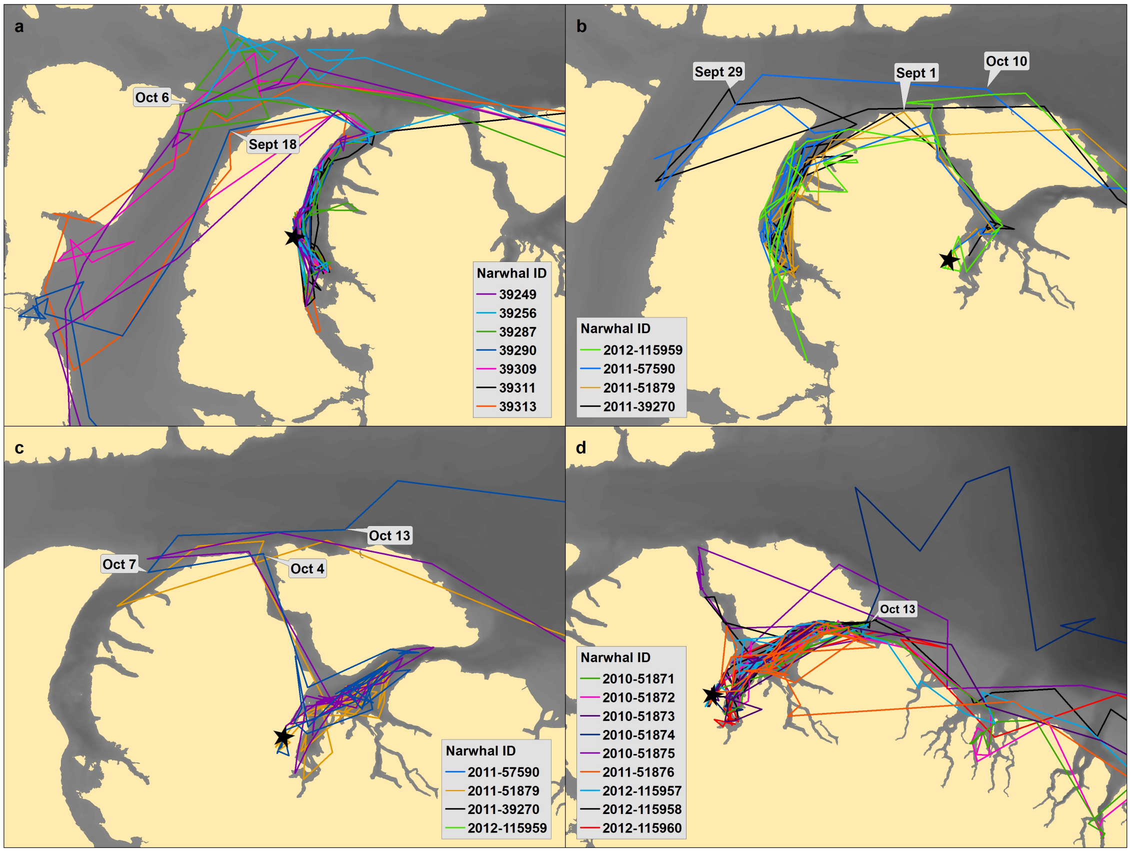

Figure 3.10: Narwhal late-summer and fall movement patterns with average dates narwhal left or entered regions. (a) Admiralty Inlet two movement paths (west and direct) are combined because only one traveled directly to the winter ground (b) Eclipse Sound early September westward movement pattern (c) Eclipse Sound early October westward movement pattern (d) Eclipse Sound direct movement pattern

remained in Eclipse Sound until at least mid-September before entering directly into Baffin Bay, often through Pond Inlet. This is the most common documented movement pattern historically (Dietz et al. 2001, Heide-Jørgensen et al. 2002) while only a little over half the narwhal from $2010 - 2012$ exhibited this movement pattern.

3.5.2 Delayed Entry into Baffin Bay

Narwhal tagged in Eclipse Sound appeared to enter Baffin Bay later than those tagged in the late 1990s. Those tagged from 1997 – 1999 that immediately travelled east upon leaving Eclipse Sound, entered Baffin Bay in mid to late September (Dietz et al. 2001, Heide-Jørgensen et al. 2002). Those that first travelled west upon leaving Eclipse Sound, and were tracked long enough to show them entering Baffin Bay did so by October 5. One narwhal's transmitter failed on Oct 4 while it was still in Prince Regent Inlet (Dietz et al. 2001, Heide-Jørgensen et al. 2002). All but two narwhal tagged in Eclipse Sound from 2010 – 2012 entered Baffin Bay between October 1 and 19, with almost one-third entering on October 18 or 19. The two narwhal that entered Baffin Bay on September 20 had an unusual fall migration where they visited Cumberland Sound prior to having localized movements over Baffin Bay. Overall there appears to have been around a two week delay entering Baffin Bay versus the late 1990s. This corresponds with the length of time Eclipse Sound narwhal resided within Admiralty Inlet between decades. Eclipse Sound narwhal tagged in the late 1990s that entered Admiralty Inlet by September 1 remained there for around two weeks, while narwhal tagged in 2011 and 2012 that entered Admiralty Inlet by September 1 remained there between four and six weeks (Heide-Jørgensen et al. 2002). While it is a small sample size for comparison, it appears that there could be a relationship between delayed fall migration and the increased residency length within Admiralty Inlet by Eclipse Sound narwhal.

3.5.3 Overlap Between Stocks

Eclipse Sound narwhal travelled extensively within the Admiralty Inlet summer-grounds during late summer and fall. The combined Eclipse Sound $(2010-2012)$ 95% summer home-range overlapped with half of the Admiralty Inlet 95% summer home-range. Narwhal tagged in Eclipse Sound that entered Admiralty Inlet resided there between 29 and 46 days, from September 1 to mid-October. During their residency Eclipse Sound narwhal travelled throughout Admiralty Inlet and all narwhal passed by Kakiak Point, the tagging ground for the Admiralty Inlet stock. As all tagging within Admiralty Inlet has occurred in August (Dietz et al. 2008, Heide-Jørgensen et al. 2013) before the arrival of narwhal from Eclipse Sound, it is unlikely that narwhal tagged within Admirably Inlet within this study or historically were from Eclipse Sound. Traveling through Admiralty Inlet during this season appears to constitute annual movement patterns for at least some portion of the Eclipse Sound stock. Therefore it should be assumed that narwhal located within Admiralty Inlet after the beginning of September could have originated either from Admiralty Inlet or Eclipse Sound. There was also extensive overlap between Eclipse Sound and the Admiralty Inlet 95% winter home-ranges in 2009 and 2011 where they almost completely overlapped, indicating that both stocks reside within the same area during the winter season. This agrees with conclusions from previous tag data from these stocks (Dietz et al. 2001, 2008, Heide-Jørgensen et al. 2002).

