Arctic Whale Mortality: Understanding Modern Population Losses for the Future

by

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Abstract:

The remote, ice-covered habitat and reclusive nature of Arctic cetaceans have led to a gap in knowledge about species ecology. In rare instances where Arctic cetaceans can be spotted, information about their population structure and biology can be gleaned through observation; however, direct observations are difficult in high ice cover. Ice entrapments, where cetaceans are crowded under increasing ice cover until escape or drowning, have given insight into cetacean populations since the 18th century, and today new genetic analyses can allow us to reexamine the population structure of these Arctic species and add to previous research on ice entrapments and narwhal social structure. In this thesis' second chapter, I first review 138 cetacean ice entrapment occurrences globally and show that ice entrapments are a significant source of mortality for cetaceans, killing more than 18,500 individuals in 13 different species since 1900. In the third chapter, I use population genetics to study the social structure of the Canadian Arctic narwhal (*Monodon monoceros*) from a 2008 ice entrapment. Through pair-wise relatedness and cluster analysis, I determined that within an ice-entrapped herd (n=245), there were 8 genetically related clusters with an average size of 30.6, indicating that the species may follow a fission-fusion social structure like other smaller, social cetaceans. This work may contribute to species management decisions and be valuable for emergency management of ice entrapments.

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Dedication

I dedicate this thesis to my family who truly are the giants on whose shoulders I stand.

To my mother for being my best friend and continually supporting me in whatever journey I chose, regardless of whether you think it is a good plan or not.

To Emily, Tommy, Jon, Jeremiah, and Ethan Alan for all of the laughter, tears, and phone calls; and for always keeping me humble.

To Miles for being my strength and stay from around the world and for deploying so I could work without distraction. Love you.

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Chapter 1: Introduction

In wildlife conservation and species management, knowledge about mortality and behaviour is essential to understanding population dynamics and predicting the future of species. Today, climate change is rapidly disrupting species ecology in ways that will have unknown consequences for animals that are strongly adapted to their climate. Climate change is currently having the biggest impact on Arctic animals, such as narwhal, which have evolved for millennia to live in ice-covered environments. These long-lived species likely cannot keep up with the pace of selection.

Ice entrapments are one of the only naturally occurring mass mortality events for cetaceans and happen when ice forms rapidly and entraps cetaceans below the ice surface where they will drown unless escape is possible (Hobbs, 2019; Heide-Jorgensen, 2022). With ice forming in increasingly unpredictable ways, seasonal migrations changing with climate change, and non-Arctic resident cetaceans staying in the polar regions longer than usual, ice entrapments may happen more frequently (Siegstand and Heide-Jørgensen, 1994). While these events can mean a dramatic and devastating loss to a population, they also give researchers a unique opportunity to look at otherwise unmeasurable or elusive cetacean species. This thesis investigates global ice entrapments through a strategic literature review and pair-wise kinship analysis of narwhal tissue samples collected from a 2008 ice entrapment in order to better understand herd sociality.

Study Species and Natural History:

Cetaceans are a monophyletic mammalian group of ~75 species that consists of Mysticeti (baleen) and Odontoceti (toothed) whales (Würsig, 1989) and can be found worldwide. Almost all members of Cetacea are threatened or endangered. Today the Monodontidae family consists of two living species, narwhal (*Monodon monoceros)* and beluga (*Delphinapterus leucas*), medium-sized whales that circumvent the Arctic Ocean, with large stocks in the Northern Atlantic Ocean (Heide-Jorgensen, 2018). Members of Monodontidae are highly adapted to life in the Arctic with notably high fat content and thick skin adapted for life as a warm-blooded mammal in cold water and lack of a dorsal fin and smaller tail flukes and pectoral flippers for maneuvering in shallow water and under ice (Harrington, 2008).

Those same charismatic adaptations that have piqued human interest also contribute to monodontid's susceptibility to climate change. Narwhal and beluga have adapted to the extreme Arctic living in areas with greater than 95% ice cover, extremely cold temperatures, and limited natural predators. Today, that habitat is changing as the surface, and air temperature warms, and with less ice and warmer water temperatures, new predators and niche competitors enter the once-restricted Arctic habitat (Lefort et al., 2020). Simultaneously with natural predators taking advantage of newly accessible water, Arctic mining and industry are advancing and threatening populations with toxic metal and organic pollutants and boat strikes (Lowry et al 2017; Heide-Jorgensen, 2018; Williams et al, 2011). As a result, narwhal and beluga whales are ranked as some of the animals most suspectable to climate change (Laidre et al, 2005).

Additionally, narwhals are one of the frequently ice-entrapped cetaceans (Williams et al., 2011). The species, which is commonly known as the unicorn of the sea for the long tusk that protrudes from most males' heads, are found in Arctic waters under pack ice in the summer and in open water with high prey availability in the winter (Laidre et al, 2004). Recent research has predicted that predation of narwhal will be an increasing threat as ice cover decreases and more aggressive predatory species, such as orca (*Orcinus orca*), establish a year-round residence in the Arctic. Orcas could predate >1,000 narwhal each year as they increase their global range, which may have dramatic effects on their total species of ~123,000 individuals (Lowry et al, 2017; Lefort et al., 2020). Yet, the same ice may be a saving grace for narwhal and entrap those same predators and continue to limit their expansion to the northern Arctic as it likely has for millennia (Matthews, 2019).

CHAPTER 2 INTRODUCTION:

Although ice entrapments are considered to be a regular occurrence with Arctic cetaceans, their range and species expanse are little understood. In order to better understand ice entrapments and species at increasing risk, Chapter 1 is a literature review of all ice entrapments globally. Through a strategic literature review of 138 references, we found that 13 species of cetacean were ice-entrapped in the waters of more than 5 countries in both hemispheres. Additionally, from 1738 to present, 20,178 cetaceans were documented to have been killed in ice entrapments, indicating that ice entrapments are a source of significant mortality for cetaceans and should be better researched.

CHAPTER 3 INTRODUCTION:

Focusing on a single ice entrapment of more than 600 narwhal in Eclipse Sound, this chapter examines herd sociality through genetic kinship. Tissue samples were collected from entrapped narwhal and genotyped at 12 microsatellite loci. Using pair-wise relatedness, internal clusters were identified and a social network was developed based on that framework. Within the 245 samples, we determined that there were 8 distinct pod clusters with an average size of 30.6 individuals with 0.24 M/F ratio. This work aligns with visual assessments and fatty-acid analysis

(Marcoux et al., 2009; Watt et al., 2019) of narwhal and indicates a fission-fusion structure similar to other Arctic *Delphinidae* species.

CHAPTER 2:

A global review of cetacean mortality due to ice entrapments

ABSTRACT

Ice entrapments constitute a significant source of natural mortality for cetaceans, and climate change is altering sea ice dynamics so entrapments may become more frequent. For polar cetaceans that are adapted to heavy ice conditions, rapid changes in ice formation could mean an increased chance of entrapment and a significant loss to their already threatened population. Ice entrapments will also threaten species and populations who have little experience with ice-covered habitats as they expand their range toward the poles. One hundred and thirty-eight references were reviewed globally for this literature review. I found that from 1738 to the present, 20,178 individual cetaceans from 13 species were killed in documented ice entrapments.

INTRODUCTION

In wildlife conservation and species management, knowledge about organisms' mortality is essential to understanding population dynamics and predicting the future of species. Today, climate change is adding complications that will have unknown consequences for animals that are adapted to ice-covered climates and have long lifespans. For example, ice entrapments are one of the only naturally occurring mass mortality events for cetaceans, and they may be happening more frequently with increasingly unpredictable ice patterns (Siegstand and Heide-

Jørgensen, 1994). In a typical ice entrapment, rapid ice forms and traps cetaceans below or near the shore so they cannot freely swim away—trapped cetaceans eventually drown or starve if escape or intervention is not possible (Hobbs, 2019; Heide-Jorgensen, 2022) (Figure 1.1). Ice entrapments have occurred throughout the evolutionary history of cetaceans and today mostly occur in polar waters (Taylor, 1957). Historical records have described ice entrapments that have stranded anywhere from 1-4000+ cetaceans at a single time and entrapments have been reported for most Arctic cetaceans species (Siegstad, 1994). The immediate cause of ice entrapments has been noted to have possible links to storms or seismic activity, but often causes are unknown (Heide-Jørgensen, 2002; Heide-Jørgensen, 2013).

Narwhal and beluga are the two most entrapped species and face different challenges from ice entrapments. Narwhal and beluga are members of Monodontidae and their ranges circumvent the Arctic and where they are subject to managed hunts in Canada, Russia, the United States, Iceland and Greenland (Heide-Jorgensen, 2018). While both species are listed by the IUCN as least concern and have populations over 125,000 individuals respectively, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), has populations of both species listed as endangered or threatened due to increased Arctic mining and industry associated pollutants, boat strikes, and climate warming (Lowry et al 2017; Heide-Jorgensen, 2018; Williams et al, 2011; COSEWIC, 2024; COSEWIC, 2020). While these species are adapted to life with high ice cover, they are still subject to large population losses because of ice entrapments (Harrington, 2008). The most famous ice entrapments in the 20th century with losses of more than 1000 individuals per entrapment were all beluga and narwhal entrapments (Watt et al, 2015; Heide- Jørgensen, 2013).

