

# THE DEMOGRAPHY OF CANADIAN ARCTIC KILLER WHALES

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## ABSTRACT

The ecosystem-level consequences of climate change-related range expansions are largely unexplored. In the Canadian Arctic, killer whale (*Orcinus orca*) occurrence is ice-restricted, and diminishing sea-ice cover has purportedly led to increased killer whale presence during the open-water season. However, the effects of increased predator presence on this Arctic marine ecosystem remain mostly unknown. In this thesis, I explore the consequences of such climate change-related predator range expansions. In chapter one, I review Canadian Arctic killer whale ecology and identify research priorities in the Canadian Arctic, two of which I address in chapters two and three. In chapter two, I whole-genome sequence twenty-nine western North Atlantic killer whales and describe two genetically distinct populations in Canadian waters: Canadian High Arctic and Canadian Low Arctic killer whales. Comparison with previously published genomes revealed Canadian High Arctic whales share a marginally significant excess of derived alleles with whales sampled in Newfoundland and Brazil, while Canadian Low Arctic whales share a significant excess of derived alleles with whales sampled in Greenland, Norway, and Iceland. In chapter three, I use photographs of sixty-three individually identifiable Canadian Arctic killer whales to estimate abundance in a capture-mark-recapture framework. The best-fitting model produced an estimate of  $163 \pm 27$ , a number of killer whales which I determine could consume >1000 narwhal (*Monodon monoceros*) during their seasonal residency in Arctic waters. Collectively, these findings provide insight into the origins of Canadian Arctic killer whales and illustrate the magnitude of ecosystem-level modification that can occur with climate change-related shifts in predator distributions.

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## THESIS FORMAT AND MANUSCRIPTS

This thesis is presented in manuscript format. Chapter one is a deme-specific review and introduces the rationale for this work. Chapters two and three, written with Abstract, Keywords, Introduction, Methods, Results, Discussion, Acknowledgements, and Literature Cited sections, describe the research completed. Chapter four summarizes the major findings.

### CHAPTER ONE

Lefort KJ, Matthews CJD, Higdon JW, Petersen SD, Westdal KH, Garroway CJ, and Ferguson SH. 2020. A review of Canadian Arctic killer whale (*Orcinus orca*) ecology. Canadian Journal of Zoology 98: 245–253. doi:10.1139/cjz-2019-0207.

*KJ Lefort wrote the manuscript. CJD Matthews, JW Higdon, SD Petersen, KH Westdal, CJ Garroway, and SH Ferguson provided comments and reviewed the manuscript before submission.*

### CHAPTER TWO

Lefort KJ, Foote AD, Garroway CJ, and Ferguson SH. In Preparation. Identification of two sympatric western North Atlantic killer whale populations: evidence for secondary contact in Arctic waters. Molecular Ecology.

*KJ Lefort conceived the study, collected and processed samples, analyzed the data, and wrote the manuscript. AD Foote assisted with data analyses. CJ Garroway and SH Ferguson provided guidance and reviewed the manuscript.*

### CHAPTER THREE

Lefort KJ, Garroway CJ, and Ferguson SH. In Press. Killer whale abundance and predicted narwhal consumption in the Canadian Arctic. *Global Change Biology*.

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*KJ Lefort conceived the study, analyzed the data, and wrote the manuscript. CJ Garroway and SH Ferguson provided guidance and reviewed the manuscript before submission.*

# CHAPTER 1. A REVIEW OF CANADIAN ARCTIC KILLER WHALE ECOLOGY

**Abstract:** The killer whale (*Orcinus orca*) is a widely distributed marine predator with a broad ecological niche at the species level with evidence of specialization and narrow ecological niches among populations. Their occurrence in Canadian Arctic waters is limited by sea ice and it has been suggested that climate warming, which has caused increases in the area of ice-free water and duration of the ice-free season, has led to an increased killer whale presence during the open-water period. In this chapter, I summarize our knowledge of Canadian Arctic killer whale demographics and ecology, synthesizing published and previously unpublished information in a single document. More specifically, I summarize our knowledge of killer whale population size and trends, distribution and seasonality (including results from recent satellite-tracking studies), feeding ecology, and threats, and identify research priorities in the Canadian Arctic. Despite increased research efforts during the past decade, our demographic and ecological knowledge remains incomplete. An improved ecological understanding is necessary for effective management of killer whales and their prey, species of ecological, economic, and cultural importance to Canadian Inuit and the marine ecosystem. This knowledge will allow us to better understand the ecological consequences of a changing Arctic climate.

**Keywords:** abundance, distribution, killer whale, *Orcinus orca*, photographic identification, predation, satellite telemetry

## INTRODUCTION

Monitoring a population's demographics and ecology is key to documenting climate-linked population-level shifts and their ecosystem-level consequences (Pershing et al. 2015). This is particularly true for shifts in top-predator populations that can cause ecosystem-scale change through top-down control and cascading ecological effects (Ripple et al. 2014). Understanding climate-linked shifts in predator populations is therefore fundamental to effective ecosystem management in the face of a rapidly changing climate.

The killer whale (*Orcinus orca*) is a globally distributed marine top predator with a broad ecological niche at the species level (Ford et al. 2000) and well-documented ecosystem-level influence (Estes et al. 1998; Springer et al. 2003, 2008; but also see DeMaster et al. 2006; Mizroch and Rice 2006; Trites et al. 2007; Wade et al. 2007). Killer whales are open-water season visitors to the Canadian Arctic and have been recorded in the region as early as the mid-1800s (Reeves and Mitchell 1988a). The frequency of killer whale sightings in Canadian Arctic waters has increased in recent years (Higdon et al. 2012, 2014), likely associated with a climate-linked increase in the extent of ice-free water and duration of the open-water season (Higdon and Ferguson 2009). Increases in abundance or shifts in the distribution of this predator could disrupt the Canadian Arctic marine ecosystem through effects on prey not historically exposed to high levels of killer whale predation (Breed et al. 2017).

Our knowledge of Canadian Arctic killer whales has been generated through a combination of Inuit knowledge studies, opportunistic encounters, and dedicated research programs. Despite increased research effort in the eastern Canadian Arctic

during the past decade (see Higdon and Ferguson 2009, 2014; Matthews et al. 2011, 2019; Young et al. 2011; Ferguson et al. 2012a, 2012b; Higdon et al. 2012, 2014; Reinhart et al. 2013; Westdal et al. 2013, 2016, 2017; Matthews and Ferguson 2014; Breed et al. 2017), many ecological questions concerning killer whales remain unanswered. This is also true in the western Canadian Arctic where killer whales, perhaps members of an Alaskan population, are sporadically observed (Higdon et al. 2013). Although occupying a broad ecological niche at the species level, narrow ecological niches are observed among killer whale populations. A region-specific understanding of killer whale ecology is therefore required for effective ecosystem management (de Bruyn et al. 2013).

In the absence of a comprehensive region-specific understanding, killer whales in the western North Atlantic (e.g., Labrador Sea, Gulf of St. Lawrence, Scotian Shelf, Bay of Fundy) and the eastern Canadian Arctic (e.g., Hudson Bay, Lancaster Sound, Baffin Bay, Davis Strait; Figure 1.1) are considered a single population listed as Special Concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2008). In this chapter, I summarize our demographic and ecological knowledge of killer whales throughout the Canadian Arctic, synthesizing published and previously unpublished information in a single document. I then present research recommendations that will inform Canadian Arctic ecosystem management and support ongoing research efforts which aim to more comprehensively understand killer whale ecological diversity worldwide.

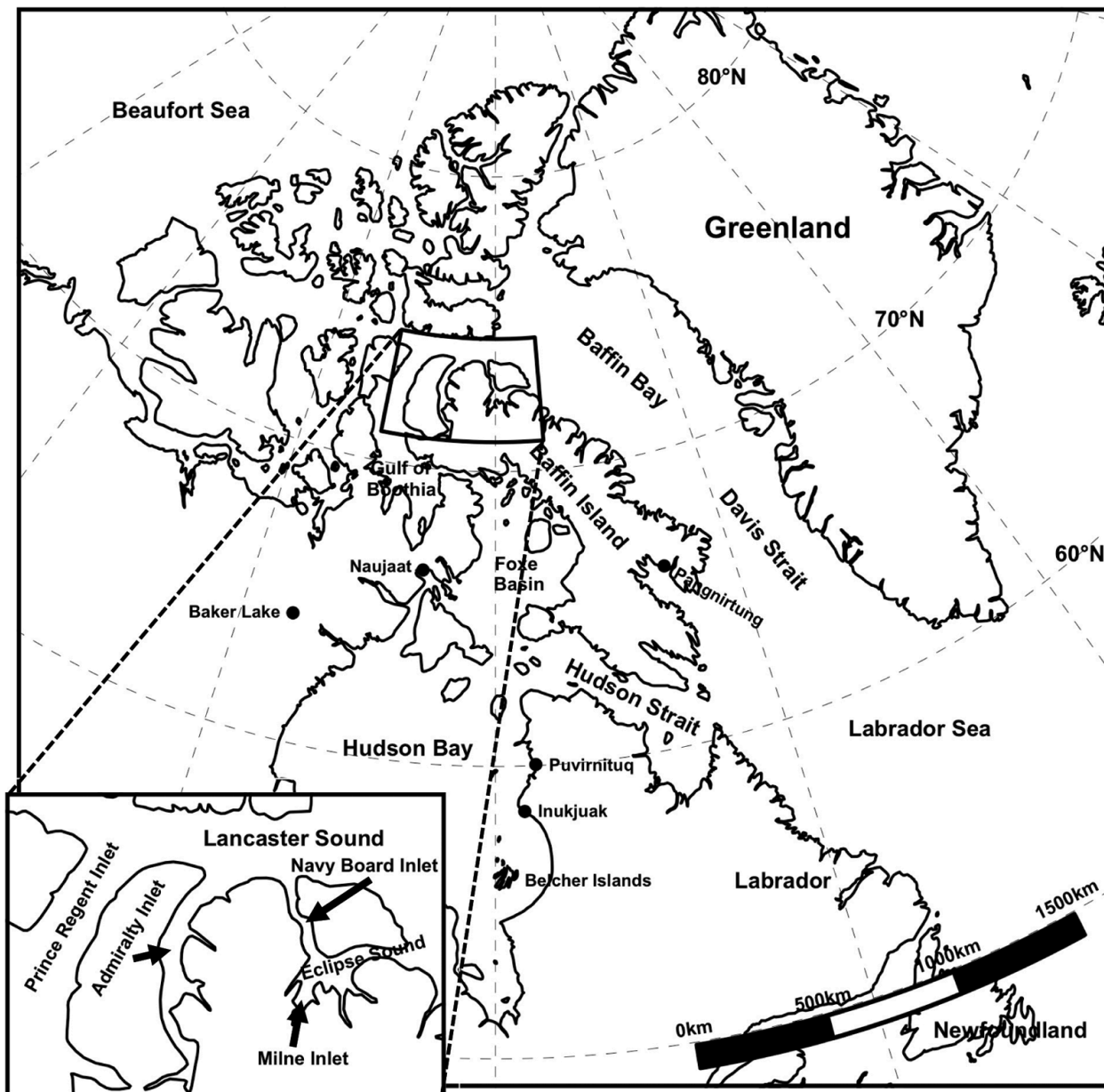


Figure 1.1. Communities and major water bodies referred to in-text.

# A REVIEW OF CANADIAN ARCTIC KILLER WHALE ECOLOGY

## *Population size*

Estimates of the number of killer whales occupying Canadian Arctic waters are required to develop a comprehensive understanding of their ecosystem influence. In the eastern Canadian Arctic, 53 individual killer whales were identified from photographs using natural features (i.e., shape, size, and colour of the dorsal fin, saddle patch, and eye patch; scars, primarily on the trailing edge of the dorsal fin and saddle patch) between 2004 and 2009 (Young et al. 2011). Only a single individual was re-sighted during this 6-year study. The cumulative number of identified individuals increased steadily with time, suggesting the actual abundance exceeds this minimum count (Young et al. 2011). Since Young et al.'s (2011) study, 45 previously unidentified killer whales were photographed in the coastal waters of northern Baffin Island (Fisheries and Oceans Canada (DFO), unpublished data). Killer whale group sizes reported in the eastern Canadian Arctic exceed these minimum counts (e.g., 100 individuals; Higdon et al. 2012). Furthermore, killer whales are occasionally reported in offshore areas where observer effort is low (Higdon et al. 2014). Such observations suggest photographic counts are underestimates of the population's size and photographic effort has been focused in a small area relative to the population's range. Much less is known concerning killer whale abundance in the western Canadian Arctic (Higdon et al. 2013).

Reliable estimates of killer whale abundance in Canadian Arctic waters do not exist; thus, population trends are difficult to assess. The frequency of reported killer whale sightings in the eastern Canadian Arctic has increased considerably since the

1950s and has been attributed to an increased number of killer whales occupying Arctic waters (Higdon et al. 2012, 2014; DFO 2014). Such an increase in abundance could be climate-linked (e.g., an increase in the number of whales exploring previously inaccessible Arctic waters; see Higdon and Ferguson 2009; Matthews et al. 2019), population growth following reduction from commercial whaling (see Sergeant and Fisher 1957; Heide-Jørgensen 1988; Mitchell and Reeves 1988; Øien 1988; Reeves and Mitchell 1988b), or growth following reduction from entrapment mortality (Reeves and Mitchell 1988a; Higdon and Ferguson 2014). Conversely, perceived increases in abundance could be the result of increased effort (see Higdon et al. 2012) or climate-linked shifts in the population's distribution (see Higdon and Ferguson 2009). Increases in abundance and shifts in distribution are difficult to parse but would have similar ecosystem-level effects.

### *Group sizes*

Sighting reports between the mid-1800s and 2008 have provided information on killer whale group sizes in the Canadian Arctic (Higdon et al. 2012). The mean-reported group size was 8.3 individuals (median = 4; range = 1–100; number of reports = 246; Higdon et al. 2012). Group sizes varied among regions with the smallest groups reported in Foxe Basin (median = 2; mean = 2.7; number of reports = 34) and the largest groups reported in the Lancaster Sound region (median = 8; mean = 13.2; number of reports = 48) and Davis Strait – Baffin Bay (median = 6; mean = 15.6; number of reports = 14; Higdon et al. 2012). Similar regional differences were noted in a photo-identification study where group sizes ranged from 5 to 10 individuals in western



Hudson Bay and from 12 to 30 individuals in the coastal waters of Baffin Island (Young et al. 2011). Killer whale group sizes also varied depending on the prey species targeted: group sizes were smallest when phocid seals were targeted (median = 2; number of reports = 9), followed by bowhead whales (*Balaena mysticetus*) (median = 4; number of reports = 13), and largest when narwhal (*Monodon monoceros*) or beluga whales (*Delphinapterus leucas*) were targeted (median = 7; number of reports = 27; Higdon et al. 2012). In contrast to these mean- and median-reported group sizes, several larger groups of 20+ killer whales have been observed preying on narwhal in the eastern Canadian Arctic (Higdon et al. 2012; C.J.D. Matthews, personal observation, 2013).