During late September and early October Admrialty Inlet narwhal traveled within regions of the Prince Regent Inlet where the Somerset Island stock have been recorded to occur (Heide-Jørgensen et al. 2003). Admiralty Inlet narwhal entered Prince Regent Inlet mid-September and remained in the area for approximately two weeks. They all travelled south along the eastern shoreline before crossing over near Brenford Bay. Four narwhal travelled through, or made localized movements within the summer home-range of the Somerset Island Stock with two visiting Bellot Strait and Creswell Bay, where Somerset Island narwhal have been tagged in August (Heide-Jørgensen et al. 2003). From the Creswell Bay area they then travelled north along the western shoreline of Prince Regent Inlet, returning to Lancaster Sound between September 29 and October 6. Somerset Island narwhal have been tracked along the western coastline between mid to late September (Heide-Jørgensen et al. 2003). It is therefore likely that there is mixing of these stocks during this time. One Admiralty Inlet narwhal travelled west but made localized movements between Maxwell Bay and Cunning Inlet from late September to early October instead of entering Prince Regent Inlet. Somerset Island narwhal have also been recorded in this area during this time period (Heide-Jørgensen et al. 2003). Therefore even though this narwhal did not enter Prince Regent Inlet, it still likely mixed with the Somerset Island stock.

While Eclipse Sound narwhal were within Prince Regent Inlet from late September to early October, it is unclear whether they would have overlapped with the Somerset Island stock during this time. These narwhal did not remain in Prince Regent Inlet as long as those tagged in Admiralty Inlet nor did they travel as extensively. They only briefly traveling south along the eastern shoreline of Prince Regent Inlet before returning to Lancaster Sound. During this time-period Somerset Island narwhal within Prince Regent Inlet have primarily occurred along the western shoreline or within their main summering area (Heide-Jørgensen et al. 2003). Eclipse Sound narwhal did not travel within either of these areas so it is unlikely that large amounts of mixing between the two stocks occurred.

3.5.4 Summer and Winter Site Fidelity

One narwhal from Admiralty Inlet and one narwhal from Eclipse Sound were tracked back to a summer ground location. A male narwhal (39256) was tagged in 2009 within Admiralty Inlet. It re-entered the mouth of Admiralty Inlet just before the transmitter failed on July 5, 2010. A female narwhal (51873) with a calf was tagged in 2010 within Eclipse Sound. Upon returning to Lancaster Sound during the end of spring migration it initially resided just east of Navy Board Inlet along the north shore of Bylot Island from June 29, 2011 to July 3, 2011. During that time period there was open water within Lancaster Sound but landfast ice blocked the entrance of Navy Board Inlet and Admiralty Inlet. It then travelled into the mouth of Admiralty Inlet and resided at the landfast edge outside the mouth of Elwin Inlet from July 5 − 8, 2011. It returned to, and travelled within Navy Board Inlet from July 10 − 27, 2011. While narwhal 51873 was within Navy Board Inlet the sea ice slowly melted until all of Eclipse Sound was primarily ice free. However this narwhal mostly remained in the northern section of Navy Board Inlet. It returned to Admiralty Inlet and remained there until the transmitter failed on October 4, 2011 even though both Eclipse Sound and Admiralty Inlet were ice free. This suggests that where narwhal summer is not an automatic decision and that other environmental factors apart from open water and previous residency influence its summer ground location. Narwhal 51873 was the first narwhal tracked to a different summer ground than it was tagged in, suggesting that Admiralty Inlet and Eclipse Sound stocks may not be as isolated from one another as previous tagging studies have concluded.

3.5.5 Conclusion

Increased variety in spatial usage typically results from greater plasticity and usually means the species will be more resilient to rapid environmental changes (Dingle and Drake 2007, Laidre et al. 2008, Williams et al. 2008, Faille et al. 2010, Descamps et al. 2017). The Eastern Canadian Arctic is currently experiencing rapid changes in a decreasing sea ice extent, which has increased the length of the ice-free season (Parkinson and Cavalieri 2008, Laidre et al. 2015, Yurkowski et al. 2016, Park et al. 2015). This has already resulted in an increased killer whale presence during the late-summer and fall season. The reduction in length of the sea ice season and decrease in sea ice extent are forecasted to continue (Wang and Overland 2012), and will likely result in a different marine species composition (Laidre et al. 2008, Higdon and Ferguson 2009, Descamps et al. 2017). Narwhal are thought to be highly sensitive to these changes because of low plasticity (Laidre et al. 2008). However they are an elusive species that are difficult to study, resulting in many life-history knowledge gaps.

This research demonstrates that Eclipse Sound and Admiralty Inlet narwhal both displayed greater flexibility in late summer movement patterns than previously recorded, using multiple movement paths before entering Baffin Bay on their fall migration. This increased flexibility resulted in the summer home-range of narwhal tagged in Eclipse Sound overlapping half of the Admiralty Inlet summer home-range, as well as Admiralty Inlet narwhal traveling through areas where Somerset Island narwhal were likely concurrently located (Heide-Jørgensen et al. 2003). Therefore the Eclipse Sound, Admiralty Inlet and Somerset Island stocks appear to be connected during September and early October. Additionally, Eclipse Sound narwhal displayed greater plasticity in their fall migration timing, entering Baffin Bay around two weeks later than what was recorded a decade earlier (Dietz et al. 2001, Heide-Jørgensen et al. 2002).

Narwhal displayed an increased flexibility in summer site fidelity, where for the first time a narwhal was tracked back to a different summering ground than where it was tagged (Heide-Jørgensen et al. 2003, 2013, 2015, Dietz et al. 2008, Westdal et al. 2010). This narwhal initially moved back and forth between the mouths of two summering grounds before selecting where it would summer, which suggests that where narwhal chose to summer is not automatic and that other environmental influences are likely involved in a decision making process. This highlights the need for continued tagging to confirm the connectivity, or separation of the Admiralty Inlet and Eclipse Sound stocks. The increased flexibility in late summer and fall movement patterns as well as site fidelity indicates that narwhal may be more able to adjust the timings and patterns of fall migration, and possibly summer ground location, in the face of changing environmental conditions than previously believed.

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Chapter 4

Baffin Bay Narwhal (*Monodon monoceros*) Select Bathymetry Over Sea Ice During Winter

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4.1 Abstract

Arctic pack ice structure and extent have been changing due to warming. Thus, understanding important habitat features for marine mammals that depend on sea ice, such as narwhal (*Monodon monoceros*), during winter will provide insight into impacts of future changes within the pack ice structure and extent. The objective of this study was to determine narwhal habitat selection for bathymetry, sea ice concentration, thickness, and floe size during the winter season. Nineteen narwhal were equipped with SPLASH tags in Admiralty Inlet and Eclipse Sound ($2009 - 2011$), with 50% of the transmitters lasting until April allowing for analysis of the entire winter season. Generalized linear mixed models indicated that both sexes selected similar bathymetric habitat corresponding to likely higher prey densities of halibut. This habitat preference for prey habitat occurred regardless of the mobile pack ice structure or amount of open water at the ocean surface. In addition we found evidence of a relationship between increased winter movements and decreased ice extent over the $2009 - 11$ period. Together these findings suggest that changes to sea ice structure likely will not negatively impact narwhal directly in the winter. However, indirect effects of changing sea ice, such as changing prey densities and distribution, increased presence of killer whales as predators, and increased interspecies competition for prey could negatively impact narwhal. In conclusion, the extensive narwhal winter movements indicate that narwhal may be more flexible in their winter ground habitat selection than previously believed.