Orca face unique challenges due to ice entrapments. Orca are rated as data deficient by the IUCN, but some populations are rated as endangered and threatened within Canada (COSEWIC, 2024; COSEWIC, 2020; COSEWIC, 2023; Esteban, 2019).Their physiological adaptations are different than ice-adapted narwhal and beluga with long dorsal fins and distinct coloration (Lefort et al, 2020). While the species has been recorded in the Arctic since the 19th century (Higdon et al., 2009), they have increased in numbers recently during ice-free seasons. As a sub-Arctic species, orca are not will suited to sea ice, but today, ice melt has opened up once restricted areas. Orca likely cannot assess climatic cues regarding sea ice change and become ice entrapped more frequently in those newly opened areas.

While ice entrapments can cause significant losses to cetacean populations, there is still a gap of knowledge regarding how ice entrapments vary through time, the relative frequency of occurrence of ice entrapments, and what the most vulnerable species and locations for ice entrapments are. In order to better understand ice entrapments, we reviewed 138 references to summarize ice entrapments in a literature review for conservation and management efforts.

METHODS

Ice entrapment data was gathered from an extensive search of scientific databases [Web of Science, Google Scholar, BIOSIS Preview, JSTOR, the University of Manitoba Library System (used to access DFO materials not accessible elsewhere)]. The keywords “whale ice entrapment”, “whale *savassat*” (savassat is an inuit term, now used in English for cetacean ice entrapment), “ice mortality whale”, and similar phrases including all cetaceans species were used. The full list of search terms is included in Appendix 1. It was considered an ice entrapment if the cetaceans were entrapped in ice and there was at least one mortality. Only papers in

English or with an immediate translation available were used in the research. Anonymous references and news articles were included if they were also cross-referenced in other literature reviews of cetacean ice entrapments.

For each ice entrapment, the following variables were recorded: reference, link to reference, species, number of cetaceans entrapped, latitude and longitude of the entrapment, first date of entrapment, last day of the entrapment, number of cetaceans harvested, how the cetaceans were harvested, number of cetaceans that escaped the entrapment, predation, samples collected, source of information (literature, oral history etc), reason entrapped, and type of ice.

Uni et al. (2005) separated ice-related mortality events into four categories: “brash-ice type”, “blockage-type”, “re-touch type”, and “fast-ice” entrapment. Brash ice-type are events where cetaceans are pushed towards shore by pack ice and trapped in between the shoreline and the ice which is more than 2 meters across (Environment Canada 2005). Blockage-type entrapments are where cetaceans are entrapped in the middle of an offshore icepack. A re-touch type entrapment is where several ice floes are pushed together and cetaceans are entrapped under ice cakes or rafted ice (Uni et al, 2005). Lastly, a fast-ice entrapment occurs in channels or bays where a rapid change in weather causes ice to form rapidly (Uni et al., 2005).

The ice entrapment data was analyzed and visualized in R (version 2023.06.2+561) using the ggplot2 and maps packages (Wickham, 2016). The complete data compilation is available in Appendix 1.

These results are limited due to language and reporting biases. We only included papers that were written in English or had an English translation, so many papers written in non-English papers were not included. Additionally, there is likely a reporting bias as large entrapments or entrapments in unusual areas and conditions may be seen as remarkable and reported in literature or news outlets compared to ice entrapments with only a few cetaceans or in an area where ice entrapments happen more frequently, so reporting would not be deemed important.

RESULTS:

One hundred thirty-eight instances of ice entrapment mortality were compiled for this chapter which recorded 20,178 individual entrapped cetaceans from 1738 to present. From 1700-1799, 1,135 cetaceans were recorded to have been killed in ice entrapments. From 1800-1899, 616 cetaceans were recorded to have been killed in ice entrapments; from 1900-1999, 17,028 cetaceans were recorded to have been killed in ice entrapments; and from 2000-2024, 1,606 cetaceans were recorded to have been killed in ice entrapments.

Most ice entrapments involved 100 or less individuals (n=106; where n is the number of entrapments), but several reports indicated entrapments of hundreds and thousands. There were five entrapments of between 200 and 300 cetaceans, four entrapments of between 300-400 cetaceans; and 3 entrapments of between 400 and500 individuals. Finally, there were five entrapments of more than 1000 individual cetaceans. The highest mortality in a single entrapment occurred in 1984 when approximately 4000 beluga cetaceans (*Delphinapterus leucas*) were entrapped in Seniavin Straight, Russia; that entrapment was one of three separate entrapments from 1955 to 1984 that each killed more than 3000 beluga in Greenland and Russia. Several occurrences of single individual ice entrapped cetaceans (n=11) were reported around the world.

In total, 13 species of cetaceans were found to have been ice-entrapped. The most entrapped species were narwhal (n=40), beluga (n=37), white beaked dolphin (n=16), and orca (n=19). Other species such as blue whales, bowhead, common dolphins and rorquals were also reported (Figure 1.2).

Cetaceans were regularly harvested from the ice entrapped populations (n=24), with the maximum harvest of 629 narwhal reported in 2008 from the Pond Inlet stock (Laidre et al, 2012). A few reports had some cetaceans escape the entrapments (n=17), with white beaked dolphins (n=8), narwhal (n=5), orca (n=5) being the most common to escape ice entrapments. The maximum number of escapees was 25 individuals (Ledwell et al., 1994). In some ice entrapments, the cetaceans were predated and killed by polar bears (n=9), no other predators were reported.

Both hemispheres were researched, although only 4 of the 138 entrapments were reported in the Southern Hemisphere (Figure 1.2). The most common countries of ice entrapment occurrence were Greenland (n=71), Canada (n=51), Japan (n=7), United States of America (n=4) and Antarctica (n=4). Several locations had multiple entrapments, notably Disko Bay, Canada and Aasiaat, Greenland. Only the entrapments in Japan were outside the polar latitudes. Of the reports that reported ice type (n=44), the most common ice type was fast ice (n=17), followed by brash-ice (n=11), re-touch ice (n=10), and lastly blockage ice (n=6).

The earliest entrapment reported occurred in 1738 and the most recent was reported in 2018 (Figure 1.4). Most of the entrapments occurred in the spring, with February being the most common month (n=41), followed by April (n=26) and March (n=25). More ice entrapments occurred in the spring (n=51) than in the fall (n=7) or winter (n=18). No ice entrapments were reported in the summer between June and September at any location or in any year. On average, ice entrapments lasted 33.8 days, with the first day reported as a day of human discovery. Several ice entrapments lasted more than four months (n=6), with entrapment of bowhead and beluga cetaceans reported in 1999 as seven months long. In many cases, it is expected that the ice entrapment lasted longer than what was reported.

DISCUSSION

This review shows that ice entrapments are a source of mass mortality in cetacean species and can occur under a variety of ice-forming conditions. Notably, in ~88% of entrapments that were recorded (n=122), no cetaceans escaped, with individuals starving and drowning over the course of weeks to months, being predated, or harvested.

Thirteen species of cetaceans were recorded to be ice-entrapped, five of which are common Arctic cetaceans, with beluga and narwhal entrapped in the highest numbers (Figure 1, Figure 3). We believe this is likely due to the fact that they are small Arctic animals that spend the majority of their lives around and under ice, but they do not have adaptations to break through ice like the bowhead whale's thick skull.

Non-Arctic residents but Arctic visitors such as orca, humpbacks, and blue whales were also commonly ice-entrapped. Size was not an obvious determining factor in ice entrapment susceptibility as cetaceans as small as white-beaked whales (~170 kg) to blue whales (~ 150,000 kg) were entrapped. With respect to blue whales, 18 individuals were killed in four separate ice entrapments off of Newfoundland and Labrador between 1986-2014 (Ledwell et al., 1986; Ledwell et al., 2014)). With a total population in the Northern Atlantic of around 250 individuals, a loss of 18 otherwise healthy and possibly reproducing individuals can be a detrimental loss to the species (Koubrak et al, 2022).

Reviewing the number of ice entrapments over time, we cannot conclude that the increase of ice entrapments in the 20th century is due to climate change because of the large reporting bias. Yet, as climate change continues to expand species ranges that were once restricted by ice cover, we predict that ice entrapment of both non-Arctic and Arctic species could become increasingly prevalent (Lefort, 2020; Marcoux, 2019). With ice cover decreasing, species that were once only summer visitors to the Arctic can use the Arctic more often as the ice-free season lengthens but may not be evolved to understand environmental cues for ice formation and become entrapped. Similarly, species that have evolved with ice entrapments may continue to become ice entrapped because environmental cues that they relied on to escape ice may no longer be reliable.

Ice entrapments may also become more common with increased industrialization and mining in polar regions. Some reports indicate that the cetaceans become disturbed by mining blasts, loud outboard motors, or seismic occurrences (Siegstad et al, 1994). More research should investigate the anthropogenic causes of ice entrapments in order to reduce preventable ice entrapments from increased industry in once inaccessible locations.

Although ice entrapment rescues have occurred with locals cutting holes in the ice, the remote and extreme nature of the habitats often makes the rescues cost-prohibitive and long-term results are not always successful on their own. Famously, Operation Breakthrough, in which three gray whales were rescued from an ice entrapment in Point Barrow, Alaska, cost over $1,000,000.00 USD in 1988 and failed when one of the three whales died days after rescue and the other two whales were never seen or tracked again (Livingstone, 2023). Ice entrapment rescues are reportedly difficult because of the often-extreme weather conditions, remote locations, and lack of ice-breaking boats and have often been reported as unsuccessful.