#### *Distribution and seasonality*

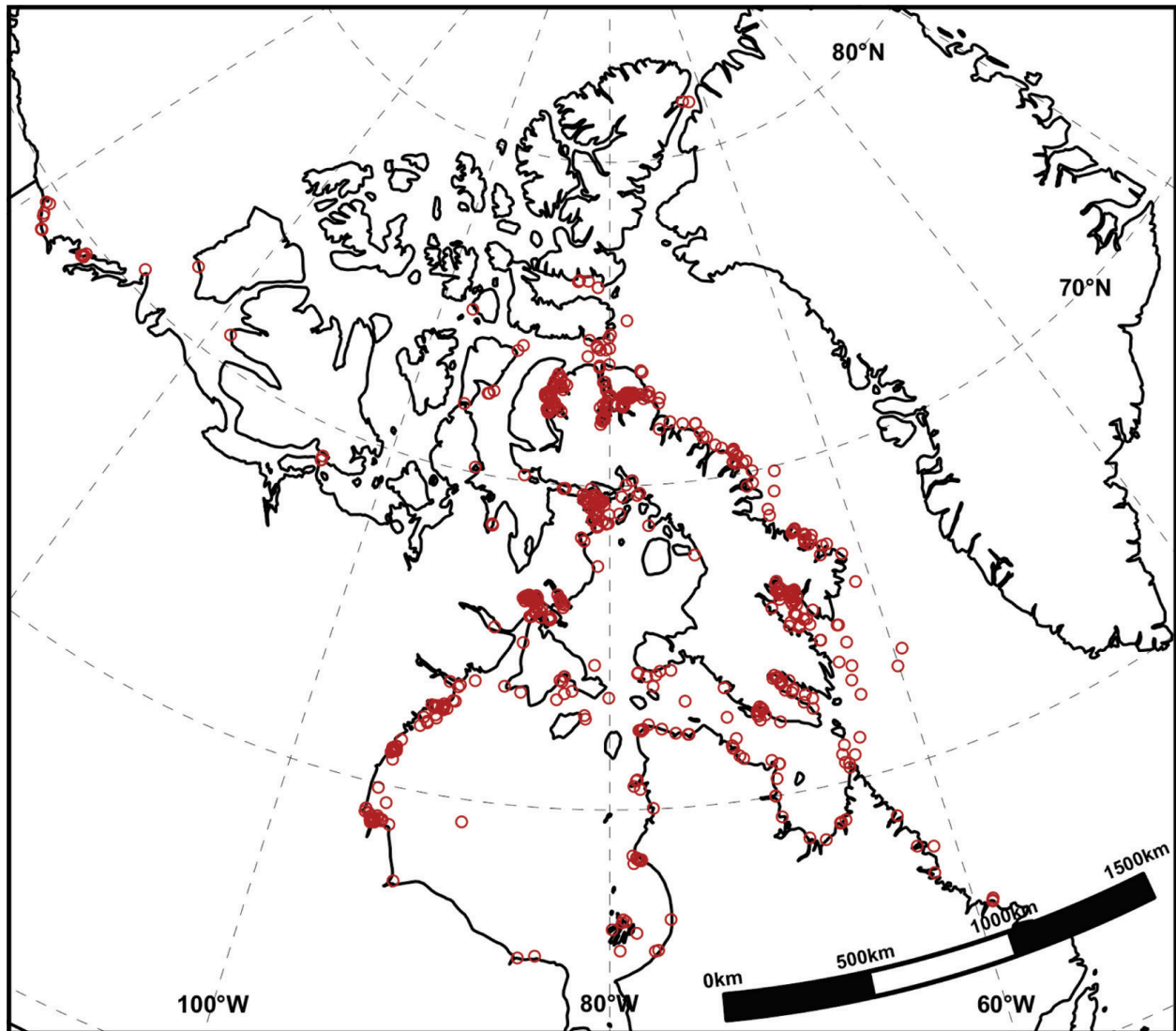
Killer whale sightings in the Canadian Arctic occur almost exclusively during ice-free or reduced-ice periods of the year (Higdon et al. 2014), suggesting their occurrence is limited by sea ice (Reeves and Mitchell 1988a). Satellite-tracking studies corroborate these observations, demonstrating that Canadian Arctic killer whales avoid heavy sea ice (Matthews et al. 2011; DFO, unpublished data). Climate warming has led to increases in the area of ice-free water and duration of the open-water season (Stroeve et al. 2014) and it has been suggested that killer whales may consequently undergo a range expansion, occupying higher latitudes for longer periods (Moore and Huntington 2008; Higdon and Ferguson 2009). Such an increase in occurrence could have considerable ecosystem-level effects (see Estes et al. 1998).

Killer whales migrate into eastern Canadian Arctic waters in late spring from overwintering areas, possibly Baffin Bay – Davis Strait, west Greenland, the Labrador Sea, or elsewhere in the North Atlantic (Sergeant and Fisher 1957; Katona et al. 1988; Reeves and Mitchell 1988a; Matthews et al. 2011). Inuit knowledge indicates that killer whale spring arrival into Arctic waters is dependent upon sea-ice conditions, occurring only once sea ice has cleared or begun to break-up (Higdon et al. 2014). Sightings near the spring floe edge are uncommon despite considerable Inuit presence in this area during this time (Higdon et al. 2014). Killer whales are often reported in a series of sightings as they travel northward along the eastern coast of Baffin Island (DFO, unpublished data). Sightings are most common between June and October, with the greatest number of observations occurring in August (Higdon et al. 2012, 2014). This seasonality is similar throughout the Canadian Arctic (Higdon et al. 2012). Killer whales depart the eastern Canadian Arctic before freeze-up, after sea ice begins to form in the fall (Matthews et al. 2011; Higdon et al. 2012, 2014; DFO, unpublished data).

There have been no winter killer whale sightings in the Canadian Arctic (Higdon et al. 2012, 2014) with the exception of those associated with ice entrapments (Higdon and Ferguson 2014; Westdal et al. 2017; Matthews et al. 2019). Winter sightings have been documented farther south in the coastal waters of Labrador (Higdon et al. 2014; Lawson and Stevens 2014), supporting the suggestion that some killer whales overwinter in this area (Sergeant and Fisher 1957; Reeves and Mitchell 1988a). Satellite-tracking studies, however, indicate that some Canadian Arctic killer whales likely overwinter farther south (see Matthews et al. 2011). There have been no photographic re-sightings between the Canadian Arctic and the coastal waters of

Newfoundland and Labrador (Young et al. 2011; Lawson and Stevens 2014) and baseline isotopic variation between killer whales from these two areas suggests two geographically non-overlapping groups, at least seasonally (Matthews and Ferguson 2014). It is possible that these are geographically non-overlapping groups during the summer, with winter-range overlap somewhere in the Atlantic.

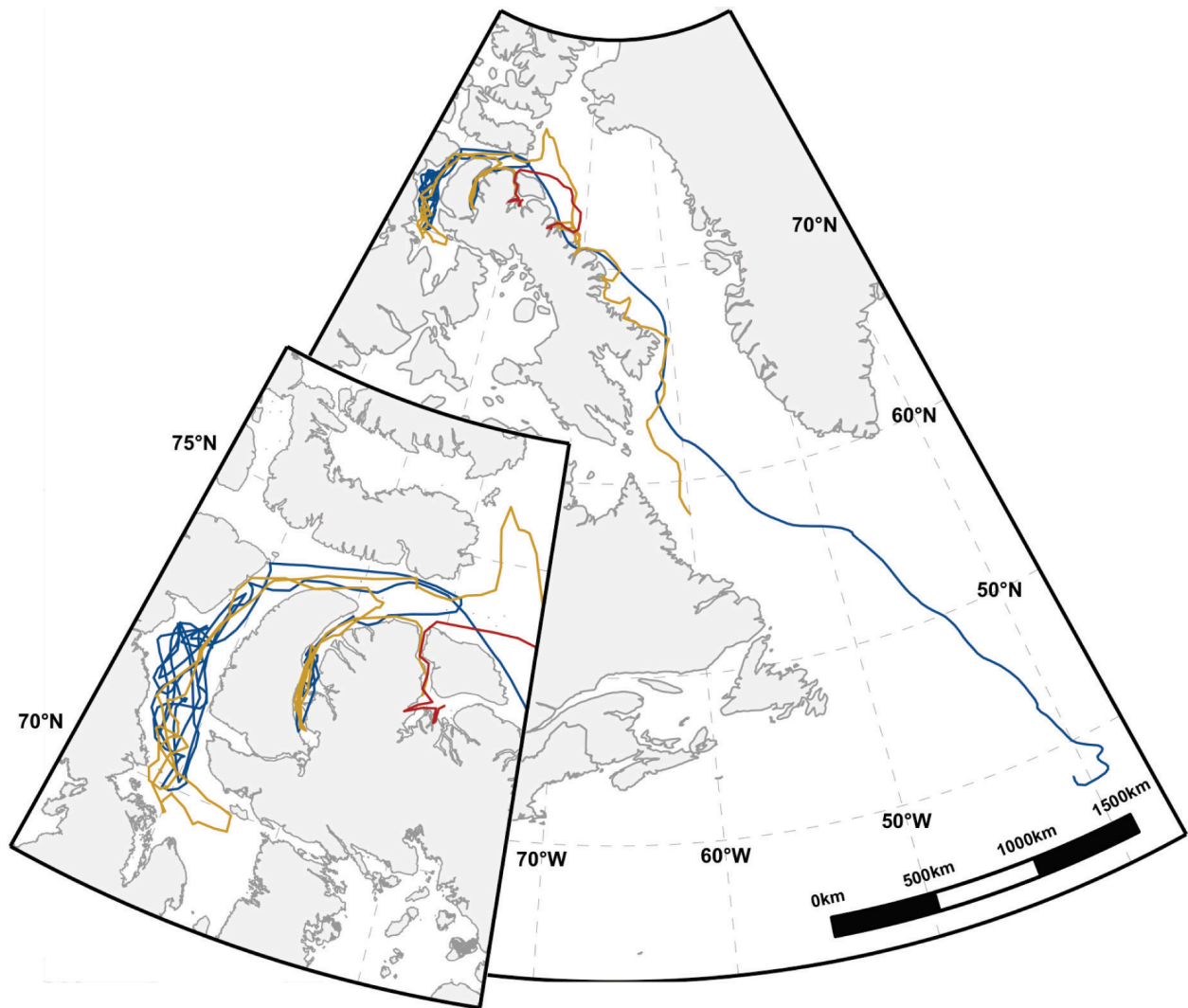
Killer whales are widely distributed across the eastern Canadian Arctic during the open-water season. Reported killer whale sightings are most common in Hudson Bay and the coastal waters of Baffin Island (Figure 1.2; Higdon et al. 2012). Nearly all participants in Inuit knowledge studies in the eastern Canadian Arctic have observed killer whales at least once (Westdal et al. 2013; Higdon et al. 2014). In contrast, sightings are uncommon in the central and western Canadian Arctic, which may reflect reduced search effort (Higdon et al. 2012), but Inuvialuit knowledge studies in the western Canadian Arctic indicate few residents have observed killer whales (Byers and Roberts 1995; Hartwig 2009; Higdon et al. 2013).



**Figure 1.2.** The distribution of killer whale (*Orcinus orca*) sightings in Canadian Arctic waters between approximately 1850 and 2018 ( $n = 643$ ) (Higdon et al. 2012; DFO, unpublished data). Location accuracy varies among sightings and represents approximate locations only.

Killer whale movement in Canadian Arctic waters has been studied using satellite telemetry (Figure 1.3). Satellite-tracking devices were deployed onto killer whales using techniques detailed in Matthews et al. (2011). Seasonal movements were investigated using first-difference correlated random walk models (Jonsen et al. 2005; Jonsen 2016) in R (R Core Team 2019). Wildlife Computers SPOT5 location-only satellite-tracking devices were deployed onto two killer whales in Admiralty Inlet, northern Baffin Island, in mid-August 2009, transmitting for 2 and 90 days, respectively (Matthews et al. 2011; Breed et al. 2017). The longest-lasting tracking device remained in Admiralty Inlet and the adjacent Prince Regent Inlet until early October before travelling along the eastern coast of Baffin Island and into the open North Atlantic by mid-November (Matthews et al. 2011; Figure 1.3). SPOT5s were deployed onto five killer whales in Milne Inlet, northern Baffin Island, in mid-August 2013, transmitting for between 9 and 59 days (DFO, unpublished data). The group remained together in Eclipse Sound and the adjacent Admiralty Inlet, Prince Regent Inlet, and Gulf of Boothia until early September before travelling east into Baffin Bay and southward along the eastern coast of Baffin Island and into the coastal waters of northern Labrador by early October (Figure 1.3). The group averaged  $104.4 \pm 44.2$  km day<sup>-1</sup> (maximum 197.5 km day<sup>-1</sup>) while in the coastal waters of northern Baffin Island (west of 80°W) and  $124.7 \pm 48.5$  km day<sup>-1</sup> (maximum 226.2 km day<sup>-1</sup>) along their southern migration (east of 80°W). One Wildlife Computers SPLASH10 satellite-tracking device was deployed onto an adult male killer whale in Eclipse Sound, northern Baffin Island, in late August 2018 (DFO, unpublished data). The tagged whale left Eclipse Sound via Navy Board Inlet in mid-September, travelling into a fjord system on the northeastern coast of Baffin Island (Figure 1.3)

averaging  $106.2 \pm 40.1$  km day<sup>-1</sup> (maximum 168.7 km day<sup>-1</sup>) during this 10-day deployment. Similar seasonal movements were observed among killer whales outfitted with satellite-tracking devices in 2009 and 2013 (although the latter group initiated their southward migration approximately 1 month earlier) but differed from those observed in 2018 (Figure 1.3). Photographic identification revealed killer whales outfitted with satellite-tracking devices in 2009 and 2018 were members of the same group (DFO, unpublished data), suggesting interannual variation in a group's seasonal movements.



**Figure 1.3.** Killer whale (*Orcinus orca*) tracks estimated from satellite-tracking data using first-difference correlated random walk models in 2009 (blue; 90-day deployment), 2013 (yellow; 59-day deployment), and 2018 (red; 10-day deployment). Each track represents the longest-lasting tracking device from that year.

## *Feeding ecology*

Observations of predation events indicate that Canadian Arctic killer whales prey on bowhead whales, beluga whales, narwhal, northern minke whales (*Balaenoptera acutorostrata*), Atlantic walrus (*Odobenus rosmarus rosmarus*), ringed seals (*Pusa hispida*), bearded seals (*Erignathus barbatus*), harp seals (*Pagophilus groenlandicus*), hooded seals (*Cystophora cristata*), and harbour seals (*Phoca vitulina*) (Stelner et al. 1984; Campbell et al. 1988; Reeves and Mitchell 1988a; Finley 1990; Laidre et al. 2006; Higdon 2007; Higdon et al. 2012, 2014; Ferguson et al. 2012a; Westdal et al. 2016). Predation events involving monodontids (beluga and narwhal) were observed most frequently, followed by bowhead whales and phocid seals (mainly ringed seals, but also harp, bearded, and hooded seals, in decreasing order of frequency; Ferguson et al. 2012a) (Higdon et al. 2012). These species are reported as killer whale prey throughout the Canadian Arctic, although the proportion of observed predation events involving each species differs among regions (Ferguson et al. 2012a; Higdon et al. 2012). Predation on bowhead whales is observed most frequently in Foxe Basin and Davis Strait – Baffin Bay (Ferguson et al. 2012a; Higdon et al. 2012). Increased predation on bowhead whales in Foxe Basin between mid-July and early September may be associated with predation on vulnerable bowhead whale calves following sea ice break-up in July (Higdon et al. 2012). Monodontid predation comprises the largest proportion of observed summer predation events but also occurs in the spring and early fall (Higdon et al. 2012). Predation on narwhal is most common in the northern Baffin Island and Hudson Bay regions and uncommon in the southern Baffin Island region, whereas predation on beluga is uncommon in the northern Baffin Island region compared with all



other regions (Ferguson et al. 2012a). The only confirmed killer whale prey species in the western Canadian Arctic is beluga whale (Higdon et al. 2012), although some western sightings suggest predation on fishes (George and Suydam 1998; Higdon et al. 2013). These apparent regional differences in prey preferences seem to be associated with the relative availability of prey (e.g., absence of narwhal in the western Canadian Arctic) and not specialization by killer whales, although these are not mutually exclusive.