4.2 Introduction

Wildlife select habitat patches within the land or seascape that enable them to maximize fitness, where high quality patches are occupied disproportionally higher in relation to their availability (Johnson 1980, Boyce et al. 2002, Johnson et al. 2006). Species are often classified as generalists or specialists, where generalists have a wide niche and quickly adapt to new opportunities. Specialists are highly adapted to survive in specialized environments or hunt particular prey and are therefore more susceptible to rapid environmental changes that affect their fitness compared to generalists (Travis 2003, Munday 2004, Clavel et al. 2011, Slatyer et al. 2013). Narwhal (*Monodon monoceros*) are a small whale endemic to the Arctic and are considered specialists and highly adapted to survive within the dense winter ice pack of Baffin Bay (Laidre and Heide-Jørgensen 2005a, 2011). Winter appears to be an important season for narwhal. After an energetically expensive, rapid fall migration of over 1000 km from the High Arctic, narwhal spend at least five months overwintering in southern Baffin Bay along the continental slope. During this season, narwhal reside within dense pack ice (sea ice concentration $> 95\%$), from January to March (Laidre and Heide-Jørgensen 2005a). They are not known to be able to break through pack ice and instead rely on leads to breathe during this period (Laidre and Heide-Jørgensen 2005a, 2011). In addition to navigating the dense ice narwhal appear to be extensively foraging during this compared to other seasons (Finley and Gibb 1982, Laidre and Heide-Jørgensen 2005a). They frequently conduct foraging-shaped dives to depths > 800 m, and occasionally dive > 1400 m (Finley and Gibb 1982, Laidre and Heide-Jørgensen 2005a, Watt et al. 2015). Greenland halibut (*Reinhardtius hippoglossoides*), Armhook squid (*Gonatus fabricii*), and potentially capelin (*Mallotus villosus*) are dominant winter prey species in this area (Laidre and Heide-Jørgensen 2005b, Watt and Ferguson 2015). Trawl surveys to 1500 m depths have found that Greenland halibut are abundant throughout Baffin Bay, with the highest densities and largest fish occurring at depths > 800 m (Jørgensen 2011, Treble 2015). Juvenile armhook squid are most abundant at depths of $400 - 600$ m while adults are primarily found at depths ranging from $400 - 1000$ m, although they have been caught at depths of 2000 m (Mansfield et al. 1975, Kristensen 1984, Zumholz and Frandsen 2006).

The ice pack within Baffin Bay has been rapidly changing. The fall freeze has been delayed, the winter sea ice extent, concentration, and thickness have been decreasing, and the spring thaw has been occurring earlier (Parkinson and Cavalieri 2008, Wang and Overland 2012, Park et al. 2015). Narwhal are thought to be poorly equipped to adapt to these rapid changes within their sea ice habitat as they have low genetic diversity and consistent migration routes and timings (Laidre et al. 2008). It is unknown if certain ice structures are favoured or avoided by narwhal as they navigate the dense pack ice. It is also unknown to what degree pack ice structure and foraging opportunities influence narwhal selection of winter ground location within Baffin Bay. Narwhal fitness could decrease if preferred sea ice habitat declines, causing narwhal to spend more time searching for or maintaining leads rather than foraging. Therefore the goal of this study was to understand narwhal habitat selection in relation to sea ice and bathymetry as a surrogate for foraging habitat during the winter season. We used generalized linear mixed models to determine relative selection of bathymetry, sea ice concentration, thickness, and floe size during this time. Bathymetry was chosen as a proxy for foraging because both halibut abundances and narwhal dive behaviour have been related to bathymetric depth (Laidre et al. 2004, Treble 2015). Our hypotheses were that narwhal would avoid landfast ice and open water, as well as select areas with bathymetric depths > 1000 m and where floe sizes were $0.5 - 10+$ km.

4.3 Methods

Nineteen narwhal were captured in black or dark green nets set up perpendicular to the shoreline. Nets had a $40x40$ cm mesh size, were anchored at the bottom, and had white floats attached to the surface (details described in Orr et al. (2001), Dietz et al. (2008), Watt et al. (2015). Tagging occurred in Admiralty Inlet at Kakiak Point (72°41'00"N, 86°41'20"W) in August 2009 and in Eclipse Sound at Tremblay Sound (72°21'23"N, 81°6'23"W) in August 2010 and 2011. Between August 15 and 19, 2009, four males and three females were captured and equipped with satellite transmitters in Eclipse Sound. Two males and three females were tagged in Eclipse Sound between August 21 and 24, 2010. One female was with a calf. Between August 6 and 20, 2011, one male and six females, two with calves, were tagged in 2011 in Eclipse Sound. Captured narwhal were equipped with SPLASH tags (Wildlife Computers, Redmond, WA, USA) and body length was recorded (Table 4.1). Sex was determined through genetic analyzation of biopsy samples . Tags were programmed to transmit daily until September 31, after which they were duty cycled at 4, 3, and 3 days during 2009, 2010, and 2011 respectively with multiple transmissions occurring each transmission day. The Argos system (CLS America) was used to receive transmissions and to assign each coordinate position an error estimate (LC values) using a least squares analysis of B, A, $0 - 3$ in increasing order of accuracy. When multiple coordinate locations had the same LC value, the first location was selected similar to Witt et al. (2010). Transmitters lasted between 166 and

Table 4.1: Narwhal stock (ES = Eclipse Sound; AI = Admiralty Inlet), deployment date (yyyy-mm-dd), date of last transmission (yyyy-mm-dd), sex, and length data

Narwhal Stock	ID	Sex	Deployment Date	Tag Duration (days)	Last Transmission	Length (cm)
AI	39249	F	2009 − 08 − 18	127	2010 − 01 − 10	386
AI	39256	M	2009 − 08 − 17	310	2010 − 07 − 05	450
AI	39287	M	2009 − 08 − 17	289	2010 − 06 − 11	439
AI	39290	F	2009 − 08 − 15	200	2010 − 02 − 23	373
AI	39309	M	2009 − 08 − 15	259	2010 − 01 − 06	376
AI	39311	M	2009 − 08 − 17	230	2010 − 05 − 02	307
AI	39313	F	2009 − 08 − 16	171	2010 − 02 − 11	391
ES	51871	M	2010 − 08 − 21	250	2011 − 04 − 28	444
ES	51872	M	2010 − 08 − 21	320	2011 − 06 − 08	461
ES	51873	F	2010 − 08 − 22	413	2011 − 10 − 04	400
ES	51874	F	2010 − 08 − 22	187	2010 − 12 − 19	390
ES	51875	F	2010 − 08 − 24	153	2011 − 01 − 25	380
ES	39270	F	2011 − 08 − 18	202	2012 − 03 − 07	394
ES	39314	F	2011 − 08 − 18	233	2011 − 03 − 31	406
ES	39315	F	2011 − 08 − 06	137	2011 − 12 − 22	389
ES	51876	F	2011 − 08 − 16	191	2012 − 02 − 13	391
ES	51878	M	2011 − 08 − 16	128	2011 − 12 − 22	310
ES	51879	F	2011 − 08 − 16	314	2012 − 06 − 26	401
ES	57590	F	2011 − 08 − 19	302	2012 − 06 − 16	404

413 days. Narwhal 39290 overwintered in Foxe Basin outside of our study area and was therefore excluded from the analysis. The winter season was defined by comparing ordinal date versus latitude similar to Dietz et al. (2008). Narwhal conducted relatively localized movements within their summer grounds in the Canadian Arctic Archipelago, as well as within their winter ground in Baffin Bay. During the fall and spring migration narwhal carry out directed movements across latitudes, presenting clearly defined arrival and departure from the winter ground (Fig. 4.1). All transmitters lasted into winter, with

77% lasting to the end of January and three transmitters per year (50%) lasting the duration of through the end of March. There was a total of 613 daily positions, of which 493 were LC= $0-3$ and 120 were LC=A−B. Prior to creation of daily positions, all transmissions per day were tightly grouped together during the winter period.