Therefore, ethical and monetary costs should be heavily considered before a rescue attempt is made.

Lastly, the impact of hunting on the same species of cetaceans is another stressor that should be considered in conjunction with ice-entrapped cetacean mortality. Between 1900-1999, it is estimated that 2.9 million cetaceans were harvested globally for human consumption and/or oil (Rocha et al, 2014). Compared to the ~18,000 cetaceans killed in ice entrapments during the same time range, the population losses due to ice entrapments pale in comparison. However, when compared to the later part of the 20th century, ~3,700 cetaceans were hunted globally from 1990-1999 (Rocha et al, 2014); while 1,169 were documented to have been ice entrapped in the same time range. While historically, ice entrapments may not have had the same impact on populations as hunting has, we may be reaching a point where they have similar impacts and should be considered jointly when managing populations. Similarly, when cetaceans are ice-entrapped, and escape is not possible, humane harvests of the entrapped populations should be prioritized to reduce overall mortality.

In the case of future entrapments, within 24 hours of the discovery of an ice entrapment, a report should be made to both the local and/or national government to verify that the entrapment is occurring and to determine if escape or rescue efforts are possible. Historic records, like those compiled in this chapter, should be referenced to decide if past ice entrapments with the species and location resulted in total mortality or escaped cetaceans. If rescue efforts are not possible and where culturally appropriate, a humane harvest such as those authorized in Canada or Greenland should be implemented or a humane euthanasia (described in Barco et al, 2016) would be appropriate. Environmental and ecological factors such as season, rate of decay, and potential environmental contaminants should be considered regarding euthanasia.

This literature review may serve as a resource for environmental managers looking at historical data for modern ice entrapment decisions. Figure 1.1 shows the number of ice entrapments in an area, and Table 1 shows the species entrapped and the outcome. This type of information may help inform those making decisions on whether to euthanize threatened species or hope for an escape.

Scientists and conservationists already struggle to help threatened species with the added burden of climate change. Ice entrapments are and will continue to be a significant source of cetacean mass mortality, so energy should be focused on how best to manage them. This review may assist in emergency management of ice entrapments.

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Figure 1.1: Image of beluga whales entrapped in Lancaster Sound in May of 1999 (Heide-Jørgensen et al, 1999)

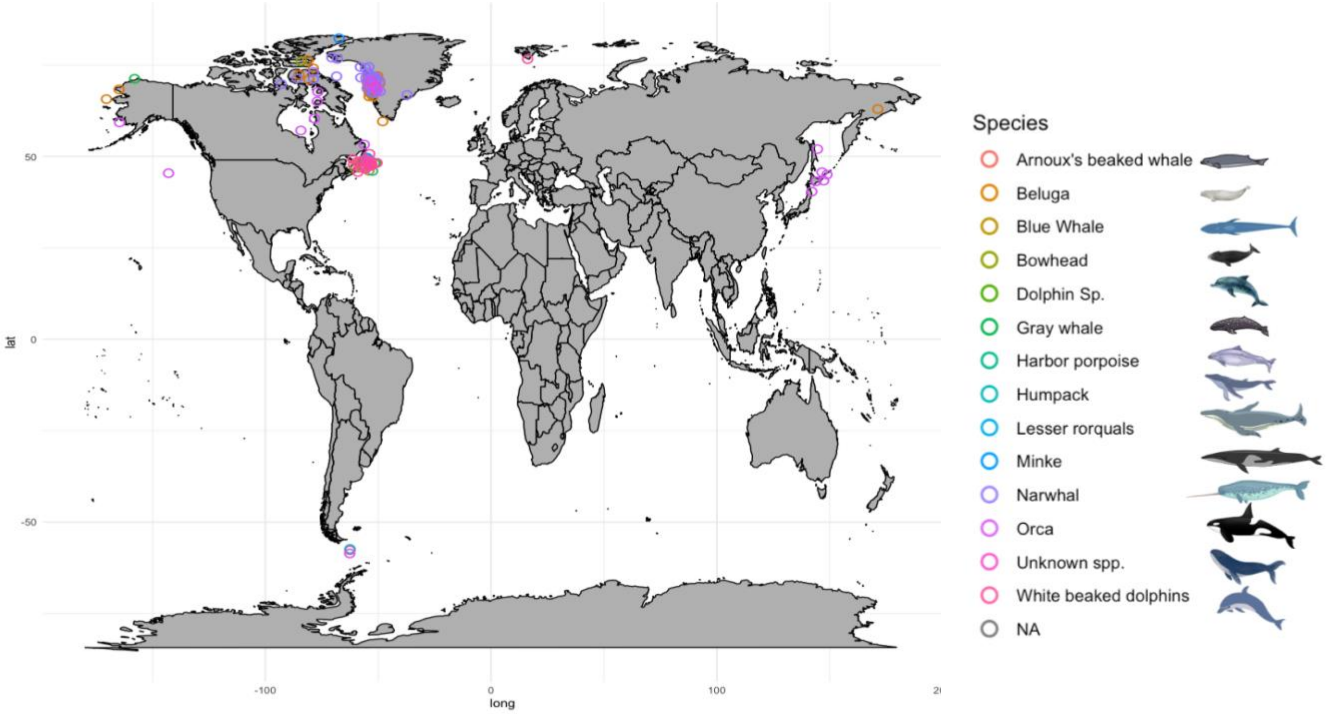

Figure 1.2: World map of ice entrapments sorted by species complied by a literature review of 138 ice entrapment references. The most entrapped species were beluga (n=37), narwhal (n=40), white beaked dolphin (n=16), and orca (n=19). Other polar species such as blue whales, bowhead, common dolphins and rorquals were also reported. The most common countries of ice entrapment occurrence were Canada (n= 51), Greenland (n=71), Japan (n=7), United States of America (n=4) and Antarctica (n=4). Several locations had multiple entrapments, notably Disko Bay, Canada and Aasiaat, Greenland. Only the entrapments in Japan were outside the polar latitudes.

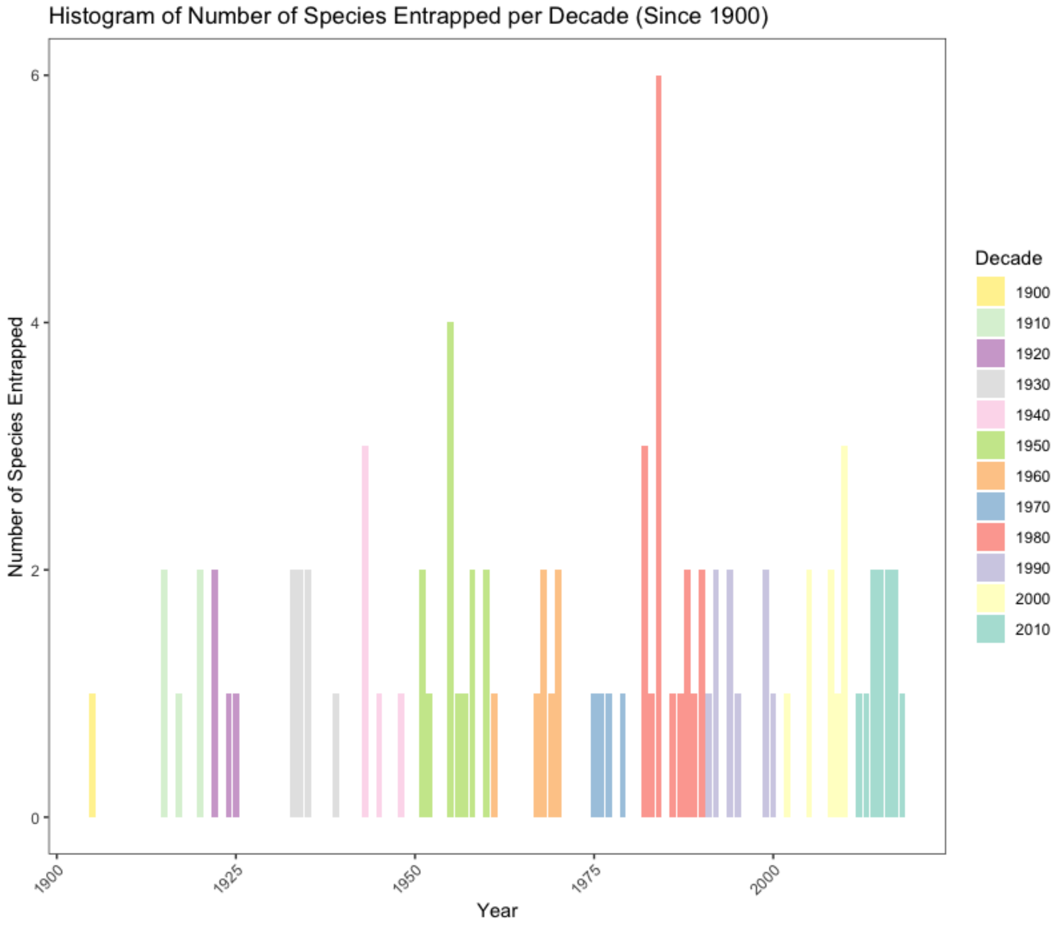

Figure 1.3: Histogram showing the number of species of cetacean that were ice entrapped per year since 1900 according to a literature review of 138 ice entrapment references. The highest mortality in a single entrapment was in 1984 when approximately 4000 beluga whales were entrapped in Seniavin Straight, Russia; that entrapment was one of three separate entrapments from 1955 to 1984 that each killed more than 3000 beluga in Greenland and Russia. In similarly high years, other large entrapments of several thousand whales occurred.