Our incomplete knowledge of Canadian Arctic killer whale population demographics (e.g., population size) and feeding ecology (e.g., the contribution of each prey species to killer whale diet) make it difficult to quantify their consumptive effects on prey populations (although see Ferguson et al. 2012b). However, Inuit throughout the Canadian Arctic are familiar with prey behaviour in response to killer whale presence (Ferguson et al. 2012a). Bowhead whales, narwhal, beluga, and several species of seal (e.g., ringed, harp) frequent shallow, nearshore waters in the presence of killer whales, presumably to avoid predation (Ferguson et al. 2012a; Westdal et al. 2013). Bowhead whales also seek refuge within ice fields (Finley 1990; Ferguson et al. 2012a). The effects of killer whale presence on their prey have also been studied using satellite telemetry (Laidre et al. 2006; Westdal et al. 2016; Breed et al. 2017; Matthews et al. 2020). In the presence of killer whales, beluga whales in western Hudson Bay reduced range size, moved closer to shore, and moved away from an attack site following a predation event (Westdal et al. 2016). In the northern Baffin Island region, narwhal moved closer to shore and exhibited transiting movement patterns (Breed et al. 2017; also see Laidre et al. 2006), whereas bowhead whales moved from open-water areas

into nearshore areas or heavy sea ice in the presence of killer whales (Matthews et al. 2020).

Despite minimal evidence to support predation on non-mammalian prey, predation on cephalopods or fishes would be much more difficult to observe than predation on large surface-breathing marine mammals (Hanson et al. 2010). Killer whales in the adjacent coastal waters of west Greenland have been reported preying on cephalopods, fishes, seabirds, and marine mammals (Heide-Jørgensen 1988; Jensen and Christensen 2003; Laidre et al. 2006). In the coastal waters of Newfoundland and Labrador, killer whales have been observed preying on fishes, seabirds, and marine mammals (Steiner et al. 1979; Lien et al. 1988; Mitchell and Reeves 1988; Reeves and Mitchell 1988b; Lawson et al. 2007). Depredation of commercial fisheries has also been reported in the coastal waters of Newfoundland and Labrador (Lawson et al. 2007). Recent observations suggest that killer whales in the eastern Canadian Arctic may feed opportunistically on Thick-billed Murres (*Uria lomvia*) (M.L. Mallory, personal observation, 2018), although such feeding events are likely uncommon, or of recent occurrence because they have never been reported in Inuit knowledge studies. Isotopic values and tooth wear observed in a stranded eastern Canadian Arctic killer whale are suggestive of predation on sharks (Matthews and Ferguson 2014); however, Inuit knowledge interviewees in this area were uncertain if killer whales preyed on fishes (Ferguson et al. 2012a). Although feeding or dietary specialization on non-mammalian prey in Canadian Arctic waters cannot be discounted, it has not been confirmed with direct observations (e.g., repeat observations of an individual or group feeding on fish). Such repeat observations are logistically challenging and unlikely in the Canadian

Arctic, and longer-term biochemical diet proxies (e.g., stable isotopes, fatty acids) will be necessary to answer questions related to dietary specialization (Matthews and Ferguson 2014).

### *Are there Canadian Arctic ecotypes?*

Killer whales in the northeastern Pacific Ocean have been grouped into ecotypes based on differences in dietary preferences, social behaviour, morphology, and genetics (Baird and Stacey 1988; Barrett-Lennard et al. 1996; Ford et al. 1998; Barrett-Lennard and Ellis 2001). Similar ecotypic groupings have been made in the Southern Ocean (Pitman and Ensor 2003; Pitman et al. 2007, 2010) and the eastern North Atlantic (Foote et al. 2009). In contrast, there are no recognized ecotypes in the western North Atlantic or the Canadian Arctic. Inuit knowledge indicates that Canadian Arctic killer whales prey on marine mammals (Ferguson et al. 2012a; Higdon et al. 2012), although isotopic values suggest that some individuals feed on non-mammalian prey (Matthews and Ferguson 2014). Observations of large killer whale groups (e.g., 20–30 individuals) are considered uncharacteristic of mammal-eating killer whales, which are typically observed in smaller groups to maximize per capita energy intake (Baird and Dill 1996). However, groups of this size have been observed feeding on narwhal in the Canadian Arctic (Higdon et al. 2012; C.J.D. Matthews, personal observation, 2013). It is possible that fish-eating killer whales seasonally shift their strategy to take advantage of energetically rich marine mammal resources in the Canadian Arctic, as has been recorded in Iceland (Samarra et al. 2017) and Greenland (Pedro et al. 2017). It is also possible that dietary specialization occurs on certain marine mammals (e.g.,

specialization on narwhal). Nonetheless, apparent regional differences in prey preferences (see Ferguson et al. 2012a; Higdon et al. 2012) are likely a function of prey availability (although these are not mutually exclusive).

Photo-identification studies (Young et al. 2011; Lawson and Stevens 2014) and isotopic analyses (Matthews and Ferguson 2014) suggest spatial segregation, although not necessarily year-round, between eastern Canadian Arctic and western North Atlantic killer whales. In contrast, satellite-tracking studies indicate geographic overlap between these two groups during the southern migration of Arctic killer whales (Matthews et al. 2011). Questions concerning connectivity between killer whales in the western Canadian Arctic and those in adjacent waters remain unanswered. The social, morphometric, and genetic components of ecotypic designation among Canadian Arctic killer whales remain unknown, and there is currently little evidence bearing on the questions of ecotypes or discrete populations in Canadian Arctic (and adjacent) waters.

### *Threats*

Two threats to Canadian Arctic killer whales are entrapments in sea ice or tidal saltwater lakes and hunting-related mortality. Three confirmed killer whale entrapments have been recorded in the eastern Canadian Arctic (Blackadar 1964; Reeves and Mitchell 1988a; Higdon 2007; Higdon and Ferguson 2014; Higdon et al. 2014; Westdal et al. 2017; Matthews et al. 2019). The first recorded entrapment occurred in northeast Foxe Basin in October during the mid-1950s, where a group of at least 5, and potentially 11 or 12, killer whales became entrapped in developing landfast sea ice (Blackadar 1964; Higdon and Ferguson 2014). At least two killer whales were harvested during this

entrapment and the rest likely died. A second entrapment occurred near Pangnirtung, Nunavut, southern Baffin Island, in 1977, where a group of 14 killer whales became entrapped in a saltwater lake and were killed by local Inuit (Reeves and Mitchell 1988a; Higdon 2007; Higdon et al. 2014). One killer whale carcass was found frozen in sea ice near Naujaat, Nunavut, northern Hudson Bay, in early October 2009. It is unknown whether this animal's death was related to sea ice or if the carcass became caught in developing sea ice after death. One ice entrapment occurred near Inukjuak, Quebec, eastern Hudson Bay, in January 2013, involving between 11 and 17 whales (Westdal et al. 2017). The whales escaped several days later; however, survival was unlikely because heavy pack ice in Hudson Strait limited the likelihood of reaching suitable open-water habitat. One killer whale was found dead the following spring (June 2013) near Puvirnituq, Quebec, eastern Hudson Bay, although it is unknown whether this whale was a member of the group entrapped near Inukjuak (DFO, unpublished data). Four killer whale carcasses were discovered near the Belcher Islands, Nunavut, southeastern Hudson Bay, in 2016 (Matthews et al. 2019). It was suggested that these animals became trapped following sea-ice formation, overwintered in the region, and starved (Matthews et al. 2019). Additional entrapments and ice-related mortality events, possibly eastern Canadian Arctic killer whales travelling to overwintering areas, have been recorded in the western North Atlantic and the coastal waters of west Greenland (see Westdal et al. 2017). Matthews et al. (2019) proposed that such ice-related mortalities may act as a natural abundance check on a population expanding their range deeper into Canadian Arctic waters.

The harvest of killer whales in the coastal waters of west Greenland may pose a threat to eastern Canadian Arctic killer whales if their range includes this area (COSEWIC 2008; also see Jourdain et al. 2018; North Atlantic Marine Mammal Commission. 1992–2018). Killer whales are occasionally the target of shootings in the Canadian Arctic (see Westdal et al. 2013), although the only confirmed mortality, aside from those associated with entrapments, was a single adult male killed near the community of Baker Lake, Nunavut, western Hudson Bay, in August 1978 (Reeves and Mitchell 1988a). Although killer whales have not traditionally been hunted in the Canadian Arctic, increasing killer whale occurrence coupled with negative attitudes towards killer whales (Westdal et al. 2013) could result in increased mortality due to management shootings. Two additional potential threats that have not been studied in the Canadian Arctic are increased contaminant levels (see Desforges et al. 2018) and increased levels of anthropogenic noise (COSEWIC 2008). Further research is required to evaluate the severity of these threats.

## FUTURE RESEARCH RECOMMENDATIONS

Studying highly mobile marine predators in remote Arctic regions is expensive and logistically challenging (Mallory et al. 2018). Consequently, much of our knowledge of Canadian Arctic killer whales has been generated through opportunistic sightings and Inuit knowledge studies. Nevertheless, a decade-long dedicated Arctic killer whale research program has also resulted in the deployment of satellite-tracking devices, as well as the collection of tissue biopsies, high-quality photographs for individual identification, and observational data. The following are recommendations for future killer whale research in the Canadian Arctic.

### *Research effort*

Increased spatial coverage in research activities is required to obtain an improved understanding of the population's ecology and natural history. Research efforts to date have focused on a small area relative to the population's range. Systematic aerial or ship-based surveys, including opportunistic cruise-ship-based studies, are one way of increasing spatial coverage, although Canadian Arctic killer whales occur at low densities making such surveys challenging. Collaborating with Inuit communities, learning from Inuit knowledge, and engaging Inuit in research activities (e.g., training community members in sampling methods) will help facilitate this objective.

## *Demography*

The long-term photo-identification database, a database which includes photographs collected during dedicated vessel-based surveys and opportunistic encounters, should be used to estimate population demographics (e.g., population size, calving intervals, age-class structure). Furthermore, the Canadian Arctic, western North Atlantic, and west Greenland killer whale photo-identification catalogues should be compared. Unmanned aerial vehicles (UAVs) equipped with high-resolution cameras should be used in photo-identification studies, thereby increasing effort for population assessments in combination with traditional vessel-based photo-identification surveys. UAV photogrammetry should also be used in ethological studies and to monitor body condition (see Durban et al. 2015).

## *Movement and distribution*

Satellite-tracking studies should continue to facilitate an improved understanding of killer whale spatial ecology (e.g., movement, distribution, and habitat selection), allowing researchers to make predictions concerning understudied areas and the consequences of future climate warming. Furthermore, archival suction-cup tags should be used to facilitate an improved understanding of finer-scale spatial ecology (Tennessen et al. 2019). Finally, a network of moored hydrophones should be established and used to identify and monitor killer whale occurrence (see Stafford 2019).



### *Feeding ecology*

Chemical biomarkers (e.g., stable isotopes, fatty acids, contaminants) should continue to be used to better understand killer whale feeding ecology. An improved understanding of feeding ecology and the ecological consequences of predation are fundamental in maintaining the sustainable harvest of killer whale prey species in the Canadian Arctic.

### *Population structure*

Genomics should be used to better understand Canadian Arctic killer whale population structure, their geographic origins, effective population size ( $N_e$ ), and the functional evolution of killer whale traits (e.g., the evolution of skin and blubber physiology to withstand cold waters; see Durban and Pitman 2012). Information concerning population structure and geographic origins will allow for the designation of discrete groups for conservation and predictions concerning killer whale expansion into Canadian Arctic waters (see Foote et al. 2019). Furthermore, bioacoustics (see Filatova et al. 2012) and chemical biomarkers (see Matthews and Ferguson 2014) should be used to explore and identify population structure (including ecotypes).

## CONCLUSIONS

Despite increased research efforts during the last decade, many questions concerning Canadian Arctic killer whales remain unanswered. This review provides an update on current knowledge and identifies areas where future research should focus. This work will provide us with an improved understanding of the ecological consequences of a changing Canadian Arctic climate and killer whale ecological diversity worldwide.

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# CHAPTER 2. IDENTIFICATION OF TWO SYMPATRIC WESTERN NORTH ATLANTIC KILLER WHALE POPULATIONS: EVIDENCE FOR SECONDARY CONTACT IN ARCTIC WATERS

**Abstract:** Questions concerning killer whale (*Orcinus orca*) population structure in the western North Atlantic remain largely unanswered. In this chapter, I whole-genome sequenced western North Atlantic killer whale tissue samples to explore within-pod and population structure. Furthermore, I computed ABBA BABA statistics to test for introgression among western North Atlantic samples and those in a previously published global dataset. I describe two western North Atlantic clusters, one among samples collected in the Canadian High Arctic and the coastal waters of Newfoundland, and a second among those collected in the Canadian Low Arctic.  $F_{ST}$  between these two clusters was 0.23, indicating limited gene flow. High Arctic killer whales shared a marginally significant excess of derived alleles with killer whales sampled in Newfoundland and Brazil, whereas Low Arctic killer whales shared a significant excess of derived alleles with killer whales sampled in Greenland, Norway, and Iceland. Coupled with previous studies, these data suggest Canadian High Arctic killer whales are related to an ancestral Atlantic population, whereas Canadian Low Arctic killer whales are related to a population that expanded into the eastern North Atlantic post-Last Glacial Maximum. These findings contribute to an improved understanding of the species' demographic history, with particular reference to the western North Atlantic.

**Keywords:** Arctic, bioinformatics, population structure, geographic expansion, western North Atlantic, whole-genome sequencing



## INTRODUCTION

Rivaled only by modern humans, killer whales (*Orcinus orca*) are among the planet's most widely distributed mammals. Like humans, killer whales display considerable ecological specialization across their near-global range. In the eastern North Pacific, sympatric resident and transient populations occupy non-overlapping ecological niches (Ford et al. 1998; Saulitis et al. 2000). This is also true in Antarctic waters among type B1, B2, and C populations (Pitman and Ensor 2003; Durban et al. 2017). Such ecological specialization forms the basis of genetic isolation among killer whale populations worldwide (Foote et al. 2016). In the eastern North Atlantic, Foote et al. (2009) proposed two populations: a generalist fish- and seal-eating type, and a specialist whale-eating type. Foote et al. (2011) later genetically identified three populations: among Norway-Iceland killer whales, among Iceland-United Kingdom killer whales, and among Gibraltar-Canary Island killer whales. Despite increased research efforts in the western North Atlantic during the past decade (see Jourdain et al. 2019 for a review), questions concerning the occurrence of genetically isolated populations in this area remain unanswered. Moreover, it is unknown if western North Atlantic killer whales represent one or multiple populations, and how they are related to killer whales worldwide.