4.3.1 Habitat Data

Data on sea ice concentration, thickness, and floe size were obtained from the Weekly Regional Ice Charts produced by the Canadian Ice Service. Ice charts were produced weekly except for January, February, and March when they were biweekly. This changed in 2012 when they were produced weekly year round. Bathymetric data with 500 m resolution was obtained from the International Bathymetric Chart of the Arctic Ocean (IBCAO; Jakobsson et al. (2012)). Habitat data were regrouped into categories using ArcGIS

(10.2, ESRI, Redlands, California, USA) to correspond with previous studies on cetacean sea ice selection, narwhal ecology, and Greenland halibut distribution (Laidre et al. 2004, Ferguson et al. 2010, Treble 2015). Sea ice concentration categories were: open water ($0-35\%$), mixed ice ($35-65\%$), closing ice ($65-95\%$), and closed ice ($95-100\%$). Sea ice thickness categories were: open water, thin ($0-30$ cm), medium ($30-70$ cm), thick first year sea ice ($70-120+$ cm), and old multiyear ice (> 120 cm). Sea ice floe size categories were: open water, small floes (< 500 m), big floes ($501-2000$ m), vast floes (> 2001 m), and landfast ice. Bathymetry categories were: shelf (< 500 m), sub ($501-1000$ m), mid ($1001-1500$ m), deep ($1501-2000$ m), and bottom (> 2000 m).

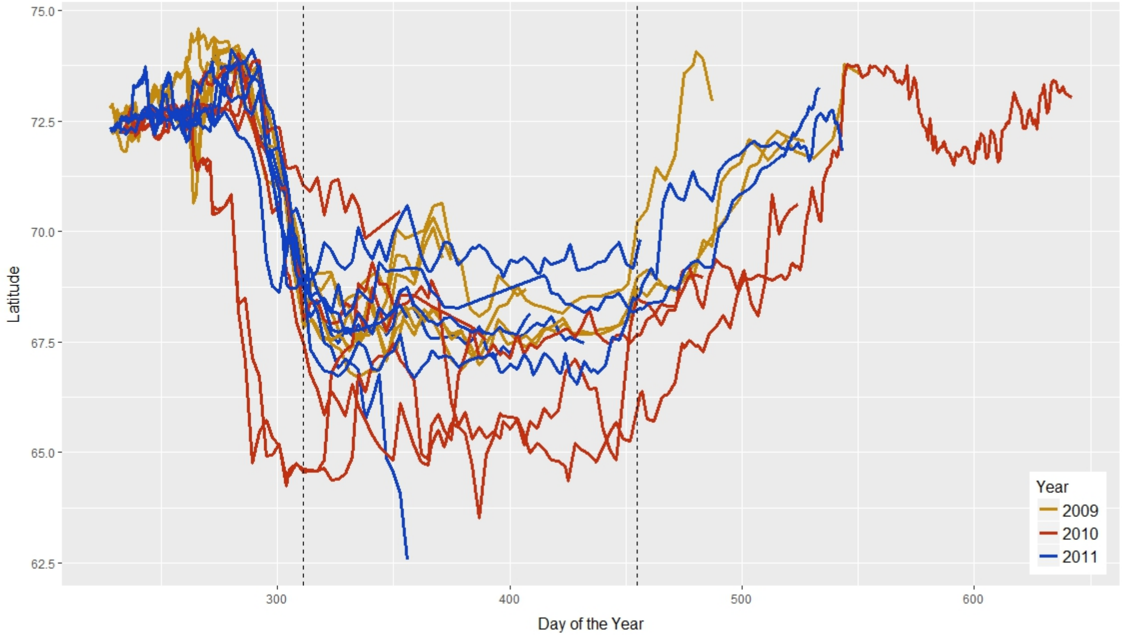

Figure 4.1: The winter season was defined by comparing the latitude of narwhal best daily locations with the day of the year (+365 after Jan 1 to maintain continuous time scale for plotting). The two vertical dashed lines represent the beginning (November 7) and end (March 31) of the defined winter season

4.3.2 Habitat Selection

Habitat selection examined used and available habitat with the assumption that high quality patches are occupied disproportionally in relation to their availability (Johnson 1980). We used narwhal locations estimates to define used habitats whereas available habitat was defined as the area that a narwhal could have travelled to between successive daily positions. The 95^{th} percentile (41 km/day) of daily winter movement distance was the radius for the available habitat buffer around each daily position. Each daily position was matched with the ice chart that was closest in date. The available and used habitat buffers were overlaid with the corresponding habitat data within as shown in Fig. 4.2. The habitat category with the largest area within the buffers was extracted using ArcMap (10.2 ESRI, Redlands, California, USA). When only one habitat category occurred within the available habitat buffer, it was recorded as both used and available (Ferguson et al. 2010). Daily positions were buffered depending on the LC value to account for coordinate position error. Buffer sizes per LC values were $3 = 0.5$ km, $2 = 1$ km, $1 = 1.2$ km, $0 = 4.2$ km, A $= 6.2$ km, and B $= 10.3$ km, as according to transmitter accuracy on marine wildlife (Hazel 2009, Costa et al. 2010, Witt et al. 2010).