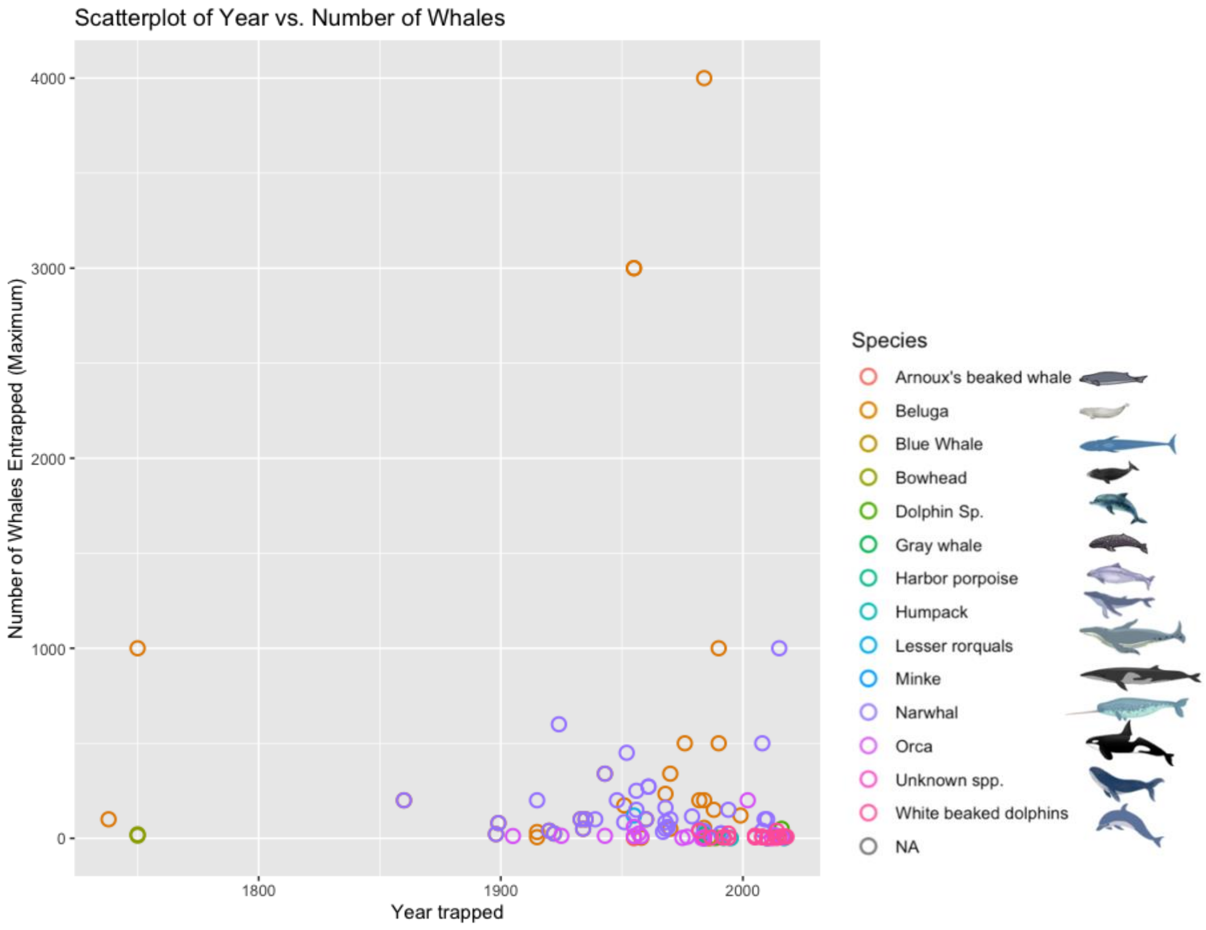

Figure 1.4: Scatterplot showing the year and the number of cetaceans ice entrapped according to a literature review of 138 ice entrapment references. The colors refer to different cetacean species entrapped.

Search Term
Ice entrapment
Ice entrapment whale
ice entrapment dolphin
ice entrapment cetecean
Ice entrapment bowhead
Ice entrapment gray whale
ice entrapment narwhal
ice entrapment belgua
ice entrapment blue whale
ice entrapment minke
Ice entrapment Orca
Ice entrapment Russia
Ice entrapment Canada
Ice entrapment USA
ice entrapment Norway
Ice entrapment Antartica
Ice entrapment Atlantic
Ice entrapment Pacific
Ice entrapment Arctic
Savassat
Savassat whale
Savassat dolphin
Savassat cetecean
Whale trapped in ice
Dolphin trapped in ice
cetecean trapped in ice
bowhead trapped in ice
gray whale trapped in ice
narwhal trapped in ice
beluga trapped in ice
blue whale trapped in ice
minke trapped in ice
orca trapped in ice
whale ice moraltiy
dolphin ice mortality
cetecean ice mortality
bowhead ice mortality
gray whale ice mortality
narwhal ice mortality
beluga ice mortaltiy
blue whale ice mortality
minke ice mortality
orca ice mortality

Appendix 1: An inclusive list of the search terms used in the Chapter 2 literature search.

Appendix 2: Chart of 138 references of cetacean ice entrapments globally.

PAPER	Species	Country	N min	N max	Year	Escapees	Harvest	Lost	Ice type
Taylor, 1957.	Arnoux's beaked whale	Antartica	1	1	1955	na	1	0	fast ice
Taylor, 1957.	Lesser rorquals	Antartica	129	120	1955	na	na	120	fast ice
Taylor, 1957.	Orca	Antartica	60	60	1955	na	na	60	fast ice
Higdon and Ferguson	Orca	Canada	5	12	19-Mar	na	2	na	na
Degerbøl, M. and Fre	Narwhal	Canada	600	600	1924	na	406	na	brash
Westdal et al, 2017	Orca	Canada	11	12	1955	na	2	5	fast ice
Dearden, J. C., 1958	Orca	Canada	25	25	1957	na	na	na	brash
Heide-Jørgensen, M.	Beluga	Canada	3	3	1958	na		na	na
Mitchell, 1988	Orca	Canada	2	2	1975	na	na	na	brash
Heide-Jørgensen, M.	Narwhal	Canada	115	115	1979	na	na	na	
Lien, J. et al, 1982.	White beaked dolphins	Canada	40	40	1982	na	na	40	na
Lien et al, 1988	Orca	Canada	1	1	1983	na	na	died	na
Lien, J., et al, 1984.	Harbor Porpoise	Canada	18	20	1984	na	na	17	na
Lien, J., et al, 1984.	Harbor Porpoise	Canada	20	25	1984	na	na	22	na
Lien, J., et al, 1984.	Minke	Canada	1	1	1984	yes	na	na	na
Lien, J., et al, 1984.	Minke	Canada	3	3	1984	3	na	0	na
Lien, J., et al, 1984.	Unknown spp.	Canada	1	1	1984	na	na	1	na
Lien, J., et al, 1986.	Blue Whale	Canada	3	3	1986	1	na	3	na
Lien, J., et al, 1986.	Blue Whale	Canada	1	1	1986	na	na	1	na
Lien et al. 1987.	White beaked dolphins	Canada	4	4	1987	na	na	4	na
Ledwell et al, 1989.	Blue Whale	Canada	2	2	1989	na	na	1	blockage
Lien, J. et al, 1990.	Dolphin	Canada	na	na	1990	na	na	na	na
Lien, J. et al, 1990.	Dolphin	Canada	na	na	1990	na	na	na	na
Lien, J., et al, 1993.	Harbor Porpoise	Canada	2	2	1992	na	na	5	na
Lien, J., et al, 1993.	White beaked dolphins	Canada	4	4	1992	na	na	4	na
Lien, J., et al, 1993.	White beaked dolphins	Canada	5	5	1992	na	na	5	na
Ledwell et al, 1994.	White beaked dolphins	Canada	3	3	1994	na	na	na	na
Ledwell et al, 1994.	White beaked dolphins	Canada	25	25	1994	25	na	no	na
Ledwell et al, 1995.	Humpack	Canada	1	1	1995	1	na	na	na
Heide-Jørgensen, M.	Beluga	Canada	na	na	1999	na	na	yes	fast ice
Sergeant and Willia	Beluga	Canada	120	120	1999	na	17	100	na
Heide-Jørgensen, M.	Bowhead	Canada	na	na	1999	na	na	yes	fast ice
Ledwell, W., et al, 2	Dolphin	Canada	na	na	2000	na	na	na	na
WDCS, 2002	Orca	Canada	100	200	2002	na	yes	na	na