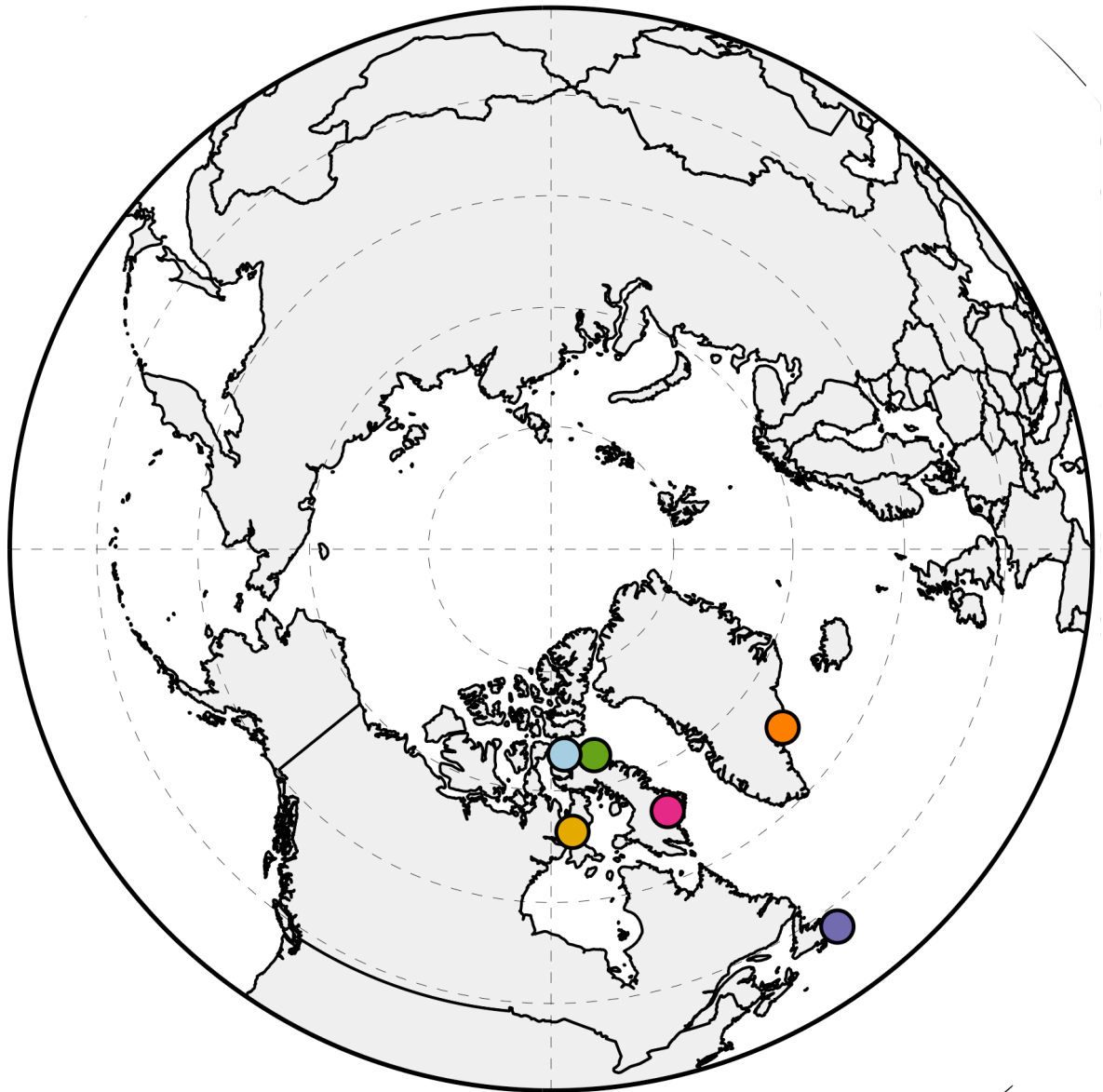
Recent advances in whole-genome sequencing have allowed for the high-resolution reconstruction of killer whale population histories (Morin et al. 2015; Foote et al. 2016, 2019). In this chapter, I adopt a similar approach and explore the population history of western North Atlantic killer whales, an area underrepresented in previous studies. I perform Principal Component Analysis (PCA) and Discriminant Analysis of

Principal Components (DAPC) to explore population structure among western North Atlantic killer whales. I compute pairwise kinship coefficients to explore within-pod (i.e., groups of whales sampled together) composition. Finally, I test for introgression among putative western North Atlantic populations and samples in a previously published global dataset (Foote et al. 2019) using ABBA BABA statistics. Ultimately, this chapter clarifies the species' global population structure with an emphasis on the western North Atlantic.

## METHODS

### *Sample collection*

Killer whale samples were collected throughout the western North Atlantic (Figure 2.1; Table 2.1). Tissue biopsies, comprising skin and blubber, were collected from free-ranging killer whales using a 150 lbs draw-weight crossbow and crossbow bolt equipped with a sterile tubular stainless steel biopsy tip ( $n = 20$ ). Additional tissue samples were collected from animals harvested in East Greenland ( $n = 6$ ). Teeth were collected opportunistically from fatally stranded killer whales ( $n = 3$ ).



**Figure 2.1.** Colored circles denote killer whale (*Orcinus orca*) tissue sampling locations throughout the western North Atlantic: Admiralty Inlet (near Arctic Bay, NU, Canada) in blue, Eclipse Sound (near Pond Inlet, NU, Canada) in green, Foxe Basin (near Repulse Bay, NU, Canada) in yellow, Cumberland Sound (near Pangnirtung, NU, Canada) in pink, Conception Bay (near Bauline, NL, Canada) in purple, and Ammasalik, Greenland in orange.

**Table 2.1.** Sample ID, sampling location, and collection year of killer whale (*Orcinus orca*) tissue samples whole-genome sequenced and included in the western North Atlantic analysis. Bolded samples were included in the global analysis.

| <b>Sample ID</b>       | <b>Location</b>                                    | <b>Year</b> |
|------------------------|--|-------------|
| ARAB-1948-MM406†       | Admiralty Inlet (near Arctic Bay, NU, Canada)      | 1948        |
| NL-1971-D118†          | Conception Bay (near Bauline, NL, Canada)          | 1971        |
| NL-2002-B042           | Newfoundland, Canada                               | 2002        |
| <b>ARRB-2009-1291†</b> | <b>Foxe Basin (near Repulse Bay, NU, Canada)</b>   | <b>2009</b> |
| EG-2012-48335          | Ammasalik, Greenland                               | 2012        |
| EG-2012-48336          | Ammasalik, Greenland                               | 2012        |
| EG-2012-48337          | Ammasalik, Greenland                               | 2012        |
| EG-2012-48338          | Ammasalik, Greenland                               | 2012        |
| EG-2012-48339          | Ammasalik, Greenland                               | 2012        |
| EG-2012-48340          | Ammasalik, Greenland                               | 2012        |
| <b>ARPI-2013-4001</b>  | <b>Eclipse Sound (near Pond Inlet, NU, Canada)</b> | <b>2013</b> |
| ARPI-2013-4002         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2013        |
| ARPI-2013-4003         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2013        |
| ARPI-2013-4004         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2013        |
| ARPI-2013-4005         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2013        |
| ARPI-2013-4006         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2013        |
| ARPI-2013-4007         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2013        |
| ARPA-2013-4001         | Cumberland Sound (near Pangnirtung, NU, Canada)    | 2013        |
| ARPI-2018-OO01         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2018        |
| ARPI-2018-OO02         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2018        |
| ARPI-2018-OO07         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2018        |
| ARPI-2018-OO10         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2018        |
| ARPI-2018-OO11         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2018        |
| ARPI-2018-OO13         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2018        |
| ARPI-2018-OO14         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2018        |
| ARPI-2018-OO15         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2018        |
| ARPI-2018-OO16         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2018        |
| ARPI-2018-OO17         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2018        |
| ARPI-2018-OO18         | Eclipse Sound (near Pond Inlet, NU, Canada)        | 2018        |

†denotes tooth samples

### *Genomic DNA library building and sequencing*

DNA was extracted from skin tissue (10-15 mg) using a Qiagen DNeasy blood and tissue kit (Valencia, CA, USA) following the Purification of Total DNA from Animal Tissues (Spin-Column Protocol) protocol. Pulp powder (or dentine powder from the surface layer of the root when pulp was not available) was collected from teeth using a hand drill and 3 mm ball-shaped diamond-coated drill bits surface-cleaned with ELIMINase Decontaminant. DNA was extracted from the powdered tooth (~100 mg) using a QIAamp DNA Investigator kit following the Isolation of Total DNA from Bones and Teeth protocol. Genomic DNA was sheared to ~150 bp using a Covaris LE220 (Woburn, MA, USA). Sequencing libraries were built using sheared DNA extracts using NEBNext Ultra II DNA Library Prep Kit for Illumina (Ipswich, MA, USA) and sequenced on the Illumina HiSeq X platform (San Diego, CA, USA).

### *Read trimming and mapping*

Read trimming, mapping, filtering, and repeat-masking were conducted following Foote et al. (2019). Briefly, Trimmomatic v0.35 (Bolger et al. 2014) was used to process reads to remove adapter sequences, trailing low-quality regions ( $Q < 20$ ), and N bases, and to drop reads  $< 31$  bases long. A high-quality reference genome assembly was used as a mapping reference (see Foote et al. 2016 for details). Processed reads were aligned to the mitochondrial genome using Burrows-Wheeler Aligner (BWA) v0.7.12 (Li and Durbin 2009). Unmapped reads were extracted using SAMtools v1.5 (Li et al. 2009) and aligned to the nuclear genome using BWA. GATK v3.7.0 was used to create an interval file for suspect indels, combined with high-confidence single-nucleotide

polymorphism (SNP) positions, and filtered to include only autosomal regions. Repeats and low-quality regions were masked using BEDtools v2.27.1. Biallelic SNPs were identified using FREEBAYES.

#### *Western North Atlantic population structure*

Principal Component Analysis (PCA) and Discriminant Analysis of Principal Components (DAPC; Jombart et al. 2010) were used to explore associations among samples, identifying groups of genetically similar individuals. These analyses were completed in the adegenet package (Jombart 2008; Jombart and Ahmed 2011) in R (R Core Team 2019). Euclidean genetic distances among samples were calculated in the poppr R package (Kamvar et al. 2014, 2015) and presented using a phylogenetic dendrogram (unweighted pair group method with arithmetic mean). The fixation index ( $F_{ST}$ ; Wright 1949; Weir and Cockerham 1984), a pairwise comparison of differences in allele frequencies among populations (where greater  $F_{ST}$  indicates greater genetic separation), was calculated among putative populations in the R package StAMPP (Pembleton et al. 2013). Pairwise kinship coefficients ( $\Phi$ ), the probability that randomly sampled homologous alleles from two individuals were identical-by-descent (i.e., copies of the same ancestral gene), among all pairs of individuals were calculated using the Maximum Likelihood Estimation Method in the R package SNPRelate (Zheng et al. 2012).

### *Global population structure*

One sample from each of the putative populations identified in this study was included in an analysis with samples representing the species' global range. SNPs from  $P_1$  (Canadian High Arctic) and  $P_2$  (Canadian Low Arctic) genomes were randomly sampled, thinning coverage to match the previously sequenced genomes. Associations among samples were investigated using PCA. ABBA BABA statistics (Patterson's D statistics) were used to test for introgression among  $P_1$ ,  $P_2$ , and samples in the global dataset (X) at sites where X had a derived allele (i.e., an allele different to that in an ancestral outgroup). The consensus genome from the common bottlenose dolphin (*Tursiops truncatus*) and the long-finned pilot whale (*Globicephala melas*), which I expected to be representative of the ancestral allele at each site (Foote et al. 2019), was used as the ancestral outgroup. I counted the number of sites where  $P_1$  (and not  $P_2$ ) shared a derived allele with X, and the number of sites where  $P_2$  (and not  $P_1$ ) shared a derived allele with X. If the initial population topology is true, neither  $P_1$  nor  $P_2$  should share a significant excess of derived alleles with samples from other regions. This test was repeated for each sample in the global dataset (see Foote et al. 2019 for details).