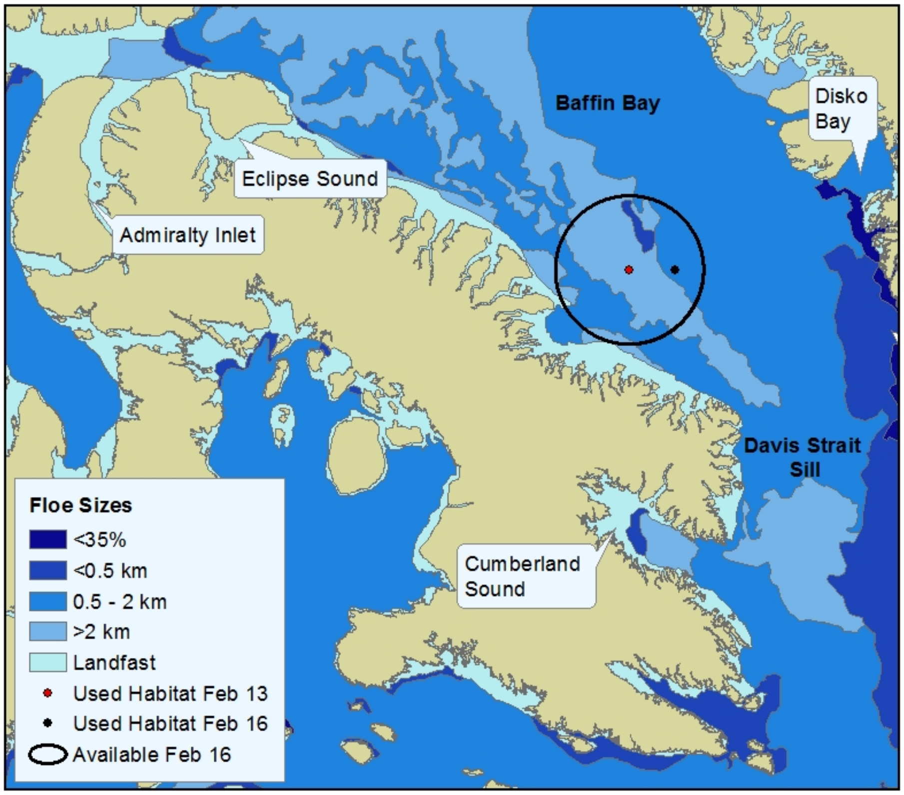

Figure 4.2: An example of the habitat selection analysis process for narwhal 39314 between Feb 13, 2012 and Feb 16, 2012. The Available Habitat Feb 16 is the area narwhal 39314 could have travelled to in between Feb 13 and Feb 16. Used Habitat Feb 16 is the area narwhal 39314 selected

4.3.3 Statistical Analysis

A generalized linear mixed model with a binomial error structure was conducted using the glmer function within the lme4 package in R (Bates et al. 2015) to analyze the relationship between narwhal occupancy (i.e. used habitat versus available habitat) and habitat variables. The fixed effects were sea ice concentration, thickness, floe size, bathymetry, and sex. No interactions were included within the fixed effects. The random effect consisted of individual whale identification. Correlation between the fixed effects were examined using the Pearsons correlation coefficient and a variance inflation factor (VIF) were the maximum limit was 0.7 and 3.0, respectively (Zuur et al. 2009). All variables fell below this threshold so all were retained for the model.

A stepwise backwards model selection format was conducted, where the model originally contains all coefficients and non-significant coefficients were removed. The Akaikes Information Criterion (AIC) was used to compare which model best fit the data, with a relatively lower AIC value indicating a better fit. To examine the amount of variation models accounted for the marginal R^2 and conditional R^2 were calculated within the MuMIn package in R (Bartoń 2016). The marginal R^2 examines the variance accounted for by the fixed effects, while the conditional R^2 examines the variance accounted for by both the fixed and random effects.

A Tukey Post Hock analysis was then conducted on the best fitted model using the glht function within the multcomp package in R (Hothorn et al. 2008) to examine narwhal occupancy in relation to availability between categories within habitat variables. Significance was examined at the 5% level.

4.4 Results

4.4.1 Narwhal Winter Movement

Narwhal tracked in 2009 and 2011 were tightly grouped throughout the winter, while narwhal tracked in 2010 had more extensive movements (Fig. 4.3). Narwhal 51871 and 51872 were within or at the mouth of Cumberland Sound from Oct 16−Nov 28 and Oct 22−Nov 16 respectively. Narwhal 51872 then entered Disko Bay on December 4 and remained there until January 4. Additionally, narwhal tracked in 2009 and 2011 spent 0% and 2% of the winter on the Davis Strait sill (south of 66°N latitude), whereas narwhal tracked in 2010 spent 43% of the winter in this region. In all years combined, narwhal generally arrived at their wintering ground by Nov 7. The beginning of the spring migration occurred throughout April but varied by year. Therefore the winter season was conservatively defined as Nov 7 to March 31 for all years. The sea ice extent covered the winter ground mid-November (2009; 2011) and mid-December (2010). Sea ice extent in 2010 was lower than in 2009 and 2011 from November to mid-January (Fig. 4.4). While 2010 sea ice extent was delayed in forming and overall lower than those of the other two years within the study, sea ice completely covered the wintering ground by December.

4.4.2 Model Selection and Validation

Sea ice concentration, floe size, and bathymetry were retained in the best fit models. Sex was not significant ($p = 0.055$). However there was little difference in AIC and r-squared values between models where it was retained and not retained (Table 4.2). Therefore sex was excluded from the final model. The final model contained fixed effects of sea ice concentration, floe size, and bathymetry, as well as a random effect of narwhal ID. The fixed and random effects explained a high amount of the variation within the model, where the marginal R^2 was 0.57 and the conditional R^2 was 0.65.

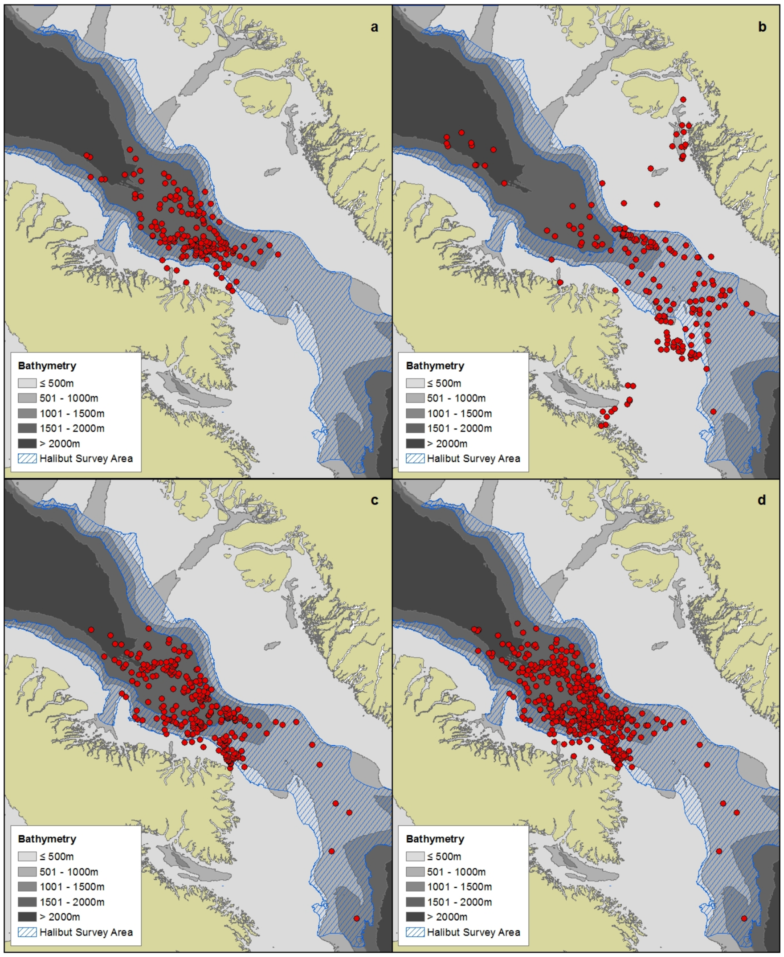

Figure 4.3: Narwhal winter locations in (a) 2009, (b) 2010, (c) 2011, and (d) 2009 and 2011. Of note are the similarities of 2009 and 2011 narwhal locations and the extensive movements recorded in 2010. The general area where halibut trawl surveys have been conducted are based off sampling locations presented within (Jørgensen et al. 2005, Jørgensen 2011, Treble 2015)