PAPER	Species	Country	N min	N max	Year	Escapees	Harvest	Lost	Ice type
Ledwell and Huntingt	White beaked dolphins	Canada	5	5	2005	2	na	3	blockage
Ledwell and Huntingt	White beaked dolphins	Canada	14	14	2005	7	na	8	blockage
Laidre, et al., 2012	Narwhal	Canada	200	500	2008	yes	629	na	fast ice
Ledwell and Huntingt	White beaked dolphins	Canada	5	5	2008	1	na	4	re-touch
Ledwell and Huntingt	White beaked dolphins	Canada	9	9	2008	na	na	9	re-touch
Ledwell et al, 2010.	Minke	Canada	1	1	2010	na	na	1	re-touch
Ledwell et al, 2010.	White beaked dolphins	Canada	1	1	2010	1	na	na	re-touch
Ledwell et al, 2012.	Unknown spp.	Canada	1	1	2012	na	na	1	blockage
Westdal, 2013	Orca	Canada	11	17	2013	yes	na	all	fast ice
Westdal et al, 2017	Orca	Canada	na	na	5-Jul	na	na		
Ledwell et al, 2014.	Blue Whale	Canada	12	12	2014	3	na	9	blockage
Ledwell et al, 2014.	White beaked dolphins	Canada	40	40	2014	na	na	40	re-touch
Watt et al, 2019.	Narwhal	Canada	1000	1000	2015	yes	229	20	fast ice
Ledwell et al, 2015.	White beaked dolphins	Canada	6	6	2015	no	na	6	re-touch
Ledwell et al, 2016.	Dolphin	Canada	50	50	2016	yes	na	5	fast ice
Ledwell et al, 2017.	Humpack	Canada	1	1	2017	na	na	yes	Brash
Ledwell et al, 2017.	White beaked dolphins	Canada	11	11	2017	5	na	3	brash
Ledwell et al, 2018.	White beaked dolphins	Canada	8	8	2018	8	na	na	re-touch
Mitchell, 1988	Orca	Canada	1	1	1900s	na	na	na	
Freeman, M. 1968.	Beluga	Canada	na	na	1940s	na	na	na	na
Egede, P. 1788.	Beluga	Greenland	100	100	1738	na	na	na	na
Gad, F. 1969.	Beluga	Greenland	1000	1000	1750	na	na	na	na
Eschricht, D.F. and R	Bowhead	Greenland	14	14	1750	na	na	na	
Gad, F. 1969.	Bowhead	Greenland	21	21	1750	na	na	na	na
Gad, F. 1976.	Unknown spp.	Greenland	na	na	1781	na	na	na	na
Gad, F. 1976.	Beluga	Greenland	na	na	1803	na	na	na	na
Gad, F. 1976.	Narwhal	Greenland	na	na	1803	na	na	na	na
Winge, 1902	Orca	Greenland	na	na	1840	na	na	na	na
Brown, R. 1868.	Beluga	Greenland	100	200	1860	na	na	na	na
Brown, R. 1868.	Narwhal	Greenland	100	200	1860	na	na	na	na
Kapel, F.O. 1979.	Beluga	Greenland	22	22	1898	na	na	na	na
Kapel, F.O. 1979.	Narwhal	Greenland	22	22	1898	na	na	na	na
Kapel, F.O. 1979.	Beluga	Greenland	80	80	1899	na	na	na	na
Kapel, F.O. 1979.	Narwhal	Greenland	80	80	1899	na	na	na	na

PAPER	Species	Country	N min	N max	Year	Escapees	Harvest	Lost	Ice type
Porsild, 1918	Beluga	Greenland	6	6	1915	na	na	na	na
Porsild, 1918	Beluga	Greenland	33	33	1915	na	na	na	na
Porsild, 1918	Narwhal	Greenland	na	na	1915	Yes	70	na	brash
Porsild, 1918	Narwhal	Greenland	200	200	1915	na	200	na	brash
Bertlesen, A. 1921.	Unknown spp.	Greenland	na	na	1917	na	na	na	na
Kapel, F.O. 1979.	Beluga	Greenland	40	40	1920	na	na	na	na
Kapel, F.O. 1979.	Narwhal	Greenland	40	40	1920	na	na	na	na
Kapel, F.O. 1979.	Beluga	Greenland	25	25	1922	na	na	na	na
Kapel, F.O. 1979.	Narwhal	Greenland	25	25	1922	na	na	na	na
Kapel, F.O. 1979.	Beluga	Greenland	100	100	1933	na	na	na	na
Kapel, F.O. 1979.	Narwhal	Greenland	100	100	1933	na	na	na	na
Kapel, F.O. 1979.	Beluga	Greenland	50	50	1934	na	na	na	na
Kapel, F.O. 1979.	Narwhal	Greenland	50	50	1934	na	na	na	na
Kapel, F.O. 1979.	Beluga	Greenland	100	100	1935	na	na	na	na
Kapel, F.O. 1979.	Narwhal	Greenland	100	100	1935	na	na	na	na
Anon. 1940.	Narwhal	Greenland	100	100	1939	na	na	na	na
Anon. 1943.	Beluga	Greenland	340	340	1943	na	na	na	na
Anon. 1943.	Narwhal	Greenland	340	340	1943	na	na	na	na
Siegstad et al, 1994.	Beluga	Greenland	na	na	1945	na	na	na	na
Siegstad et al, 1994.	Narwhal	Greenland	200	200	1948	na	na	na	na
Golfodnoff, M. 1956.	Beluga	Greenland	173	173	1951	na	na	na	na
Golfodnoff, M. 1956.	Narwhal	Greenland	85	85	1951	na	na	na	na
Anon. 1953-1988.	Narwhal	Greenland	450	450	1952	na	na	na	na
Anon. 1953-1988	Beluga	Greenland	3000	3000	1955	na	na	na	na
Golfodnoff, M. 1956.	Beluga	Greenland	3000	3000	1955	na	na	na	fast ice
Hadrup, G. 1971.	Narwhal	Greenland	250	250	1956	na	na	na	na
Knudsen, H. 1958. Frc	Narwhal	Greenland	100	150	1956	na	na	na	na
Anon. 1961	Beluga	Greenland	100	100	1960	na	na	na	na
Anon. 1961	Narwhal	Greenland	100	100	1960	na	na	na	na
Kapel, F.O. 1979.	Narwhal	Greenland	272	272	1961	na	na	na	na
Siegstad et al, 1994.	Narwhal	Greenland	272	272	1961	na	na	na	na
Siegstad et al, 1994.	Narwhal	Greenland	34	34	1967	na	na	na	na
Berliner, F. 1968.	Beluga	Greenland	234	234	1968	na	na	na	na
Berliner, F. 1968.	Narwhal	Greenland	161	161	1968	na	na	na	na

PAPER	Species	Country	N min	N max	Year	Escapees	Harvest	Lost	Ice type
Kapel, F.O. 1979.	Narwhal	Greenland	50	50	1968	na	na	na	na
Kapel, F.O. 1979.	Narwhal	Greenland	84	84	1968	na	na	na	na
Haller, A.A. 1986.	Narwhal	Greenland	60	60	1969	na	na	na	na
Siegstad et al, 1994.	Narwhal	Greenland	na	na	1969	na	na	na	na
Anon. 1970a.	Beluga	Greenland	340	340	1970	na	na	na	na
Kapel, F.O. 1979.	Beluga	Greenland	50	50	1970	na	na	na	na
Kapel, F.O. 1979.	Narwhal	Greenland	100	100	1970	na	na	na	na
unpublished data - Si	Beluga	Greenland	500	500	1976	na	na	na	na
Siegstad et al, 1994.	Beluga	Greenland	50	200	1982	na	na	na	na
Siegstad et al, 1994.	Narwhal	Greenland	45	45	1982	na	na	na	na
Anon. 1984.	Beluga	Greenland	200	200	1984	na	na	na	na
Siegstad et al, 1994.	Beluga	Greenland	20	20	1984	na	na	na	na
Siegstad et al, 1994.	Narwhal	Greenland	38	38	1984	na	8	25-30	na
Siegstad et al, 1994.	Beluga	Greenland	100	150	1988	na	100	na	na
Anon. 1990a	Beluga	Greenland	500	500	1990	na	na	na	na
Siegstad et al, 1994.	Beluga	Greenland	300	1000	1990	na	400	na	fast ice
Tobiassenet al, (1994	Narwhal	Greenland	26	26	1991	na	na	na	na
Siegstad et al, 1994.	Narwhal	Greenland	26	26	1991	na	26	1	na
Heide-Jørgensen, M.	Narwhal	Greenland	150	150	1994	na	100	50	fast ice
Laidre, et al., 2012	Narwhal	Greenland	30	40	2008	na	80	na	fast ice
Laidre, et al., 2012	Narwhal	Greenland	50	100	2009	yes	38	na	fast ice
Laidre, et al., 2012	Narwhal	Greenland	30	100	2010	yes	35	na	re-touch
Siegstad et al, 1994.	Beluga	Greenland	na	na	1920-1930s	na	na	na	na
Uni et al, 2017.	Orca	Japan	13	13	1925	2	11	na	brash
Yamada, 2000	Orca	Japan	13	13	1943	na	na	na	brash
Uni et al, 2017.	Orca	Japan	10	10	1958	3	8-Jan	na	brash
Uni et al, 2017.	Orca	Japan	8	8	1977	na	8	na	fast ice
Amano, Masao, et al.	Orca	Japan	9	9	2005	2	yes	no	re-touch
Uni et al, 2017.	Orca	Japan	4	5	2016	4	na	na	brash
Uni et al, 2017.	Orca	Japan	5	5	na	na	yes	na	na
Aars, Jon, et al. 2015	White beaked dolphins	Norway	2	2	2014	na	na	2	fast ice
Mymrin, 1999	Beluga	Russia	3000	4000	1984	na	na	na	na
Burns and Seaman, 1	Beluga	USA	40	55	1984	na	na	48	na
Burns and Seaman, 1	Beluga	USA	na	na	1984	na	na	numerous	na