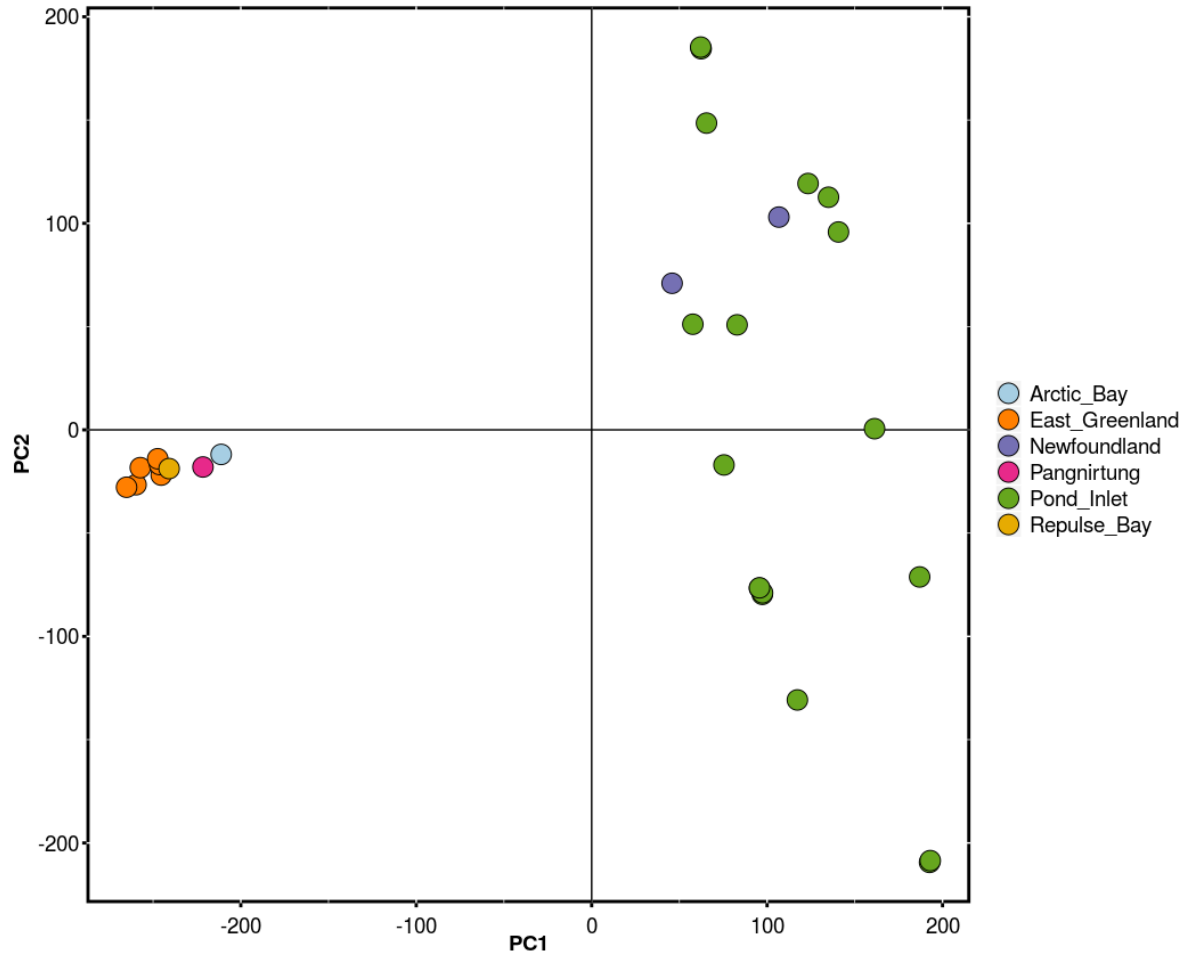
## RESULTS

### *Western North Atlantic population structure*

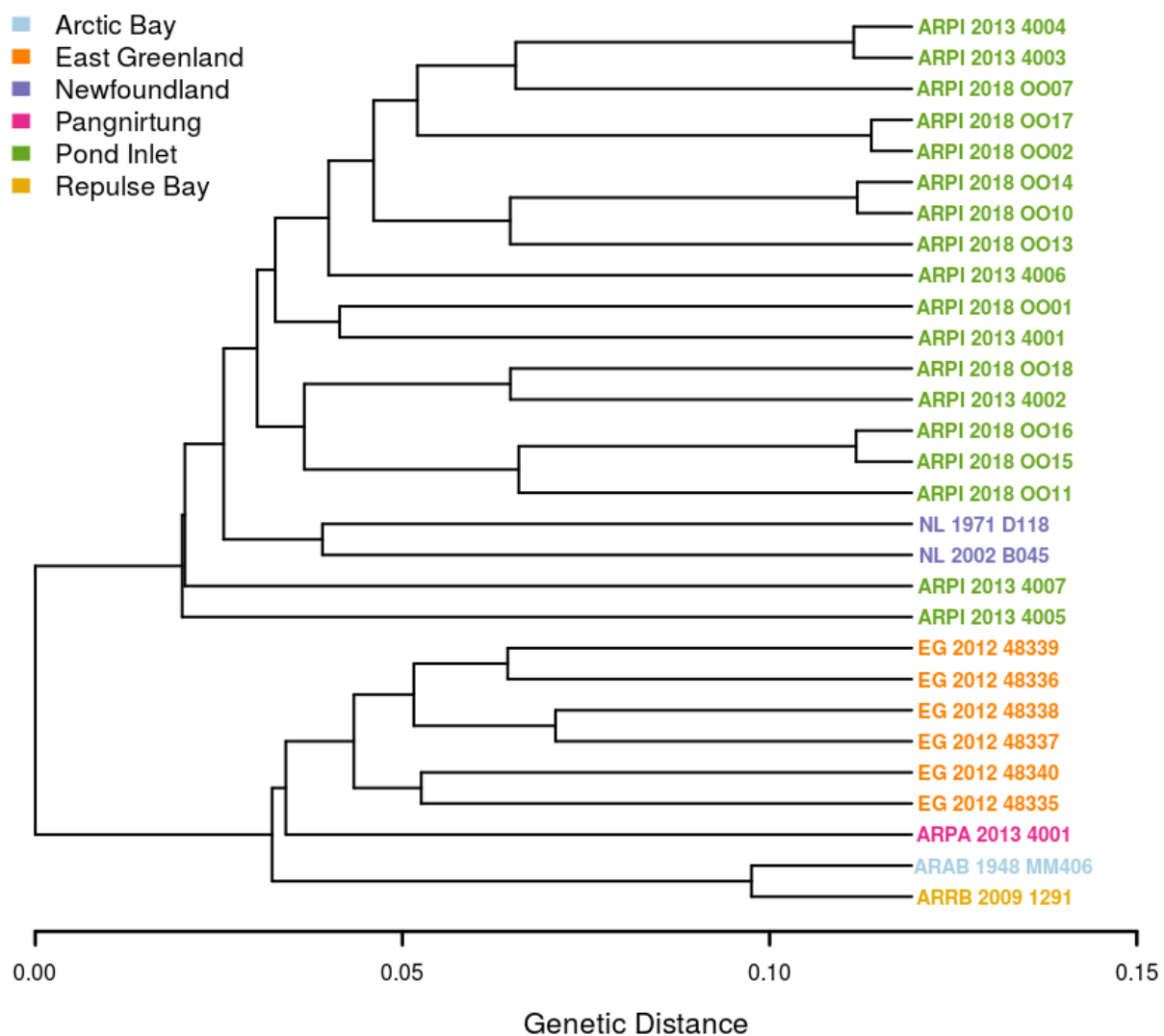
Principal component one (PC1), which explained 23.6% of the total observed variation, indicated two western North Atlantic clusters, one among samples collected in the Canadian High Arctic and the coastal waters of Newfoundland ( $P_1$ ), and a second among those collected in the Canadian Low Arctic and Greenland ( $P_2$ ) (Figure 2.2). PC2 (8.2%) indicated greater genetic diversity among  $P_1$  samples than among  $P_2$  samples (Figure 2.2). DAPC supported PCA inference: when  $K = 2$ , one cluster formed among  $P_1$  samples, and a second among  $P_2$  samples (also see Figure 2.3).  $F_{ST}$  between these two clusters was 0.23. Together, these data suggest two genetically distinct killer whale populations in the Canadian western North Atlantic.

Kinship coefficients supported PCA and DAPC inference. When kinship coefficients were calculated among all individuals from both populations, no identical-by-descent homologous alleles, thus no relatives, occurred between High Arctic and Low Arctic whales ( $\Phi = 0$ ; data not shown). When kinship coefficients were calculated within each cluster, distant relatives occurred between Newfoundland and Canadian High Arctic whales ( $\Phi \leq 0.02$ ; Figure 2.4). Both Canadian High Arctic pods comprised relatives ( $\Phi = 0.02-0.23$ ) and non-relatives (Figure 2.4). Relatives ( $\Phi = 0.01-0.23$ ) and non-relatives occurred between the two Canadian High Arctic pods (Figure 2.4). The Greenland pod comprised relatives ( $\Phi = 0.05-0.20$ ) and non-relatives and were not related to Canadian Low Arctic whales (Figure 2.5). Two Canadian Low Arctic whales were inbred ( $\Phi = 0.36$ ; Figure 2.5).

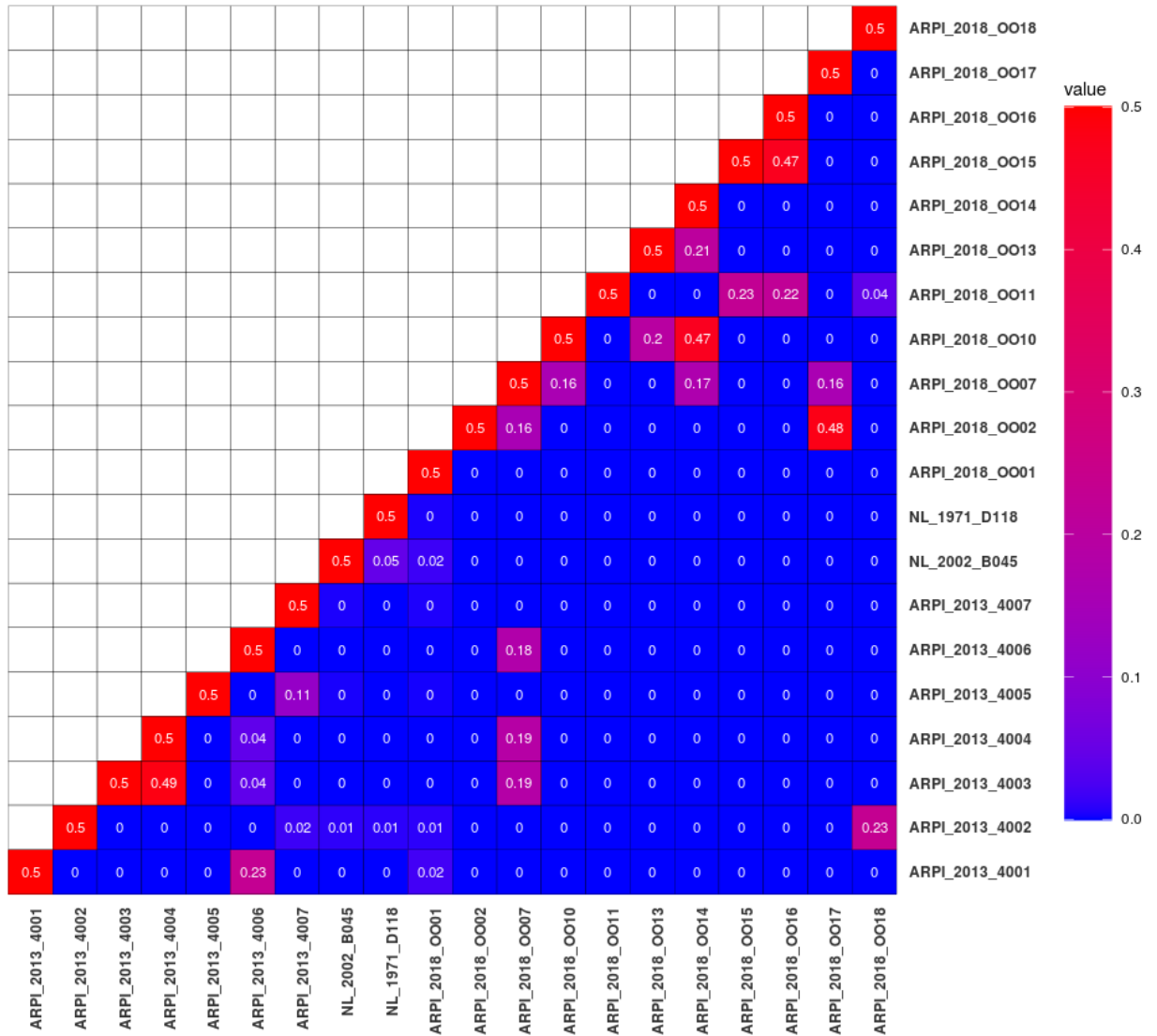




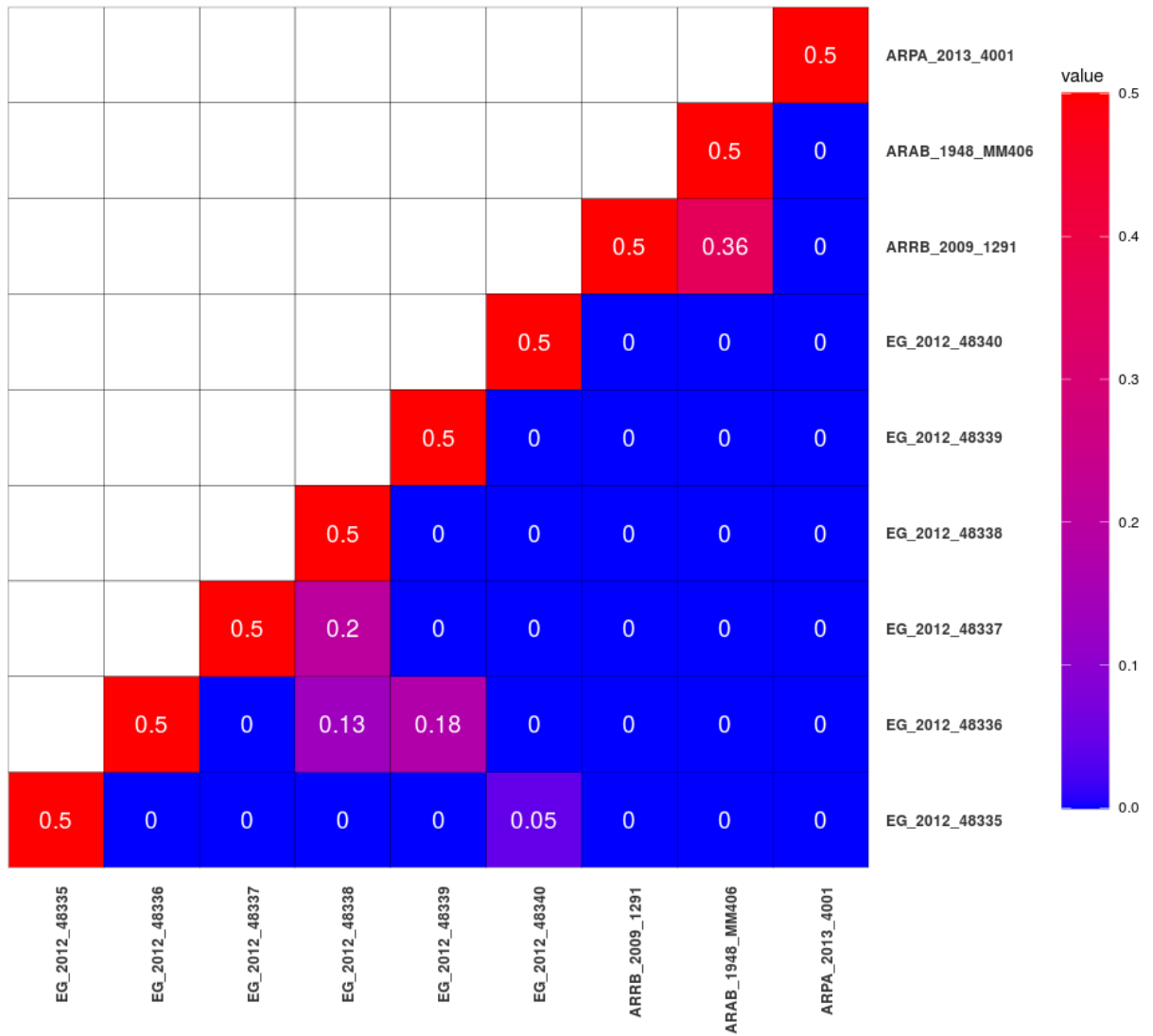
**Figure 2.2.** Principal components one (23.6%) and two (8.2%) demonstrate genetic divergence among whole-genome sequenced western North Atlantic killer whales (*Orcinus orca*).



**Figure 2.3.** Phylogenetic dendrogram (unweighted pair group method with arithmetic mean) displaying Euclidean genetic distances among whole-genome sequenced western North Atlantic killer whales (*Orcinus orca*).



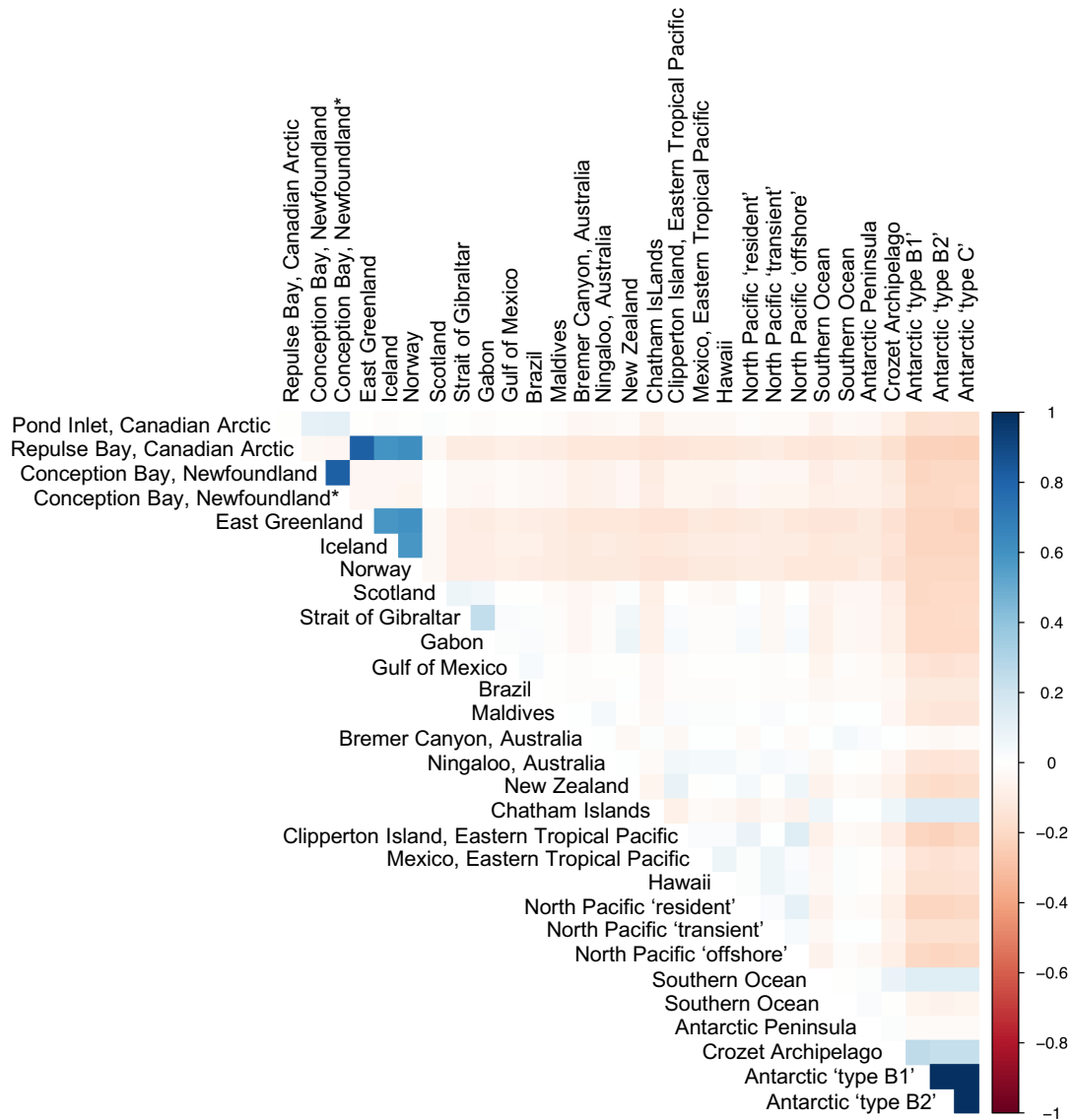
**Figure 2.4.** Pairwise kinship coefficients among Canadian High Arctic killer whales (*Orcinus orca*) calculated using the Maximum Likelihood Estimation Method.