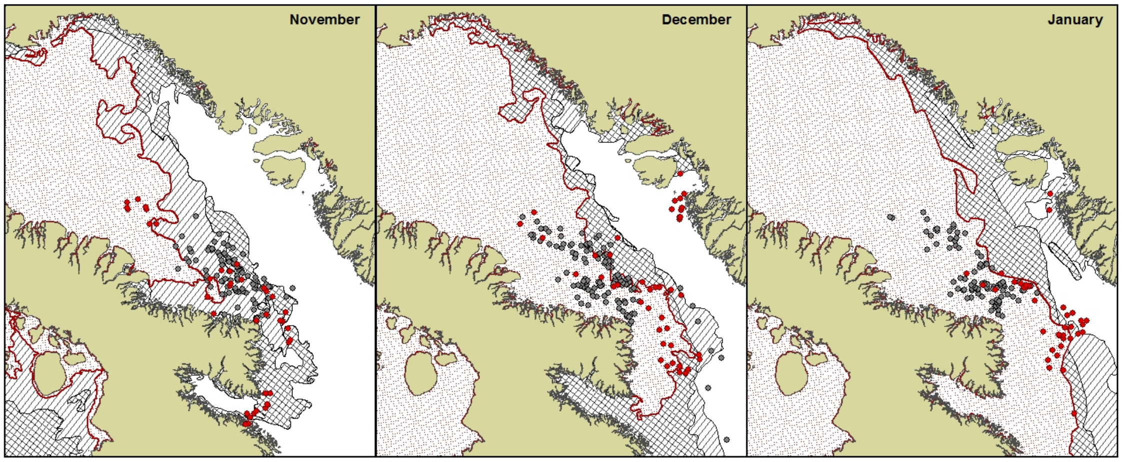

Figure 4.4: Sea ice extent mid-month 2009 (cross-hatch), 2010 (dots with red outline), and 2011 (diagonal) with corresponding monthly narwhal used habitat 2009 (grey), 2010 (red), 2011 (grey). While 2010 extent is smaller it covered most 2009 and 2011 used habitat locations by mid-December. For analysis used habitat was overlaid with weekly ice charts, rather than monthly

Narwhal disproportionately occupied closed ice ($> 95\%$ concentration) and open water ($0 - 35\%$ concentration) in relation to their availability (Table 4.3). Closed ice and open water were selected over closing ice ($65 - 95\%$; $p = < 0.001$). Landfast ice was not occupied disproportionately in relation to its availability. Open water, small floes (< 500 m), big floes ($501 - 2000$ m), and vast floes (> 2000 m) were selected over landfast ice ($p = < 0.001$). narwhal disproportionately occupied big floes compared to small

Table 4.2: Generalized linear mixed effect models of narwhal habitat selection between sea ice concentration (CON), sea ice thickness (TH), floe size (FLOE), and bathymetry (BATH). Variables that were significant are bolded

Model	AICc	Δ i	w_i	marginal r^2	cond r^2
CON + **FLOE** + **BATH** + SEX	1126.0	0.00	0.60	0.57	0.65
CON + **FLOE** + **BATH**	1127.4	1.38	0.30	0.57	0.64
CON + **FLOE** + TH + **BATH** + **SEX**	1129.6	3.54	0.10	0.58	0.64

Table 4.3: Tukey post hoc test results of the final habitat selection model (CON + FLOE + BATH) identifying significance within the categorical variables sea ice concentration (CON), floe size (FLOE), and bathymetry (BATH). Note that with positive z-values variables in the left column are selected over the variables in the right column while negative z-values are the opposite

Predictor Variables	Value	SE	z-value	p-value
CON				
Mixed Ice - Open Water	-0.676	0.484	-1.395	0.488
Closing Ice - Open Water	-1.450	0.357	-4.063	< 0.001***
Closed Ice - Open Water	0.112	0.354	0.316	0.988
Closing Ice - Mixed Ice	-0.774	0.414	-1.867	0.231
Closed Ice - Mixed Ice	0.788	0.423	1.862	0.234
Closed Ice - Closing Ice	1.561	0.230	6.777	$<$ 1e$-$04***
FLOE				
Small - Open Water	-0.052	0.343	-0.151	1.000
Big - Open Water	0.784	0.354	2.217	0.155
Vast - Open Water	0.656	0.401	1.637	0.443
Landfast - Open Water	-3.695	0.669	-5.523	< 0.001***
Big - Small	0.836	0.221	3.784	0.001**
Vast - Small	0.708	0.288	2.460	0.088
Landfast - Small	-3.643	0.603	-6.038	< 0.001***
Vast - Big	-0.128	0.249	-0.515	0.984
Landfast - Big	-4.479	0.591	-7.579	< 0.001***
Landfast - Vast	-4.351	0.615	-7.076	< 0.001***
BATH				
Sub - Shelf	1.308	0.218	5.996	$<$ 1e$-$04***
Mid - Shelf	2.481	0.268	9.272	$<$ 1e$-$04***
Deep - Shelf	3.700	0.294	12.565	$<$ 1e$-$04***
Bottom - Shelf	3.278	0.484	6.777	$<$ 1e$-$04***
Mid - Sub	1.173	0.300	3.907	< 0.001***
Deep - Sub	2.392	0.334	7.167	$<$ 1e$-$04***
Bottom - Sub	1.970	0.510	3.862	< 0.001***
Deep - Mid	1.219	0.260	4.682	$<$ 1e$-$04***
Bottom - Mid	0.797	0.457	1.745	0.381
Bottom - Deep	-0.422	0.412	-1.024	0.830

Note: '*' $p < 0.05$; '**' $p < 0.01$; '***' $p < 0.001$

floes ($p < 0.01$). Bathymetric depths < 1000 m were disproportionately unoccupied in relation to their availability. Sub ($500 - 501$ m), mid ($501 - 1000$ m), deep ($1500 - 2000$ m), and bottom waters (> 2000 m) were selected over shelf waters (< 500 m; $p = < 0.0004$). Mid, deep, and bottom waters were selected over sub waters ($p = 0.0007$, $p = < 0.0004$, and $p = 0.0009$ respectively). Narwhal occupied deep waters disproportionately in relation to mid waters ($p = < 0.0004$).

4.5 Discussion

Narwhal did not appear to be selecting or avoiding particular pack ice types. Instead they selected areas with deeper bathymetry and avoided shallower areas. These regions with deeper bathymetry appear to correspond with high densities of winter prey species (Jørgensen 1997, 2011, Bjørke 2001, Treble 2015). This suggests that during winter both sexes of narwhal are likely targeting areas with high prey densities regardless of the mobile pack ice structure above.

4.5.1 Sea Ice Selection

While narwhal are unable to break through pack ice, leads occur more frequently within thinner moving ice (Smith et al. 1990, Richter-Menge et al. 2002, Laidre and Heide-Jørgensen 2005a, Assmy et al. 2017). Therefore, it was hypothesized that narwhal may prefer relatively thinner ice due to the greater abundance of leads. However, narwhal did not preferentially select thinner sea ice in our models suggesting that narwhal are adapted to locating leads within different pack ice thicknesses, and that this is not an important habitat component while navigating through habitat patches.

The mobility of the ice floes through winds and currents are influenced by floe size, which altogether influences lead formation. Additionally floe diameter is an important predictor of the likelihood of floes breaking apart (Smith et al. 1990, Hopkins and Thorndike 2006, Asplin et al. 2014, Perovich and Jones 2014). Floe size was predicted to be an important habitat component as narwhal navigate dense pack ice in the winter. However, narwhal did not select for particular floe types even though there was large variability in floe sizes available among and within years. Narwhal instead demonstrated strong avoidance of landfast ice, likely because of the complete lack of access to the air surface.