PAPER	Species	Country	N min	N max	Year	Escapees	Harvest	Lost	Ice type
Lowry et al, 1987	Orca	USA	5	5	1984	na	na	na	re-touch
Sullivan, 2002.	Gray whale	USA	3	3	1988	2	na	1	blockage

CHAPTER 3:

Narwhal Ice Entrapment Sociality: Using Microsatellite Genomics to Infer Narwhal Social Structure

ABSTRACT: For reclusive Arctic species like narwhal, a high degree of sociality has been assumed, but their specific social structure is poorly understood. Their ice-covered habitat has shielded the species from long-term observation and has granted only glimpses and limited visual observation of potential narwhal social structure in the summer months. In November 2008, more than 600 narwhal were entrapped off of Eclipse Sound and were humanely harvested by surrounding communities. Nearly 250 tissue samples were collected and banked at the Department of Fisheries and Oceans. The data was genotyped at 12 microsatellite loci and kinship was calculated with a Lynch and Ritland estimator. Using network matrix analysis, we constructed a social network for narwhal in that entrapment which had a herd size of 245 individuals with 8 clusters of an average size of 30.6 individuals, then was filtered to the first, second and third-order relatives. This research indicates that narwhal may follow fission-fusion social structure and may be useful in narwhal stock management and social history evolution.

INTRODUCTION

All members of *Delphinidae* are known for their social behavior such as the eeks and shrills of their vocal communication, their large pod communities, and the presence of menopause in *Mondontidae* species (Gowans et al., 2007). All of these adaptations suggest that in their evolutionary history, social behavior was beneficial and selected for, and that disrupting whale pods can have negative impacts on the entire pod (Williams et al., 2006). Unlike other more accessible species, studies of narwhal social structure are made difficult by their extreme habitat, which limits direct observation and long-term study of identifiable individuals.

Climate change and hunting pressures have placed narwhals amongst the most vulnerable Arctic species (COSEWIC, 2024). Early studies on narwhal social structure have produced varying results about narwhal kinship, pod size, and other intraspecies interactions (Watt et al, 2015). These visual studies have described narwhal social structure as being cluster and herd-based. A cluster is the most basic unit made up of 1-25 individuals of mixed sex and age (Marcoux et al, 2009). A herd consists of many clusters and can be tens or thousands of individual narwhal (Marcoux et al. 2009). Kinship, or the degree of relatedness between individuals, has not been thoroughly studied in a narwhal herd or cluster (Watt et al, 2015).

Narwhal have been thought to follow a fission-fusion social structure, but more concrete data is needed (Watt et al, 2015). Bottlenosed dolphins (*Delphinus truncatus)* and white-beaked dolphins are classic examples of highly social cetaceans that follow fission-fusion social structure (Bertulli et al, 2021). In these examples, a larger population of dolphins separate into smaller groups of variable size, age, and sex ratio and then fuse back several times throughout the year when it is ecologically beneficial. Fission–fusion structure is beneficial in times of low resources when whales can separate and reduce hunting competition. It is beneficial in times of high food (typically in the summer months in the Arctic) when the smaller groups can fuse together for more efficient group hunting and mating (Aureli, 2008; Connor, 2000; Tsai et al., 2013).

Genetic kinship has been used to determine relatedness, build a social network of Francisca Dolphin (*Pontoporia blainvillei*), and infer social structure (Costa-Urrutia et al, 2012).

Narwhal tissue samples from a 2008 ice entrapment within the Pond Inlet Community have been sequenced at 12 microsatellite loci and represent the most extensive narwhal pod sampling possible to date. This allowed us to ask the question: what is the narwhal social structure within a pod? How does relatedness reflect broader social structure? We hypothesize that as described in literature with visual observation, within the pod there will be a high degree of kinship between individuals in the same cluster and that the overall herd will have several clusters of differing relatedness.

METHODS

Sample collection:

On November 15, 2008, a pod of narwhal was entrapped from the Pond Inlet, Eclipse Sound stock and discovered within a pressure ridge 17 km from shore. The temperature was decreasing to nearly -32 °C , and the closest open water was more than 50 km away, so Fisheries and Oceans Canada (DFO) and local officers authorized a humane harvest of the entrapped whales (Laidre, 2012). From November 19 - December 2, 2008, 629 whales were harvested with a recorded 68 calves, 210 juveniles, and 288 adults (Laidre, 2012) (Figure 2.1).

Of those harvested whales, 276 blubber and skin samples were banked at the Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, Manitoba. All samples were stored frozen at -20 °C until analysis. DNA was extracted from the tissue samples using DNeasy spin columns (Qiagen Inc.) using kit and manufacturer protocols at the Assiniboine Zoo Conservation Genetics Lab. Molecular sex was then determined using Shaw et al. (2013) universal primers for X and Y chromosomes on PCR as done for narwhal in Petersen et al. (unpublished data), which resulted in 202 females and 48 males. The tissue samples (n=276) were then genotyped using microsatellite loci developed for cetaceans (Ev14, FCB1, 3, 4, 5, 10, 13, GT39, KWM2, 12, MK8, 9) as previously used for narwhal in Watt et al (2015).

We cannot directly observe narwhal social networks, so we will use genetic relationships to estimate social network structure. We used the microsatellite data to calculate relatedness among the entrapped whales using a Lynch and Ritland estimator which is commonly used to determine the relatedness between individuals in populations where allele and microsatellite repetition frequency can be estimated (Lynch and Ritland, 1999; Van de Casteele, et al., 2001). To build a network, we then used pair-wise relatedness functions in GenalEX 6.1 to determine the relationships between all individuals in the entrapment (Peakall and Smouse 2006, 2012). We removed the zeroes, and the remaining data (n=245) was then filtered to first (0.5), second (0.25) , and third-order (0.125) relatives.

To understand the family groups determined by the pairwise relatedness factors, we used a clustering algorithm to build a network of relatedness within the population. Under the definition that a cluster determines a family group within the larger herd, we used the fast-greedy clustering algorithm in iGraph 2.0 (Csardi, 2024). This algorithm builds clusters by looking for groups with more links within than between. To visualize the size and differences between family groups, the clusters were determined with the first, second and third order relative filters from the previous paragraph. The clusters were graphed onto matrixes to determine cluster structure where individuals were nodes linked by their degree of relatedness and the total amount of related individuals determined the internal clusters of the herd (Csardi, 2006; Csardi et al, 2023). In order to see the alignment of the microsatellite genetic strategy with historic observation based social network research, the data was then compared against existing narwhal social structure literature.

RESULTS

Pairwise relatedness for all of the individuals had a range of 0.001-0.5 (mean=0.055, number of pairs=22,367). Within the herd, there were 20 first order pairs, 280 second order pairs, and 1192 third order pairs. Within the kinship network based on links without pruning, the genotyped samples (n= 245) were calculated to have eight genetically related family groups (clusters) with an average group size of 30.6 individuals and a M/F sex ratio of 0.24 for the entire herd. The relatedness matrices (Figure 2.2) were based on first (r=0.5, siblings), second (r=0.25, cousins) and third-order (r=0.125, second cousins) relatives and determined the internal clusters of the entrapped Eclipse Sound herd at each degree of relatedness (Figure 2.2). Within the first-order cluster, there were 19 clusters with a group size of 1.05 individuals and an M/F sex ratio of 0.57. In the second-order cluster, there were 45 groups with an average size of 3.5 individuals and a sex ratio of 0.23, and in the third-order cluster, there were 9 clusters with an average group size of 27.1 individuals and an overall M/F ratio of 0.24.

DISCUSSION

To provide evidence for fission-fusion social structure, we would expect the genotyped samples to represent a variety of degrees of relatedness in each cluster and have a relatively evenly distributed cluster size within the overarching herd. In other social cetaceans, the social structure has been examined with kinship analyses of pods or clusters, and this work supports the same results of fission-fusion structure based on clusters of small family size with mixed sex and age in this ice entrapment (Costa-Urrutia et al., 2012). In comparison with other narwhal social structure research, the average cluster size of this herd (30.6 individuals) may align with visual assessments (~9 individuals) (Watt et al., 2015) and supports the early findings of fission-fusion sociality using fatty-acid analysis (Watt et al., 2015) (Table 1).

The November 2008 ice entrapment gives us a glimpse into narwhal habits during the fall and winter months. The combined presence of males and females, in addition to adults and juveniles, indicates that neither sex disperses from their parents and, at least in the fall months, they travel as a mixed-sex group. In some instances, all-male narwhal groups that were identified by the presence of tusks have been spotted in the summer months in large congregations (Marcoux et al, 2009). This work may indicate that those observations and occurrences were a behavior in which males separate from their herd for hunting or mating competition. Behavioral congregations like that further support the fission-fusion social structure.