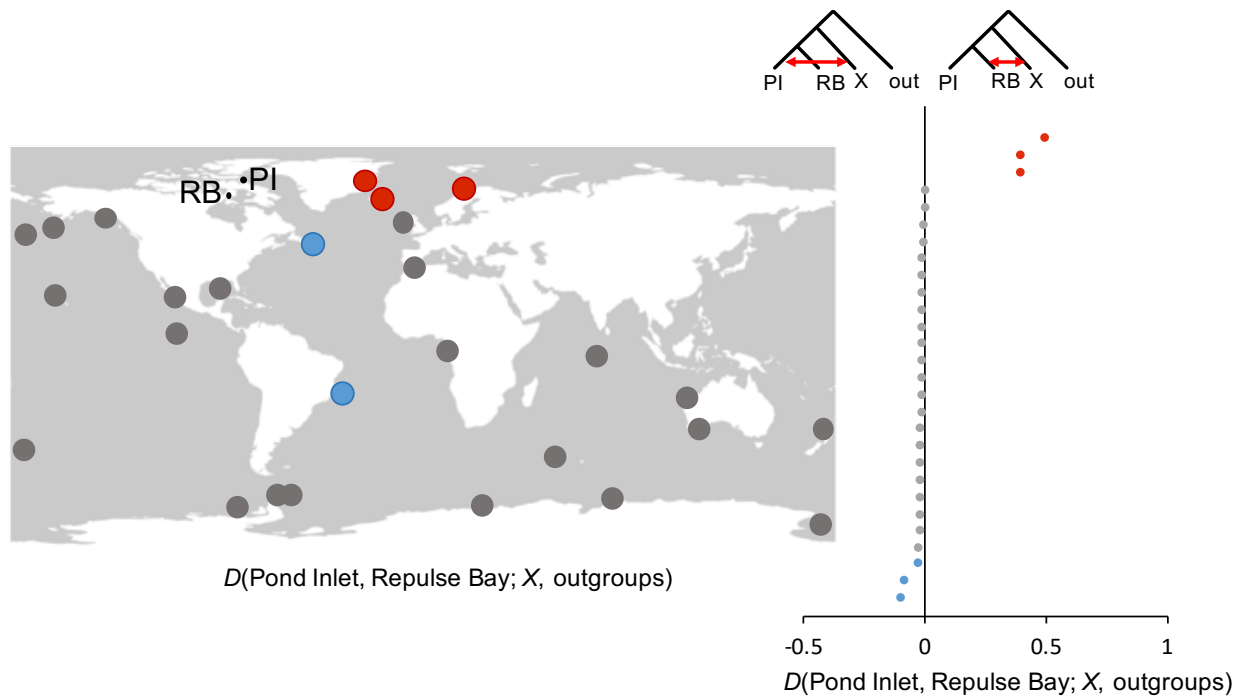
**Figure 2.5.** Pairwise kinship coefficients among Canadian Low Arctic killer whales (*Orcinus orca*) calculated using the Maximum Likelihood Estimation Method.

### *Global population structure*

Results from the global analysis supported those from the regional western North Atlantic analysis: the two western North Atlantic populations ( $P_1$ : Canadian High Arctic (Pond Inlet); and  $P_2$ : Canadian Low Arctic (Repulse Bay)) showed no covariance (Figure 2.6). High Arctic whales showed some covariance with Newfoundland, and Low Arctic whales showed strong covariance with eastern North Atlantic whales (Greenland, Norway, and Iceland). Neither High Arctic nor Low Arctic whales showed strong covariance with other regions. ABBA BABA statistics corroborated these findings. High Arctic whales shared a marginally significant excess of derived alleles with a whale sampled in Newfoundland, and Low Arctic whales shared a significant excess of derived alleles with whales sampled in Greenland, Norway, and Iceland (Figure 2.7; Table 2.2). Furthermore, I observed a marginally significant excess of derived alleles shared between High Arctic whales and a whale sampled in Brazil. All other comparisons were non-significant, indicating no excess sharing with other regions (Figure 2.7; Table 2.2).



**Figure 2.6.** Covariance matrix among whole-genome sequenced killer whales (*Orcinus orca*) from each of the two putative populations identified in this western North Atlantic study (P<sub>1</sub>: Pond Inlet, Canadian Arctic; and P<sub>2</sub>: Repulse Bay, Canadian Arctic) and those in a previously published global dataset (Foote et al. 2019). Figure created by Andrew Foote.



**Figure 2.7.** Whole-genome sequenced killer whales (*Orcinus orca*) included in the global ABBA BABA analysis, colour-coded based on the value of  $D(\text{Pond Inlet (PI), Repulse Bay (RB)}; \text{X, outgroup})$  and considered significant if  $Z > 3$  (red) or  $Z < -3$  (blue).

Figure created by Andrew Foote.

**Table 2.2.** nABBA, nBABA, jackknife-estimated D statistics, standard error, and Z scores among Canadian High Arctic (ARPI-2013-4001) and Canadian Low Arctic (ARRB-2009-1291) killer whales (*Orcinus orca*) and samples in the global dataset (see Foote et al. 2019). Bolded samples share a significant excess of derived alleles with one of the two Canadian Arctic populations.

| <b>Sample</b>           | <b>nABBA</b>  | <b>nBABA</b>  | <b>D Statistic</b> | <b>SE</b>     | <b>Z</b>        |
|-------------------------|---------------|---------------|--------------------|---------------|-----------------|
| <b>Greenland</b>        | <b>184152</b> | <b>61715</b>  | <b>0.4980</b>      | <b>0.0062</b> | <b>80.6499</b>  |
| <b>Iceland</b>          | <b>102320</b> | <b>43699</b>  | <b>0.4015</b>      | <b>0.0080</b> | <b>50.3432</b>  |
| <b>Norway</b>           | <b>102071</b> | <b>43430</b>  | <b>0.4030</b>      | <b>0.0082</b> | <b>49.2925</b>  |
| Scotland                | 63065         | 62784         | 0.0022             | 0.0084        | 0.2672          |
| ETP - Mexico            | 59801         | 59605         | 0.0016             | 0.0067        | 0.2457          |
| Antarctic Peninsula     | 59642         | 59727         | -0.0007            | 0.0066        | -0.1072         |
| Chatham Islands         | 57703         | 58556         | -0.0073            | 0.0069        | -1.0641         |
| Hawaii                  | 59858         | 60808         | -0.0079            | 0.0070        | -1.1278         |
| Transient               | 59781         | 60944         | -0.0096            | 0.0068        | -1.4219         |
| New Zealand             | 59153         | 60515         | -0.0114            | 0.0075        | -1.5083         |
| Bremer Canyon           | 58516         | 59837         | -0.0112            | 0.0066        | -1.6799         |
| Offshore                | 58454         | 60056         | -0.0135            | 0.0075        | -1.8009         |
| type B1                 | 52619         | 54169         | -0.0145            | 0.0078        | -1.8717         |
| type C                  | 53313         | 54835         | -0.0141            | 0.0074        | -1.8916         |
| Ningaloo                | 59251         | 60830         | -0.0131            | 0.0066        | -1.9931         |
| Maldives                | 57255         | 58904         | -0.0142            | 0.0069        | -2.0568         |
| Gabon                   | 60971         | 62800         | -0.0148            | 0.0070        | -2.0996         |
| resident                | 58175         | 60084         | -0.0161            | 0.0074        | -2.1791         |
| Southern Ocean          | 57268         | 59030         | -0.0152            | 0.0067        | -2.2725         |
| ETP - Clipperton Island | 61032         | 63520         | -0.0200            | 0.0081        | -2.4526         |
| Gulf of Mexico          | 61491         | 63791         | -0.0184            | 0.0074        | -2.4918         |
| type B2                 | 53920         | 56051         | -0.0194            | 0.0075        | -2.5978         |
| Southern Ocean          | 58167         | 60418         | -0.0190            | 0.0067        | -2.8186         |
| Gibraltar               | 60491         | 63252         | -0.0223            | 0.0078        | -2.8527         |
| Crozer                  | 56319         | 58670         | -0.0204            | 0.0061        | -3.3747         |
| <b>Brazil</b>           | <b>60320</b>  | <b>63118</b>  | <b>-0.0227</b>     | <b>0.0067</b> | <b>-3.3889</b>  |
| <b>Newfoundland</b>     | <b>58790</b>  | <b>70732</b>  | <b>-0.0922</b>     | <b>0.0084</b> | <b>-10.9827</b> |
| <b>D118_2</b>           | <b>92761</b>  | <b>108334</b> | <b>-0.0774</b>     | <b>0.0057</b> | <b>-13.5733</b> |



## DISCUSSION

### *Western North Atlantic population structure*

These results revealed two genetically distinct killer whale populations in the western North Atlantic: a Canadian High Arctic and Newfoundland population ( $P_1$ ) and a Canadian Low Arctic and Greenland population ( $P_2$ ) (Figure 2.2; Figure 2.3).  $F_{ST}$  between these two populations indicated greater genetic separation than between some of the better-studied Antarctic ecotypes (Foote et al. 2016); this level of separation strongly suggests no recent gene flow. Connectivity between the Canadian High Arctic and Newfoundland likely results from Arctic killer whales traversing eastern Canadian waters during their north-south seasonal migrations (Matthews et al. 2011; Lefort et al. 2020). Connectivity between Greenland and the Canadian Low Arctic presumably results from geographic overlap and possible seasonal east-west migrations.

Canadian High Arctic ( $P_1$ ) killer whales may have historically occurred in the western North Atlantic (Higdon et al. 2012; Lawson and Stevens 2014) and may be adapted to navigate unpredictable sea-ice environments (e.g., knowledge of when to depart to avoid sea ice; Matthews et al. 2011). I anticipate High Arctic killer whales will continue to be successful in Canadian Arctic waters, especially given forecasted decreases in seasonal sea-ice cover. Conversely, Canadian Low Arctic ( $P_2$ ) killer whales may be relatively new to Canadian Arctic waters (Higdon and Ferguson 2009); thus, may not be behaviorally adapted to navigate this unpredictable sea-ice environment. The frequency of killer whale ice entrapments in Hudson Bay, where Low Arctic killer whales occur during the summer, is increasing (Matthews et al. 2019). Matthews et al. (2019) suggested reduced sea-ice cover in Hudson Bay has allowed

killer whales increased summer access. However, without the culturally inherited geographic knowledge of this unpredictable sea-ice environment, Low Arctic whales may be subject to an increased risk of ice entrapments. In contrast, High Arctic killer whales may possess matrilineal knowledge of sea-ice formation patterns (Matthews et al. 2019).

Both Canadian High Arctic pods (ARPI-2013-400x and ARPI-2013-00xx) and the Greenlandic pod (EG-2012-483xx) comprised relatives and non-relatives (Figure 2.4; Figure 2.5), uncharacteristic of this cetacean often observed in matrilineal groups (Barrett-Lennard 2000). Williams and Lusseau (2006) demonstrated network fragmentation following removals from killer whale social networks, while Busson et al. (2019) demonstrated surviving members of pods responded by associating with other pods following removals. Taken together, it is possible pod composition observed in this study is an artifact of anthropogenic mortality in the Canadian Arctic (Lefort unpublished data), in the coastal waters of Greenland (NAMMCO), or residual effects from North Atlantic commercial whaling (Øien 1988).

### *Global population structure*

Coupled with Foote et al.'s (2019) findings, these data suggest Canadian High Arctic killer whales are related to an ancestral Atlantic population, whereas Canadian Low Arctic killer whales are related to a population that expanded into the eastern North Atlantic (Greenland, Iceland, Norway) post-Last Glacial Maximum (Figure 2.6; Figure 2.7). High Arctic and Low Arctic killer whale co-occurrence in Canadian Arctic waters is thus secondary contact between an ancestral Atlantic population and a derived sub-

Arctic population that drifted following a post-Last Glacial Maximum range expansion. Moreover, neither High Arctic nor Low Arctic killer whales showed strong covariance with any other non-Atlantic samples (Figure 2.6); thus, there is no evidence of secondary colonization of the North Atlantic (such as in the Eastern Tropical Pacific; Morin et al. 2015) and the separation detected among Canadian Arctic killer whales is likely driven by processes within the Atlantic.

### *Conclusions*

In this chapter, I identified two sympatric western North Atlantic killer whale populations: a Canadian High Arctic (and coastal Newfoundland) population ( $P_1$ ), and a Canadian Low Arctic population ( $P_2$ ). My results suggest limited gene flow between these populations. These may face population-specific threats and require population-specific conservation initiatives. For example, the Canadian High Arctic killer whale population size is small (Lefort et al. In Press); thus, should be a closely monitored. Moreover, Canadian Low Arctic killer whales have relatively low genetic diversity (Figure 2.2). Since Low Arctic killer whales are harvested in East Greenland (see NAMMCO) and are vulnerable to ice entrapments in Hudson Bay (see Matthews et al. 2019), then perhaps Low Arctic killer whales should be a conservation priority. However, even though few samples represent Low Arctic killer whales in this study, the Greenland-Iceland-Norway population(s) number in the hundreds of individuals (Samarra et al. 2017; Jourdain and Karoliussen 2018; Jourdain et al. 2019).

Additional samples, particularly from the Canadian Low Arctic, are required to further investigate population structure in the western North Atlantic. I do not discount

the possibility of additional population structuring in the western North Atlantic: killer whales in the coastal waters of Newfoundland have broad dietary niches, feeding on seabirds, fishes, and marine mammals (Lawson et al. 2007), whereas those in the Canadian Arctic have much narrower niches, feeding exclusively on marine mammals (Higdon et al. 2012; although see Matthews and Ferguson 2014). Such dietary differences, albeit coupled with genetic separation, have been used to discern population structure elsewhere, for example, fish-eaters and mammal-eaters in the eastern North Pacific (Ford et al. 1998; Saulitis et al. 2000).

Continued climate warming will promote shifting distributions as individuals track suitable conditions. This is particularly true in polar regions where climate warming has led to substantial ecosystem-level change. In the Canadian Arctic, previously inaccessible areas are becoming accessible (Stroeve et al. 2014). Species may shift poleward into these newly accessible areas resulting in modifications to the composition of biological communities. Previously non-overlapping closely related species (or in this case, populations) may hybridize (e.g., Garroway et al. 2010; Kelly et al. 2010), or single species (or populations) may radiate through peripatric or parapatric speciation as new habitat becomes available. Understanding how species are responding to climate change is required to predict and mitigate the effects of future change. Furthermore, a detailed understanding of killer whale population structure in Canadian Arctic waters is necessary for the effective management and conservation of this lesser-known Arctic cetacean.

## ACKNOWLEDGEMENTS

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# CHAPTER 3. KILLER WHALE ABUNDANCE AND PREDICTED NARWHAL CONSUMPTION IN THE CANADIAN ARCTIC

**Abstract:** Range expansions and increases in the frequency of killer whale (*Orcinus orca*) sightings have been documented in the eastern Canadian Arctic, presumably the result of climate change-related sea-ice declines. However, the effects of increased numbers of predators on this marine ecosystem remain largely unknown. In this chapter, I explore the consequences of climate change-related range expansions by a top predator by estimating killer whale abundance and their possible consumptive effects on narwhal (*Monodon monoceros*) in the Canadian Arctic. Individual killer whales can be identified using characteristics such as acquired scars and variation in the shape and size of their dorsal fins. Capture-mark-recapture analysis of 63 individually identifiable killer whales photographed between 2009 and 2018 suggests a population size of  $163 \pm 27$ . This number of animals, given our region-specific understanding of killer whale bioenergetics and feeding, could consume  $1290 \pm 214$  narwhals during their residency in Arctic waters. The effects of such mortality at the ecosystem level are currently uncertain, but trophic cascades caused by top predators, including killer whales, have been documented elsewhere. These findings illustrate the magnitude of ecosystem-level modifications that can occur with climate change-related shifts in predator distributions.