Sea ice concentration formation and distribution were consistent within and among years. The predominant concentration was closed ice ($> 95\%$), with closing ($65 - 95\%$) and mixed ice ($35 - 65\%$) creating the pack ice edge. Open water ($< 35\%$) occurred along the most eastern strip of Baffin Bay and Davis Strait where the warm waters of the West Greenland current flow along the coast north. Narwhal selected for both closed ice, as well as for open water. While previous studies have documented narwhal occupying closed ice for much of the winter, no studies have documented narwhal occupying open water disproportionate to its availability (Laidre and Heide-Jørgensen 2005a, 2011) and no tracking study of Baffin Bay narwhal has indicated any affiliation for open water during the winter (Heide-Jørgensen et al. 2003, Dietz et al. 2008).

There are three possible explanations for why narwhal occupied open water disproportionately to its availability. It could be related to narwhal occupying open water for parts of November before the sea ice extent covers the winter ground. A second explanation is that the delayed sea ice growth observed in $2010 - 2011$ resulted in the winter ground having areas where sea ice $< 30\%$ throughout the winter season. Finally the open water selection could be related to the extensive movements documented from narwhal tracked in 2010. When the model was reanalyzed without the 2010 data, the selection for open water did not occur while other parameters remained consistent, indicating that the open water selection was either an artifact of the 2010 anomalous ice year or the extensive narwhal movements. While there was delayed growth in sea ice extent in 2010 compared to 2009 and 2011, in all three years the winter ground was primarily covered with sea ice $> 95\%$ by mid-December, as has historically occurred (Laidre and Heide-Jørgensen 2005a). It is therefore unlikely that the delayed growth in sea ice extent was the primary cause of the winter selection of open water. Narwhal tracked in 2009 and 2011 arrived at the winter ground and remained relatively stationary throughout the winter season. However, narwhal tracked in 2010 conducted extensive movements until early January. This occurred concurrent to the delayed growth in sea ice extent. Between early January and mid-March three of the five narwhal were tracked along the ice edge or within one days movement away in open water. Narwhal 51871 and 51873 were at the ice edge, or travelled between the ice edge and open water until mid-February and late January respectively when the pack ice expanded southward. Narwhal 51872 was highly mobile, traveling between the pack ice and open water until mid-March when it remained within the pack ice. Therefore, the selection of open water was predominately explained by the extensive movements, as well as narwhal remaining one day from the ice edge from January until mid-February. This indicates that narwhal are not primarily targeting for a particular sea ice concentration, as they are adapted to closed ice which is the predominant feature within the pack ice.

4.5.2 Bathymetry

Our habitat model showed that narwhal targeted $1500 - 2000$ m bathymetry and avoided bathymetry < 1000 m. This corresponds both with depths of energetically expensive foraging-shaped dives conducted by narwhal, as well as high densities of mature sized prey species during the winter. It is therefore reasonable to assume that narwhal were selecting for areas with bathymetric depths of $1500 - 2000$ m due to likely higher prey densities. During winter, narwhal dive behaviour and main prey species abundance are both related to depth, therefore bathymetry was included as a proxy for prey density and foraging behaviour (Laidre et al. 2004, Jørgensen 2011, Treble 2015, Watt et al. 2015). Foraging shaped dives between 800 and > 1400 m depths are frequently conducted by narwhal throughout the winter season (Laidre et al. 2003, 2004, Watt et al. 2015). Greenland halibut, armhook squid (*Gonatus fabricii*), and potentially capelin (*Mallotus villosus*) are important winter prey species (Laidre and Heide-Jørgensen 2005b, Watt and Ferguson 2015). Trawl surveys conducted across Baffin Bay to 1500 m depths show that Greenland halibut are abundant and prevalent in all regions and depths with the highest densities and largest fish found in depths > 800 m. Halibut travel to deeper waters both as they grow larger, as well as during the winter season (Jørgensen 1997, 2011, Treble 2015). While halibut trawl surveys had maximum depths of 1500 m, it is likely Greenland halibut occur at depths > 1500 m (Jørgensen 1997, 2013). Immature armhook squid are most abundant at depths of $500 - 600$ m along the West Greenland shelf, while adults are primarily found in depths ranging from $400 - 1100$ m along the continental slopes and have been caught down to depths of 2000 m (Kristensen 1984, Bjørke 2001, Zumholz and Frandsen 2006). Little is known about capelin distribution within Baffin Bay itself as they are historically not abundant in this area, preferring fjords in West Greenland and southern Baffin Island. However since the 2000s they have become a dominant prey species within Hudson Bay and are now frequently observed in thick-billed murre (*Uria lomvia*) diets near Qikiqtarjuag, Baffin Island, NU which is at similar latitudes as the narwhal winter ground (Provencher et al. 2012, Chambellant et al. 2013, Gaston and Elliott 2014). They have also been increasing in proportion within the diets of ringed seals (*Pusa hispida*) and beluga (*Delphinapterus leucas*) within Cumberland Sound (Marcoux et al. 2012, Yurkowski et al. 2016).

4.5.3 Conclusion

Climate change is predicted to continue the trend of decreasing ice concentration, thickness, and extent (Wang and Overland 2012). It was unclear how these changes within the pack ice structure would limit narwhal as they rely on leads while navigating the dense pack ice. No sea ice metrics were found to influence used versus available habitat, which suggests that narwhal are adapted to multiple sea ice types and that this is not the primary reason for habitat selection. Narwhal instead were strongly selecting for deep areas in Baffin Bay along the shelf break that likely supported higher prey densities. This suggests that it is unlikely that changes within the mobile pack ice structure itself will directly impact narwhal as they appear to be able to manage in a variety of sea ice thicknesses, floe sizes, and concentrations. However, climate-driven changes to prey populations and distributions in Baffin Bay during the winter could directly impact narwhal in terms of their choice of habitat features.

In November and December 2010 narwhal conducted extensive movements outside the pack ice coinciding with reduced sea ice extent. This is suggestive of a potential relationship between low sea ice extent early in the winter and the documented extensive movements, but further research is warranted. Additionally, once the sea ice extent grew to match previous years, narwhal remained < 1 day outside the ice edge for another month. This indicates that as the sea ice extent decreases, narwhal could remain in areas with high prey densities rather than following the sea ice. However, the presence of sea ice would likely deter the presence of killer whales that are known to attack and consume narwhal (Higdon and Ferguson 2009, Breed et al. 2017), as well as other non-ice adapted marine species that may compete for similar prey (Laidre et al. 2008). Nevertheless, the increased movement documented during the lower sea ice extent indicates that narwhal may be more adaptable to these changes than previously thought.