Although this entrapment (0.24 M/F) is within the range of observed sex ratios (0.22 M/F) of other microsatellite ice-entrapped populations (Watt et al., 2015) (Table 1), we suspect bias in sampling. Male narwhal have a higher myoglobin content and a higher ratio of slow twitch oxidative fibers than female narwhal and thus a better ability to swim farther and deeper to escape ice entrapments (Williams et al, 2011). We would expect that the sex ratio for a non-entrapped herd would include more males. In previous entrapments, there was a bias towards harvesting narwhal with tusks, which are predominantly male (Porsild, 1918). Similarly, the 2008 entrapment harvest period was confined to a three-day period because of harsh weather conditions, so they possibly harvested more males with tusks and a higher volume of meat despite no reported bias (Laidre, 2012). Additionally, the sex ratio for the 2008 entrapment (.24) differs from visual survey sex ratios (90% single-sex and .72-1.44) (Marcoux et al., 2009; Cousens et al., 1991). This may indicate an entrapment bias or a reporting bias from visual surveys that fail to consider male narwhal without tusks and female narwhal with tusks.

Although this sample represents the largest genetic-based social study of the narwhals to date, sampling from an ice-entrapped group of whales is inherently biased. While inherently difficult to accomplish, an ideal study would use tissue from herds in the summer months and also winter months to better understand the role of resource availability. A simpler study would be to combine genetic samples across several ice entrapments within the same narwhal stock and compare kinship and infer social structure from the entire group.

From a conservation perspective, research has shown that disrupting the social structure in orca has had a significant impact on the survivability of the entire group (Busson et al., 2019). In this study, individual whales were killed by fishermen who thought the whales were eating their catch while simultaneously researchers studied social structure and hierarchy in the same pod. The study found that in social groups (pods) where individuals are killed or lost, the surviving members are less associated and have reduced fitness (Busson et al, 2019). While this research has not been repeated in narwhal, their similar highly social nature indicates that sociality is important for their survival and that it may be an important part of future management of decreasing populations. Understanding social structure can help population managers understand the population-level consequences of the loss of individuals to harvest. As with the other member of Monodontidae, beluga, a matrilineal hierarchy would suggest limiting the harvest of the oldest and likely highest-ranking females (O’Corry-Crowe et al., 2020).

Although narwhal are not an endangered species, they are one of the most threatened species due to climate change (Laidre et al, 2005). Narwhal are facing unique challenges like increasing predation from species whose ranges are increasing alongside decreasing ice cover (Lefort, 2020), decreasing food species and supply as dietary a specialist (Watt, 2013), and increasing human presence in their once isolated habitat. With those external pressures, it is predicted that narwhal will continue to follow ice deeper and deeper into the Arctic until their habitat and arctic prey are so reduced that species reaches the point of extinction (Chambault, et al 2020).

With the added challenge of climate change and increased industry and human presence in the Arctic, we may reach a point where each individual in a population matters for the survival of the stock or species. A deeper understanding of narwhal social structure and kinship helps uncover the inner-workings of a herd which may be increasingly important in future management decisions for hunting and stock management.

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Figure 2.1: Photo of a narwhal harvested from the 2008 Pond Inlet ice entrapment. Taken by Brian Koonoo.

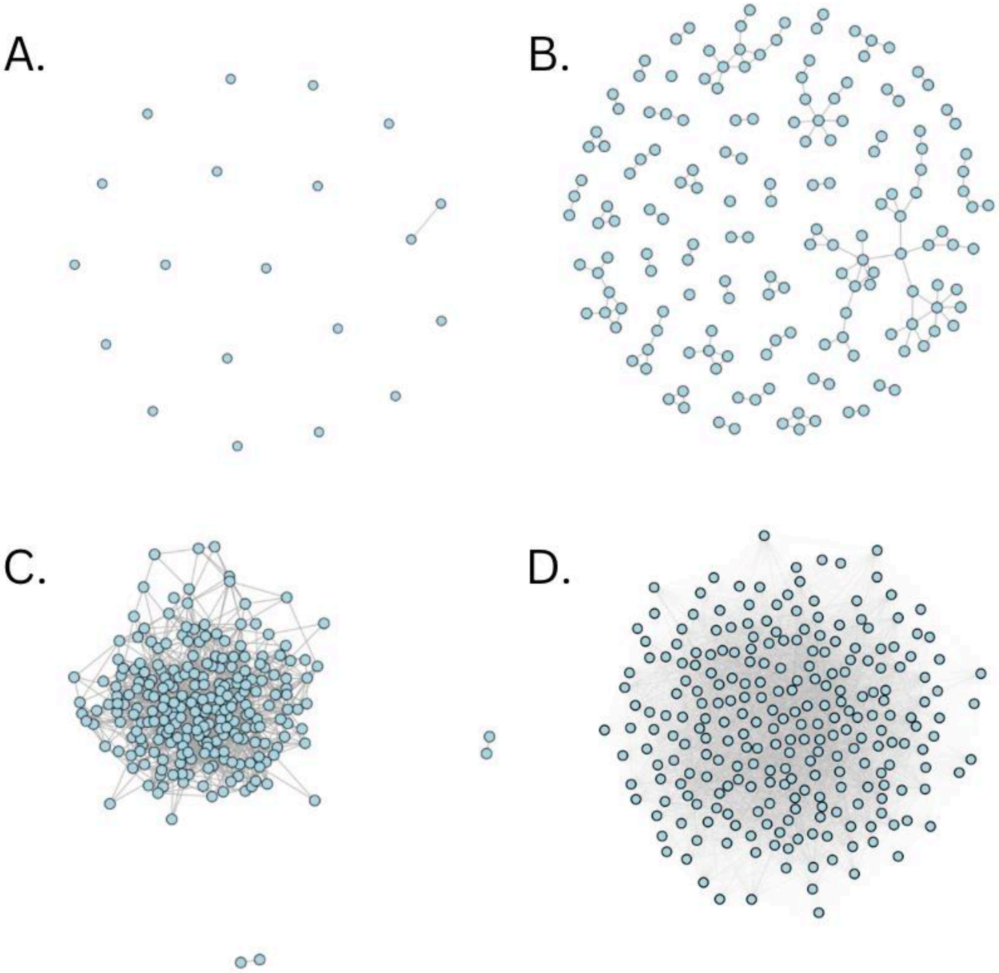
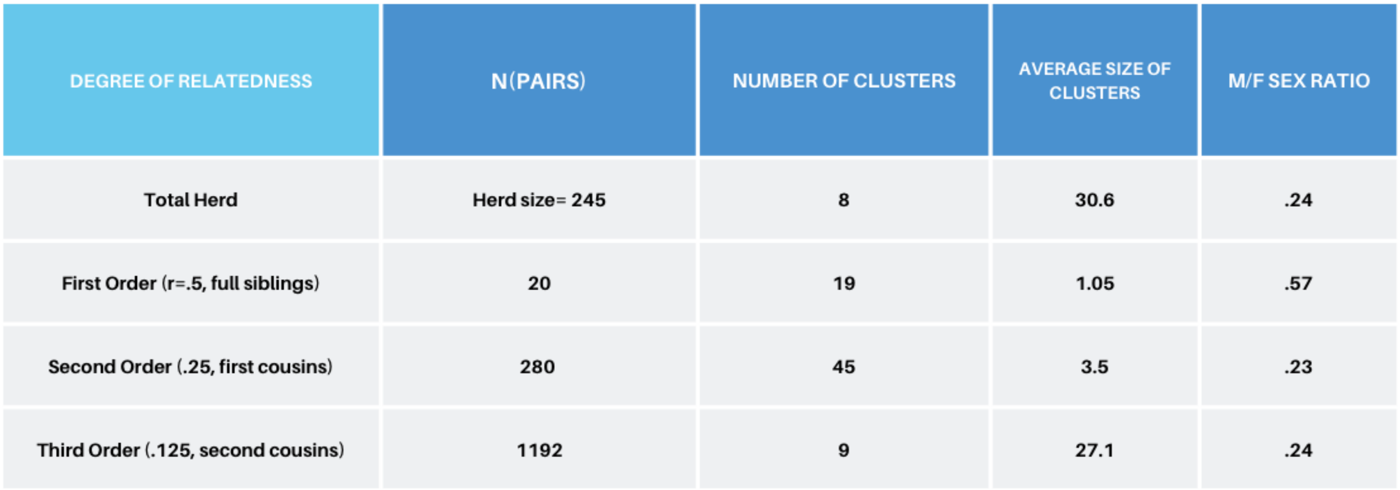
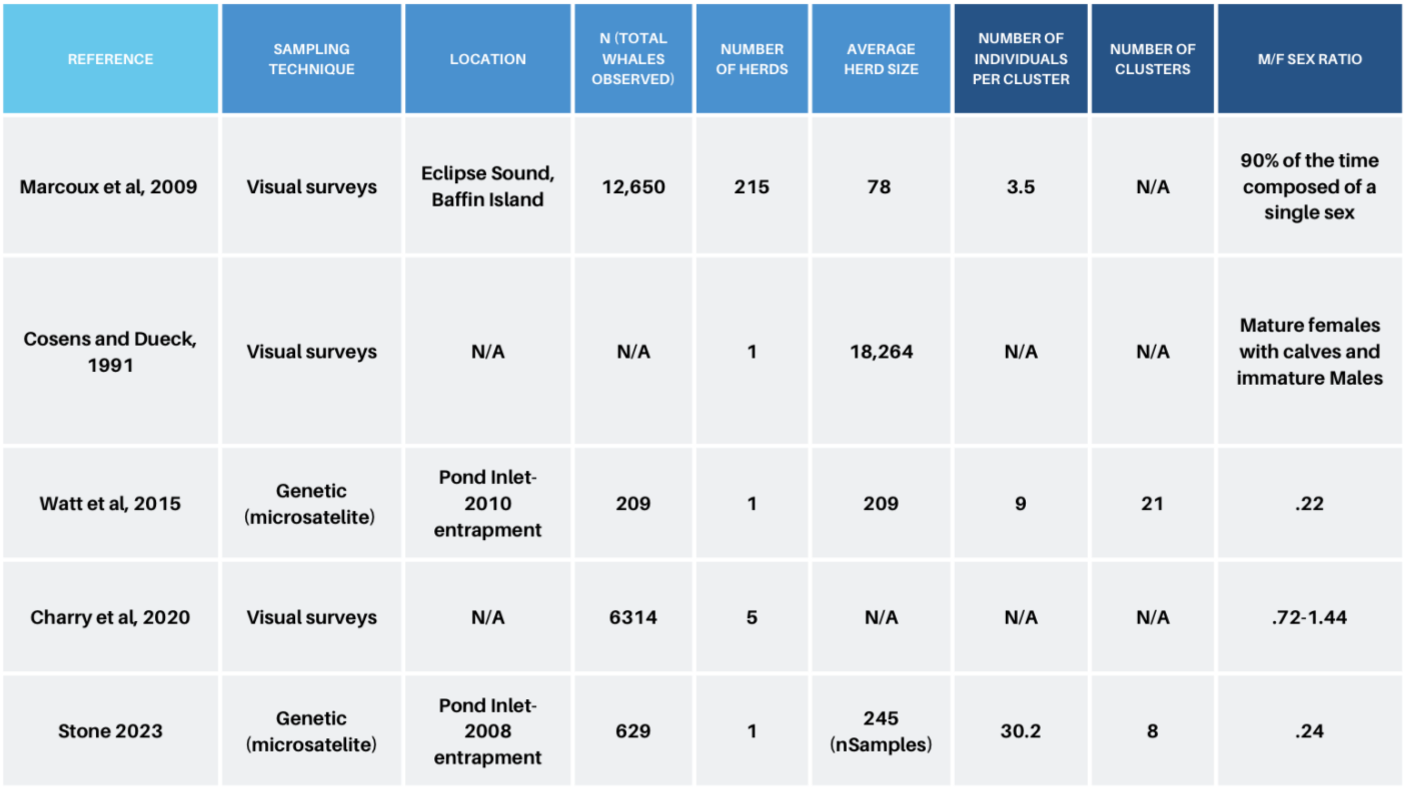