**Keywords:** bioenergetics, capture-mark-recapture, photographic identification, predation, range shifts, trophic cascades

## INTRODUCTION

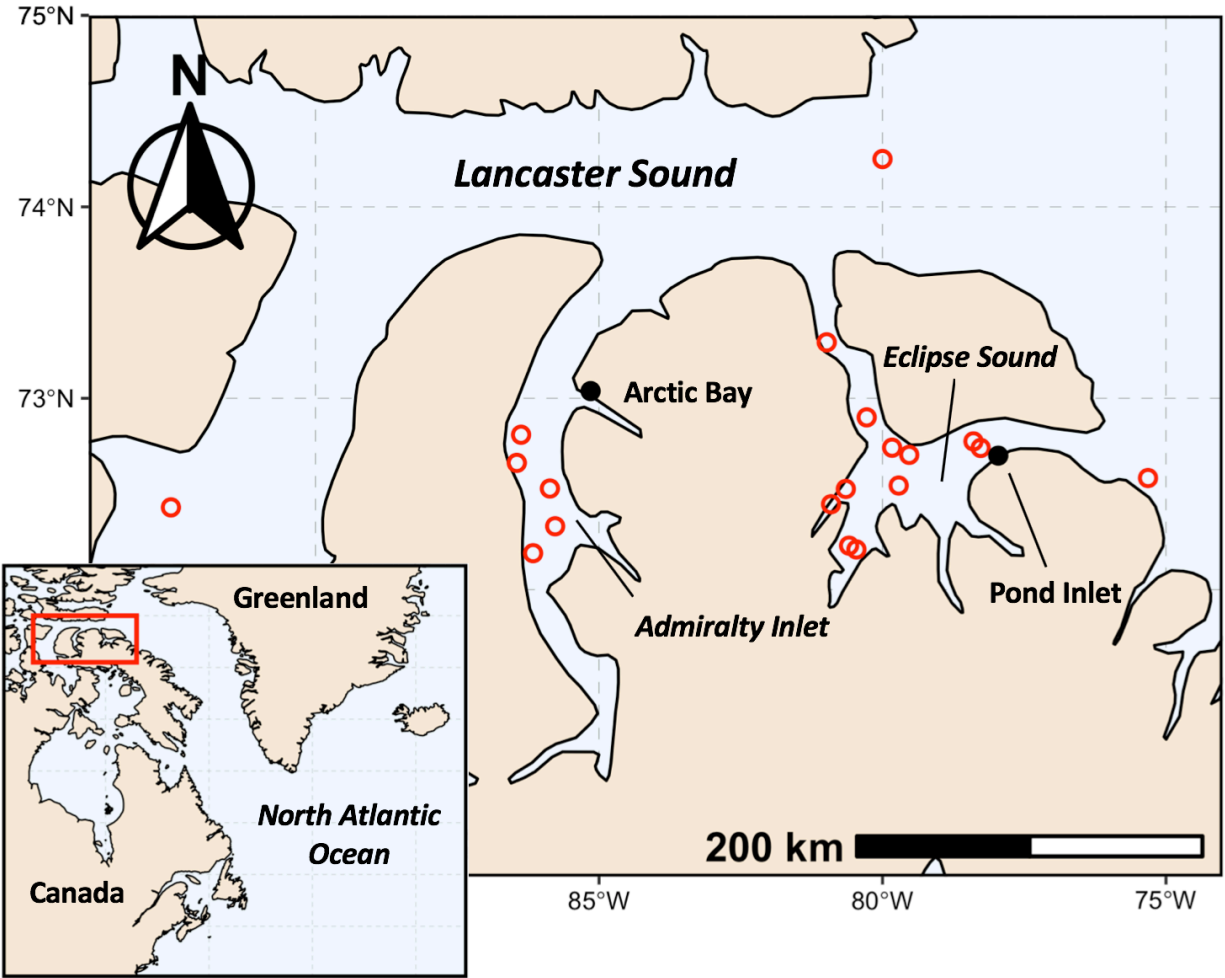
Climate warming and the resulting modifications to ecosystem structure have caused widespread shifts in species' distributions (Parmesan and Yohe 2003; Parmesan 2006), thereby altering the species composition of communities and interactions within communities (Hoffmann and Sgrò 2011). Generally, species' high-latitude range boundaries are defined by climate, whereas their low-latitude range boundaries are defined by interactions with competing species (MacArthur 1972). Thus, climate change-related expansions at species' high-latitude range boundaries may cause contractions in resident species whose ranges are being invaded (MacArthur 1972). The consequences of invaders are well documented and include the displacement of residents (e.g., Morse 1971) and interbreeding between invaders and residents (e.g., Garroway et al. 2010; Kelly et al. 2010). However, ecosystem-level consequences of invaders, particularly Arctic marine predators invading ecosystems supporting vulnerable prey, remain comparatively unexplored. Paine (1966) published the first account of ecosystem transformation via top-down trophic cascade. In Paine's influential study, mussel (*Mytilus californianus*) -consuming sea stars (*Pisaster ochraceus*) were removed from an experimental site. In control sites, sea stars dominated, mussels declined, and vegetation thrived. In experimental sites, mussels dominated and vegetation declined, demonstrating sea stars' top-down control of the rocky intertidal ecosystem. Five decades later, there is now indisputable evidence for predator's ecosystem influence via top-down processes (Pace et al. 1999; Ripple et al. 2014).

The killer whale (*Orcinus orca*) is a globally distributed marine predator with a broad ecological niche when considered at the species level, but with narrow well-differentiated niches among populations (Ford et al. 2000). Mammal-eating killer whales are summer visitors to eastern Canadian Arctic waters whose occurrence is purportedly ice restricted (Reeves and Mitchell 1988; Matthews et al. 2011). Questions concerning killer whale abundance in Canadian Arctic waters remain largely unanswered (Lefort et al. 2020). Killer whales have been reported as common in eastern Canadian Arctic waters (0.20-0.40 individuals per 100 km<sup>2</sup>; Forney and Wade 2006) and Young et al. (2011) identified 53 individuals during a six-year photographic-identification study. Range expansions and increases in the frequency of killer whale sightings are thought to have begun in the mid-1900s and have been attributed to climate change-related sea-ice declines (Higdon and Ferguson 2009). In Canada's northern Baffin Island region, killer whales are now regular summer occupants (Higdon et al. 2014) and remain in the region for the duration of the open-water season (Matthews et al. 2011; Lefort et al. 2020). During this time, killer whales feed primarily on narwhal (*Monodon monoceros*) and ringed seals (*Pusa hispida*) (Ferguson et al. 2012). Large mammalian predators are capable of influencing ecosystems via top-down processes (Ripple et al. 2014) — killer whales are no exception (Estes et al. 1998; Springer et al. 2003, 2008; although see DeMaster et al. 2006; Mizroch and Rice 2006; Trites et al. 2007; Wade et al. 2007).

The narwhal is an endemic Arctic whale with a pan-Arctic distribution. In the late spring, thousands of narwhal migrate to summering areas off Baffin Island's northern coast, returning to offshore overwintering areas in Baffin Bay in the late fall (Doniol-

Valcroze et al. 2015). These narwhal are harvested predominantly by the Canadian Indigenous communities of Pond Inlet and Arctic Bay (Figure 3.1); although they are also occasionally harvested by other northern Canadian and Greenlandic communities in other areas during other seasons (Watt et al. 2019). Northern Baffin Island narwhal summering areas (e.g., Admiralty Inlet and Eclipse Sound; Figure 3.1) were historically partially ice-covered into the late summer (Dyke et al. 1996), providing narwhal with access to refugia from ice-restricted killer whales — this is no longer available.

In this chapter, I assess the consequences of marine predator range expansions by estimating killer whale abundance in Canada's northern Baffin Island region using capture-mark-recapture analysis of photographically identifiable killer whales. This estimate is used to parameterize a bioenergetics model to explore the potential consumptive effects of killer whale predation on narwhal in the Canadian Arctic. My results offer insight into the possible predator-mediated effects of killer whales on a culturally valuable prey species.



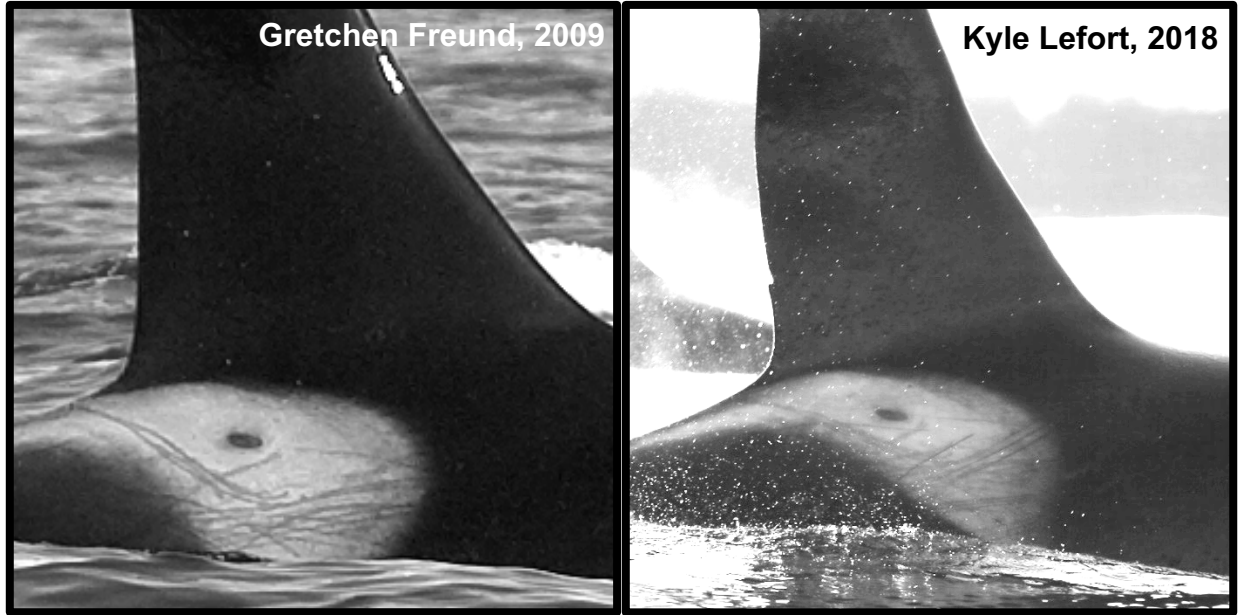
**Figure 3.1.** Canada's northern Baffin Island region with the approximate location of killer whale (*Orcinus orca*) encounters where photographs were collected (2009-2018).



## METHODS

### *Photograph collection and processing*

Individual killer whales can be identified using characteristics such as variation in the shape, size, and color of their dorsal fins, saddle patches, and eye patches; and scars, primarily on the trailing edge of their dorsal fins and saddle patches (Bigg et al. 1986; Figure 3.2). Dedicated boat-based surveys, which varied in their spatiotemporal coverage of the study area, were completed during the open-water season. Effort was focused in areas where killer whales had been previously sighted, and therefore was non-random and biased towards areas adjacent to coastal communities (Figure 3.1). Photographs for individual identification were collected using a Canon EOS-1DX DSLR camera equipped with either a 24-70 mm lens, a 70-200 mm telephoto lens with 1.4x or 2.0x extender, or a 400 mm fixed lens. Additional photographs were collected by citizen scientists during opportunistic encounters (i.e., cruise ship-based encounters). When possible, all individuals in an encountered group were photographed. I produced a photographic-identification catalog containing all identified individuals using right-side photographs. Left-side photographs were excluded to avoid double-counting individuals and because right-sides were preferentially photographed. Only high-quality photographs suitable for individual identification were included in this analysis. A matrix of identification histories was constructed with each cell assigned the value of 1 or 0 to indicate whether an individual was captured during a given survey year.



**Figure 3.2.** An example of saddle patch markings used to identify individual killer whales (*Orcinus orca*).

### *Estimating abundance*

I used Jolly-Seber POPAN capture-mark-recapture models to estimate population size from individual capture histories. In these models, apparent survival ( $\Phi$ ), capture probability ( $\rho$ ), and the probability of entry into the population ( $\beta$ ) are used to estimate the cumulative number of animals born into the population, hereafter super-population size ( $N$ ). I selected open Jolly-Seber models as immigration-emigration and births-deaths were likely during this ten-year study (Schwarz and Arnason 2019). I made the following assumptions: (1) all individuals had equal capture probabilities, (2) all individuals had equal survival probabilities, (3) markings used for identification remained constant, (4) sampling occasions were instantaneous, and (5) the study area remained constant. Eight variations of the model were fit with constant or time-dependent  $\Phi$ ,  $\rho$ , and  $\beta$  (Table 1). Akaike's Information Criterion corrected for small sample sizes (AICc) was used to select the best-fitting model while accounting for model complexity (Burnham and Anderson 2002). All analyses were conducted in Program MARK using the RMark interface (Laake 2013) in R (R Core Team 2019).

Similar studies have corrected their population size estimates according to an estimate of the proportion of the population lacking characteristics allowing for individual identification (Durban et al. 2010; Kuningas et al. 2014). In such studies, unidentifiable individuals are excluded from the analysis, but the resulting estimates are divided by the proportion of identifiable individuals in photographs (and thus, identifiable individuals in the population). In this study, the proportion of identifiable individuals in the population was unknown due to a large number of low-quality photographs; thus, I present the model-estimated number of identifiable individuals, as well as a corrected estimate

assuming the proportion of identifiable individuals in the population was  $\frac{2}{3}$ . This correction follows similar studies completed around the Aleutian Islands and Gulf of Alaska (Durban et al. 2010) and in northern Norway (Kuningas et al. 2014).

### *Estimating energetic requirements*

I used a length-at-age Gompertz growth function [Equation 1] in combination with a mass-at-length power function [Equation 2] to estimate killer whale mass-at-age in all sex-age classes (see Williams et al. 2011). Field metabolic rates (FMRs) for killer whales in each sex-age class were calculated from body mass ( $m$ ) assuming daily field metabolic rates of 5.5x Kleiber (1975) -predicted basal metabolic rates [Equation 3]. This method was selected as the FMRs of similar marine mammals range from five to six times Kleiber-predicted basal metabolic rates (see Noren 2011). For comparison, Noren (2011) assumed northern resident killer whale FMRs to range between five and six times Kleiber-predicted basal metabolic rates (according to the equations  $FMR = 350 \times m^{0.75}$  and  $FMR = 420 \times m^{0.75}$ , respectively, where  $m$  is body mass in kg), while Williams et al. (2004) assumed adult Alaskan transient killer whale FMRs to be 5.8x Kleiber-predicted basal metabolic rates (according to the equation  $FMR = 406 \times m^{0.756}$ ). Daily prey energetic requirements (DPERs) for killer whales in each sex-age class were calculated by dividing FMRs by 0.847 to account for killer whale's digestive efficiency [Equation 4] (Williams et al. 2004). The relative contribution of each age-sex class to the population's DPERs was calculated as the product of the proportion of the population (generated using survival probabilities at-age of the better-studied northeastern Pacific northern resident population; Olesiuk et al. 2005) and the DPERs for an individual in

each age-sex class. The sum of these products,  $DPER_{total}$ , are the DPERs for an individual of weighted-mean age and sex.

$$[1] L = a \times e^{-b \times e^{-c \times A}}$$

where  $L$  is length in cm,  $A$  is age in years,  $a_{male} = 629.1$ ,  $a_{female} = 558.7$ ,  $b = e^{-0.22}$ ,  $c_{male} = e^{-1.7}$ , and  $c_{female} = e^{-1.3}$  (generated using data from captive killer whales of Icelandic origin caught in the live-capture fishery).

$$[2] m = a \times L^b$$

where  $m$  is body mass in kg,  $L$  is length in cm,  $a = 6.7^{-5}$ , and  $b = 2.8$  (generated using data from northeastern Pacific northern resident, southern resident, and transient killer whales; and killer whales of Icelandic origin caught in the live-capture fishery).

$$[3] FMR = 385 \times m^{0.75}$$

where FMR is in kcal/d and  $m$  is body mass in kg.

$$[4] DPER = 454.5 \times m^{0.75}$$

where DPER is in kcal/d and  $m$  is body mass in kg.