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Chapter 5

Conclusion

The Arctic environment is rapidly changing with decreasing sea ice extent and concentration as well as increasing ocean temperatures (Barber et al. 2012, Laidre et al. 2015, Park et al. 2015). Marine mammal and fish species seasonal distribution have already been shifting and this pattern is anticipated to continue doing so (Higdon and Ferguson 2009, Provencher et al. 2012, Gaston and Elliott 2014, Yurkowski et al. 2016). Narwhal (*Monodon monoceros*) are thought to be highly sensitive to climate change because they have been recorded conducting long migrations with regular migration routes and timings, and have shown high summer site fidelity (Laidre et al. 2008). These spatial use patterns suggest that narwhal would have low plasticity to adjust their routes and timings of migration as well as summer and winter ground location if those areas become degraded (Laidre et al. 2008, Faille et al. 2010, Monteith et al. 2011, Cherry et al. 2013). However few narwhal have been equipped with satellite transmitters compared to the narwhal population so there could be movement patterns or behaviour that have not been recorded (Dietz et al. 2001, Heide-Jørgensen et al. 2002, 2003, 2013, Dietz et al. 2008, Doniol-Valcroze et al. 2015). The results of this thesis indicate that narwhal have a higher plasticity in terms of late summer movement patterns and fall migration routes, the timing of fall migration, summer ground location, and winter ground location than previously believed.

5.1 Major Conclusions

Admiralty Inlet and Eclipse Sound narwhal have higher plasticity in terms of adjusting the late-summer movements and fall migration timings with changing conditions. Narwhal from both stocks conducted two to three late-summer movement patterns. One movement pattern of narwhal tagged in Admiralty Inlet was to leave Admiralty Inlet mid-September and travel west towards, or within Prince Regent Inlet and then enter Baffin Bay. The second movement pattern was to immediately begin the fall migration towards Baffin Bay upon leaving Admiralty Inlet. Narwhal tagged in Eclipse Sound left the sound by early September and travelled west into Admiralty Inlet where they remained for four to six weeks before heading to Baffin Bay. The second movement pattern was for narwhal to leave Eclipse Sound mid-September and travel west within Lancaster Sound before heading to Baffin Bay. The third group of narwhal travelled directly to Baffin Bay from Eclipse Sound in early October. Additionally, narwhal tagged in Eclipse Sound entered Baffin Bay at least two weeks later than that of Eclipse Sound narwhal tracked the previous decade.

For now it should be assumed that narwhal occurring in Admiralty Inlet after September 1 could be from either Admiralty Inlet or Eclipse Sound stocks. Multiple narwhal tagged in Eclipse Sound remained within Admiralty Inlet for over four weeks from September 1 to mid-October. The Eclipse Sound 95% summer home-range also overlapped half of the Admiralty Inlet 95% summer home-range.

For the first time one narwhal tagged in Eclipse Sound summered in Admiralty Inlet the following year. Not only does this indicate lower site fidelity and increased connectivity between the two stocks, the behaviour of this narwhal also indicates that summer ground location is not an automatic decision. This narwhal first remained outside of Navy Board Inlet and then Admiralty Inlet as landfast ice blocked both areas. It then returned to Navy Board Inlet and entered it as leads developed. However it remained in Navy Board Inlet while sea ice within Eclipse Sound decayed and open water become prevalent. When Eclipse Sound was ice-free it switched over to Admiralty Inlet, which was also ice-free, where it remained until the transmitter failed in October. Therefore the narwhal did not automatically return to the same summer ground and it did not switch summer grounds due to ice constraints. When this narwhal was tagged it did have a calf and it is unclear if this influenced the decision of summer ground location the subsequent year. This decision making process highlights that interpretation of where narwhal summer prior to them conducting residency behaviour within the summer ground should be treated cautiously.

During the winter season narwhal were selecting areas with bathymetric depths $1500-2000$ m and avoiding areas with bathymetric depths < 1000 m regardless of the structure of the mobile pack ice. Narwhal dive behaviour indicates that the frequency and depth of dives increase with increasing bathymetric depth, and that during this season narwhal are frequently conducting foraged shaped dives at depths > 800 m (Laidre et al. 2003, 2004, Watt et al. 2015). Trawl surveys indicate that Greenland halibut densities are highest at depths > 800 m (Treble 2015, Jørgensen 2011). And while little is known about squid at depths < 600 m, adult squid have been caught to depths up to 2000 m (Kristensen 1984, Bjørke 2001, Zumholz and Frandsen 2006). Therefore it appears that narwhal are primarily selecting areas with that likely contain higher prey densities during the winter season and are not favoring or avoiding particular mobile pack ice structures. Therefore as pack ice structure changes in response to climate change, it is unlikely to directly impact narwhal fitness. However it could indirectly impact narwhal if it changes prey distribution or density.

Narwhal also demonstrated increased flexibility in winter movement than previously recorded. During the 2010 tag year narwhal conducted increased movements coinciding with a delayed growth in sea ice extent. Narwhal remained along the ice edge even when the sea ice extent had grown to be similar to the other years. This indicates that narwhal could remain in areas that likely contain high prey densities as ice extent decreases. However decreasing sea ice extent could change prey distribution, increase the number of predatory killer whales, and increase interspecific competition from subarctic cetaceans, all of which could influence narwhal behaviour (Laidre et al. 2008, Higdon and Ferguson 2009, Breed et al. 2017).

Therefore the results of this thesis conclude that narwhal have more flexible movement patterns, migration timings, summer site fidelity, and winter ground location than previously believed. This indicates that narwhal likely have greater plasticity and may have some ability to adjust to climatic changes.

5.2 Future Work

Understanding whether Admiralty Inlet and Eclipse Sound stocks are indeed separate stocks is important both for accurate population estimates and for sustainable harvest quotas (Bethke et al. 1996). As narwhal are an important cultural and nutritional species accurate sustainable harvest quotas are important to both ensure that communities are able to have harvest traditional food while ensuring that stock abundance does not decrease. This will be increasingly challenging as narwhal adjust to climate change. There are two aspects to understanding this question. Do narwhal switch summer ground location on subsequent years, and do they travel between these summer grounds within one summer? The question regarding narwhal summer site fidelity has proven difficult to answer as the longevity of satellite transmitters are unpredictable despite efforts to maximize battery life like implementing a duty cycle for most of the year. Continued work on unique photographic identification through scarring might be the fastest way to answer this particular question, despite the large size of both populations (Auger-Méthé et al. 2011, Doniol-Valcroze et al. 2015). The successful use of quad-copter drones in these regions in taking photographs and videos of cetaceans below the water surface may make this method more cost-effective.

A possible method to understand how many narwhal travel between Admiralty Inlet and Eclipse Sound summer grounds from July to September would be to set-up an acoustic mooring near the shoreline of the Borden Peninsula between the two stocks. Narwhal traveling from Eclipse Sound to Admiralty Inlet always travelled quickly along the shoreline and would be recorded by the mooring.

It is important to continue to equip narwhal with satellite transmitters to increase the sample size and confidence levels for narwhal spatial patterns year round from stocks that have previously been studied. There are also stocks within the Baffin Bay population that have not been successfully equipped with satellite transmitters. Therefore their migration routes and winter ground locations are unknown.

The potential relationship between delayed pack ice growth and extensive narwhal movement merits its own study. This would involve statistically examining narwhal movement speeds and sea-ice growth rate from early November to at least late December for all years with narwhal tag data. This study could be combined with an examination of the relationship between the growth of sea ice extent and when narwhal enter Baffin Bay during the fall to see if there is a relationship between later ice development and the delay in when narwhal entered Baffin Bay.

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