Figure 2.2: 2008 Pond Inlet ice entrapment herd clusters separated by degree of relatedness. Panel A is all first order relatives, B is second order relatives, C is third order relatives, and D is the entire herd.



DEGREE OF RELATEDNESS	N(PAIRS)	NUMBER OF CLUSTERS	AVERAGE SIZE OF CLUSTERS	M/F SEX RATIO
Total Herd	Herd size= 245	8	30.6	.24
First Order (r=.5, full siblings)	20	19	1.05	.57
Second Order (.25, first cousins)	280	45	3.5	.23
Third Order (.125, second cousins)	1192	9	27.1	.24

TABLE 1: Within the herd, there were 20 first order pairs, 280 second order pairs, and 1192 third order pairs. Within the kinship network based on links without pruning, the genotyped samples (n= 245) were calculated to have eight genetically related family groups (clusters) with an average group size of 30.6 individuals and an M/F sex ratio of 0.24 for the entire herd. The relatedness matrixes (Figure 2.2) were based on first (r=0.5, siblings), second (0.25, cousins) and third-order (r=0.125, second cousins) relatives and determined the internal clusters of the entrapped Eclipse Sound herd at each degree of relatedness (Figure 2.2). Within the first-order cluster, there were 19 clusters with a group size of 1.05 individuals and an M/F sex ratio of 0.57. In the second-order cluster, there were 45 groups with an average size of 3.5 individuals and a sex ratio of 0.23, and in the third-order cluster, there were 9 clusters with an average group size of 27.1 individuals and an overall M/F ratio of 0.24. To sum up, this information shows that within a narwhal herd, there are clusters of differing degrees of relatedness (down to immediate siblings), and the number of pairwise relatedness clusters to the first and second degree show that individuals in a herd maintain close proximity and social ties with their extended family.



REFERENCE	SAMPLING TECHNIQUE	LOCATION	N (TOTAL WHALES OBSERVED)	NUMBER OF HERDS	AVERAGE HERD SIZE	NUMBER OF INDIVIDUALS PER CLUSTER	NUMBER OF CLUSTERS	M/F SEX RATIO
Marcoux et al, 2009	Visual surveys	Eclipse Sound, Baffin Island	12,650	215	78	3.5	N/A	90% of the time composed of a single sex
Cosens and Dueck, 1991	Visual surveys	N/A	N/A	1	18,264	N/A	N/A	Mature females with calves and immature Males
Watt et al, 2015	Genetic (microsatelite)	Pond Inlet-2010 entrapment	209	1	209	9	21	.22
Charry et al, 2020	Visual surveys	N/A	6314	5	N/A	N/A	N/A	.72-1.44
Stone 2023	Genetic (microsatelite)	Pond Inlet-2008 entrapment	629	1	245 (nSamples)	30.2	8	.24

TABLE 2: Table compares narwhal sociality literature and results of Chapter 3. The sex ratio for the 2008 entrapment (0.24) differs from visual survey sex ratios (90% single-sex and .72-1.44) (Marcoux et al., 2009; Cousens et al., 1991), which may indicate an entrapment bias or a reporting bias from visual surveys. The size and number of clusters are similar to that recorded by Watt et al., 2015, another genetic survey.

DISCUSSION CHAPTER

In this thesis, I used ice entrapments to better understand whale mortality and social structure. Ice entrapments are unique occurrences that mostly occur in the polar regions that grant a glimpse into otherwise healthy whale populations (Chapter 2). Over the past 50 years, whale conservation has helped restore populations to their highest numbers in decades, but for animals that are adapted to extreme climates without significant human interference from extensive hunting or industry, a more comprehensive approach needs to be taken in order to better support the species.

This thesis contributes to global knowledge of cetaceans in two major ways:

1. Compiling global ice entrapments for emergency management reference
2. Investigation Narwhal sociality within an ice-entrapped herd

In Chapter 2, I investigate cetaceans in ice entrapments globally in order to better understand species at risk. Through a strategic literature review of 138 references, 13 different species of cetacean were ice-entrapped in the waters of more than 5 different countries in both hemispheres. From 1738 to the present, more than 20,000 whales were killed in ice entrapments. This chapter further examines the survival rate, escape rate, timing and hunts during the entrapments; and may have implications in conservation and species management.

In Chapter 3, I focus on a 2008 ice entrapment of more than 600 narwhal in Eclipse Sound and use genomic relatedness to examine narwhal herd sociality. More than 245 tissue samples were collected from entrapped narwhal and genotyped at 12 microsatellite loci. Using pair-wise relatedness, internal clusters were estimated, and a social network was developed based on that framework. Within the 245 samples, we determined that there were 8 distinct pod clusters with an average size of 30.6 individuals with M/F ratio of 0.23. This work aligns with earlier genetic analysis of narwhal and suggests a fission-fusion social structure like other Arctic *Delphinidae* species.

Broader Impact

Even within the past six months, emergency management of ice entrapped Orca whales in Hokkaido, Japan has made global news (NBC News, 2024). As climate change continues to expand species ranges that were once restricted by total ice cover and polar industry increases, we expect ice entrapment of non-Arctic and Arctic cetacean species to become increasingly prevalent. It is my hope that this thesis helps change the perspective of cetaceans and ice entrapments by providing evidence that they are a semi-frequent occurrence that can be a prodigious source of mortality for cetaceans and may serve as a reference (Chapter 1) for emergency management decisions.

Chapter 3 used tissue sampled during a 2008 narwhal ice entrapment in Eclipse Sound and gives insight into narwhal sociality from minimally known and high cost study species. The tissue samples were collected by members of the Fisheries and Oceans Canada (DFO), and were brought into this thesis more than ten years after collection. For cetaceans and other species that are highly vulnerable to climate change and live in remote habitats, ice entrapments are an incredibly valuable resource for many questions pertaining to evolutionary biology and ecology. If anything, I hope that Chapter 3 gives perspective on what is possible with such inclusive samples of otherwise unknown and threatened species.

The threat of extinction is a real possibility for many polar cetaceans that have been adapted to a predictable habitat and ice formation pattern for millennia. The total mortality of recorded ice entrapment events in the last 200 years is more than 20,000 individuals, often in species with threatened and already low population sizes or stocks. Looking deeper at an ice entrapped population of narwhal in 2008, Chapter 3 indicates that social groups of narwhal have a high degree of kinship and follow fission-fusion social structure. The sociality focus highlights the importance of understanding the social structure of threatened populations of cetaceans and may be important in environmental management decisions. In general, we predict ice entrapments to increase as ice formation and maintained ice patterns change, and as a result, a deeper understanding of ice entrapments will become a more critical part of cetacean conservation.