### *Estimating narwhal mortality*

To estimate the number of narwhal killed by killer whales, I divided the killer whale population's seasonal energetic requirements by a single narwhal's energy content, under several scenarios, using the following calculation:

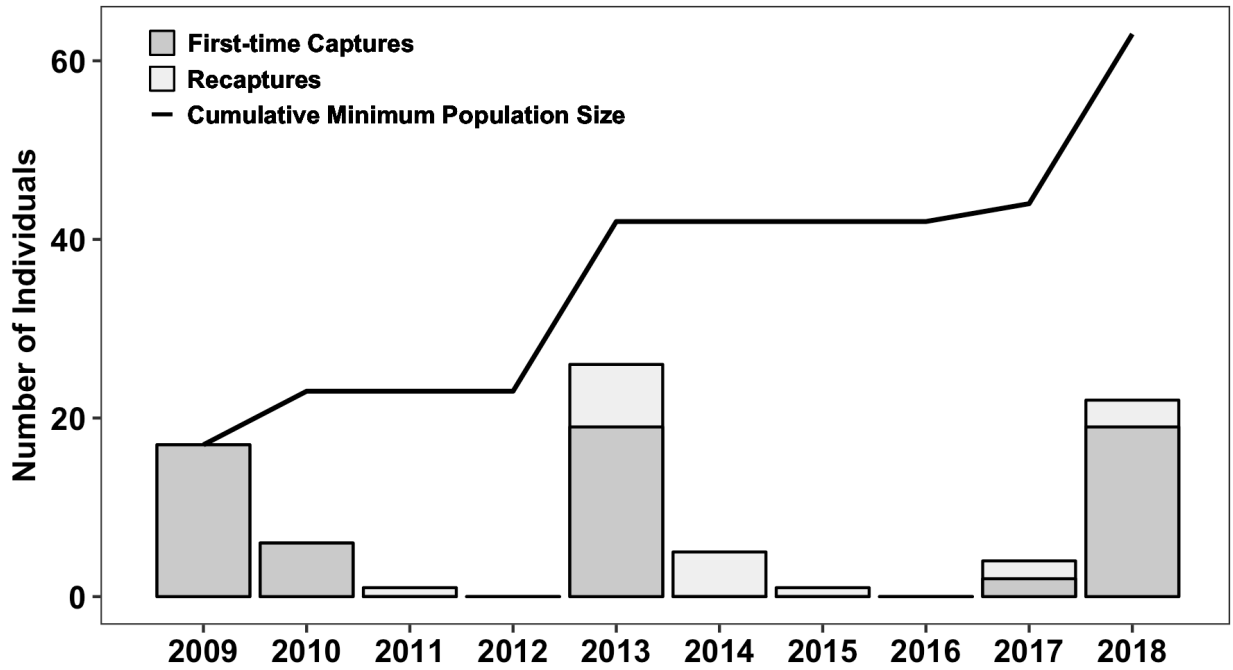
$$\# \text{ narwhal killed} = \frac{DPERS_{total} \times N \times t \times pDiet}{U_{Nar} \times m_{Nar} \times pConsumed}$$

where  $DPERS_{total}$  are the daily prey energetic requirements of a killer whale of weighted-mean age and sex,  $N$  is the super-population size,  $t$  is the number of days killer whales occupy the study area,  $pDiet$  is the proportion that narwhal contributes to killer whale diet,  $U_{Nar}$  is narwhal energetic density,  $m_{Nar}$  is narwhal mass, and  $pConsumed$  is the proportion of a narwhal consumed during a predation event.

Killer whale sightings are reported in the northern Baffin Island region between June and October (Higdon et al. 2012; Ferguson unpub. data). Satellite-tracking studies confirm that killer whales depart the region between mid-September and early October (Matthews et al. 2011; Lefort et al. 2020); thus, I assumed a 90-day residency. I assumed narwhal energetic density ( $U_{Nar}$ ) was 2500 kcal kg<sup>-1</sup>; this estimate has been used in similar studies (Estes et al. 2009) and matches the energetic densities of similar marine mammals (Williams et al. 2004). Mature male and female narwhals weigh 1600 kg and 900 kg, respectively (Heide-Jørgensen 2017). Indigenous knowledge suggests killer whales prey exclusively on females (Higdon et al. 2012); however, predation on males has been observed (C.J.D. Matthews personal observation, 2013). In this study, I assumed the mass of each narwhal consumed ( $m_{Nar}$ ) was 800 kg, accounting for probable selective predation on females, and for predation on non-adults (K.J. Lefort personal observation, 2019). The number of narwhal killed by killer whales was estimated as a function of  $pConsumed$  under ten  $pDiet$  scenarios where narwhal accounted for 0-100% of killer whale diet, in increments of 10%.

## RESULTS

Sixty-three individual killer whales were identified from photographs collected during this ten-year study (Figure 3.3), eleven of which were recaptured at least once (Figure 3.4). The number of years during which an individual was sighted at least once ranged from one to four; thus, some individuals are returning to the eastern Canadian Arctic seasonally. The best-fitting Jolly-Seber model had constant apparent survival ( $\Phi$ ), constant probability of entry into the population ( $\beta$ ), and time-dependent capture probability ( $\rho$ ), and produced a population size estimate of  $109 \pm 18$  (Table 3.1). Correction for unidentifiable individuals yielded a total population size estimate of  $163 \pm 27$ . While time-dependent capture probabilities in the best-fitting model indicate interannual variability in the probability of capturing whales, this is likely due to variable annual survey effort. These are impossible to parse. Male (486–4597 kg) DPERs ranged from 47,053 to 253,803 kcal day<sup>-1</sup>, while female (349–3297 kg) DPERs ranged from 36,673 to 197,816 kcal day<sup>-1</sup>. DPERs<sub>total</sub>, the DPERs for an individual of weighted-mean age and sex, was 175,876 kcal day<sup>-1</sup>. In one possible scenario ( $p_{\text{Diet}} = \frac{3}{4}$  and  $p_{\text{Consumed}} = \frac{3}{4}$ ), this number of killer whales would consume  $1290 \pm 214$  narwhal during a 90-day residency (Figure 3.5).

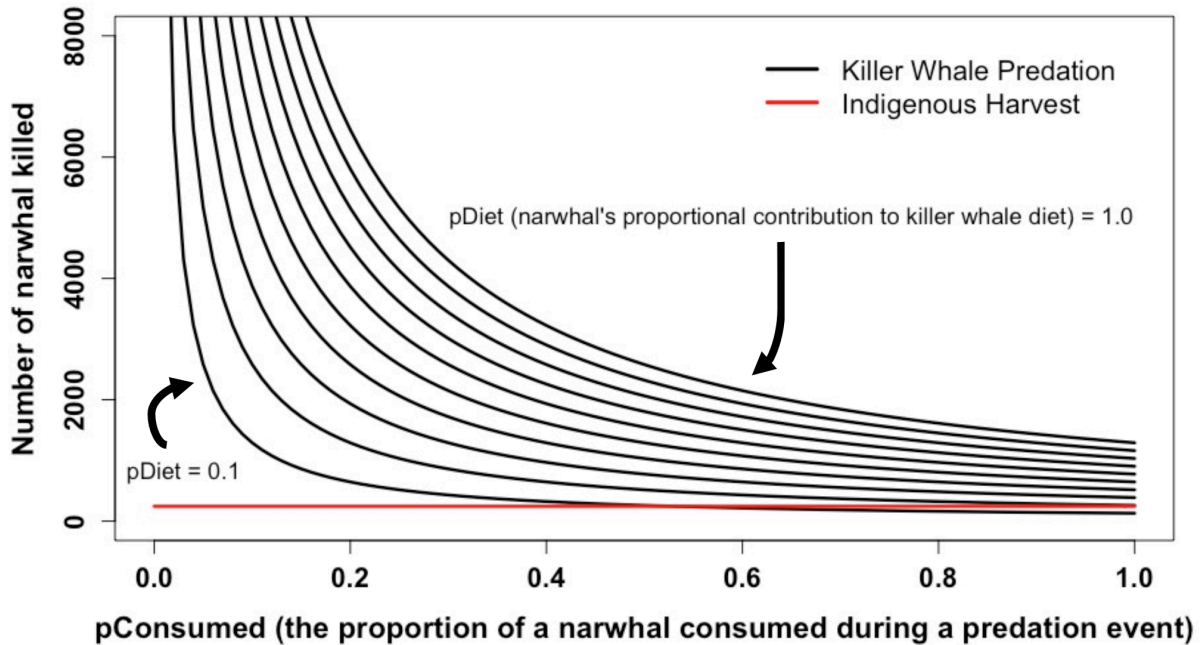


**Figure 3.3.** Cumulative minimum number of killer whales (*Orcinus orca*), number of first-time captures, and number of recaptures in Canada's northern Baffin Island region (2009-2018).



| <i>n</i> | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 |
|----------|------|------|------|------|------|------|------|------|------|------|
| 19       |      |      |      |      |      |      |      |      |      | ■    |
| 15       | ■    |      |      |      |      |      |      |      |      |      |
| 15       |      |      |      |      | ■    |      |      |      |      |      |
| 3        |      |      |      |      | ■    | ■    |      |      |      |      |
| 3        |      | ■    |      |      | ■    |      |      |      |      |      |
| 2        |      |      |      |      |      |      |      |      | ■    |      |
| 1        | ■    |      |      |      | ■    |      |      |      | ■    | ■    |
| 1        | ■    |      |      |      | ■    |      | ■    |      |      | ■    |
| 1        |      | ■    | ■    |      | ■    | ■    |      |      |      |      |
| 1        |      | ■    |      |      |      |      |      |      |      |      |
| 1        |      | ■    |      |      | ■    | ■    |      |      |      | ■    |
| 1        |      |      |      |      | ■    |      |      |      | ■    |      |

**Figure 3.4.** Individual Canadian Arctic killer whale (*Orcinus orca*) capture histories. Filled squares denote years during which individuals were captured. *n* denotes the number of individuals with each unique capture history.



**Figure 3.5.** The number of narwhal (*Monodon monoceros*) killed by killer whales (*Orcinus orca*) in Canada’s northern Baffin Island region, estimated as a function of  $p_{\text{Consumed}}$  (the proportion of a narwhal consumed during a predation event) under ten  $p_{\text{Diet}}$  (the proportion that narwhal contributes to killer whale diet) scenarios:  $x_n = x_{n-1} + 0.1$  where  $x_1 = 0.1$ . For context, the red horizontal line shows the region’s mean annual Indigenous narwhal harvest (2006-2015; Watt and Hall 2018).

**Table 3.1.** Jolly-Seber POPAN capture-mark-recapture model AICc values, estimated killer whale (*Orcinus orca*) super-population sizes ( $N$ )  $\pm$  standard errors (Std Err), lower confidence levels (LCL), and upper confidence levels (UCL). Time-dependent and constant apparent survival ( $\Phi$ ), capture ( $\rho$ ), and entry ( $\beta$ ) probabilities are denoted by the subscripts "t" and ".", respectively. Models are ordered according to AICc values.

| <b>Model</b>                             | <b>AICc</b> | <b><math>N \pm</math> Std Err</b> | <b>LCL</b> | <b>UCL</b> |
|--|-------------|-----------------------------------|------------|------------|
| { $\Phi(\cdot)\rho(t)\beta(\cdot)$ }     | 164.48      | 108.85 $\pm$ 18.22                | 84.65      | 160.10     |
| { $\Phi(t)\rho(t)\beta(\cdot)$ }         | 176.78      | 103.36 $\pm$ 42.55                | 70.41      | 282.73     |
| { $\Phi(\cdot)\rho(t)\beta(t)$ }         | 179.68      | 120.43 $\pm$ 23.56                | 89.51      | 187.41     |
| { $\Phi(t)\rho(t)\beta(t)$ }             | 199.83      | 65.24 $\pm$ 3.61                  | 63.25      | 83.54      |
| { $\Phi(t)\rho(\cdot)\beta(t)$ }         | 208.06      | 131.23 $\pm$ 24.95                | 97.08      | 199.61     |
| { $\Phi(\cdot)\rho(\cdot)\beta(t)$ }     | 216.13      | 131.50 $\pm$ 24.46                | 97.74      | 198.06     |
| { $\Phi(t)\rho(\cdot)\beta(\cdot)$ }     | 245.01      | 142.30 $\pm$ 28.50                | 103.04     | 220.02     |
| { $\Phi(\cdot)\rho(\cdot)\beta(\cdot)$ } | 268.20      | 145.53 $\pm$ 28.65                | 105.61     | 222.85     |

## DISCUSSION

In this chapter, I generate estimates of mammal-eating killer whale abundance and their consumption of narwhal in the Canadian Arctic. Forney and Wade (2006) report killer whales as common (0.20-0.40 individuals per 100 km<sup>2</sup>) in the eastern Canadian Arctic. Northern Baffin Island narwhal occupy 60,000 km<sup>2</sup> during the summer (COSEWIC 2004). If we assume killer whales occupy this same area, this study's estimate of 163±27 is comparable to Forney and Wade's (60 000 km<sup>2</sup> \* 0.20-0.40 individuals per 100 km<sup>2</sup> = 120-240 individuals). Even under a conservative scenario, this population of killer whales could consume >1000 narwhal during the open-water season (Figure 3.5). While I cannot speak to the likelihood of narwhal population declines in Canadian Arctic waters with this data, the potential for killer whale-mediated prey population declines have been recorded elsewhere (e.g., Estes et al. 1998; Reisinger et al. 2011). Furthermore, killer whale's non-consumptive effects on narwhal in the Canadian Arctic are known to be substantial (see Breed et al. 2017).

Canadian Arctic killer whales avoid sea ice (Reeves and Mitchell 1988; Matthews et al. 2011), presumably due to the risk of entrapment (Matthews et al. 2019). Furthermore, recent studies suggest some high-latitude killer whales may not possess the physiological ability to tolerate cold water for extended periods (Durban and Pitman 2012; Pitman et al. 2019). Continued Arctic warming may allow killer whales increased access to a spatiotemporally greater open-water season (Higdon and Ferguson 2009). Consequently, killer whales may extend their distribution farther into the Canadian Arctic Archipelago, and remain in Arctic waters for longer, as documented in the North Pacific Arctic (see Stafford 2019). Increased predation in areas now lacking seasonal sea ice

may result in increased narwhal mortality, narwhal population declines, and a range contraction as narwhal's southern range boundary shifts poleward into areas with greater sea-ice cover. Narwhal population declines or shifts in their distribution could have socioeconomic and food security consequences for Indigenous communities reliant on narwhal both in Canada and Greenland.

Few recaptures, likely an artifact of low killer whale density, hindered the use of more-informative capture-mark-recapture models (e.g., spatially explicit models) which require more data; nonetheless, our estimates appear reasonable given the frequency of killer whale sightings and reported group sizes in the eastern Canadian Arctic (Ferguson unpublished data). Improvements to these estimates will require additional survey effort to overcome the challenges associated with studying mobile marine predators in difficult-to-access areas (Mallory et al. 2018). Additional uncertainty arises due to limited knowledge of the proportion that narwhal contributes to killer whale diet ( $p_{\text{Diet}}$ ) and the proportion of a narwhal consumed during a predation event ( $p_{\text{Consumed}}$ ). Underestimates of the number of narwhal killed could result from the partial consumption of narwhal, surplus killing, or if killer whales are feeding exclusively on narwhal (alternatively, killer whales may be feeding on other prey, such as ringed seals). Observational data bearing on these potential issues do not exist. Underestimates of the number of narwhal killed could also result from increased feeding rates during the short productive summer, or if residency time is  $> 90$  days. An improved region-specific understanding of killer whales will allow for strengthened estimates and for consumptive effects on other prey species to be considered.

Despite uncertainties, quantifying the effects of killer whale predation on narwhal, a species of cultural significance to Indigenous communities in northern Canada and Greenland, is necessary for effective narwhal management. Narwhal are listed as Special Concern by the Committee on the Status of Endangered Wildlife in Canada due to uncertainty in the population's size, population trends, and life history parameters; the potential effects of climate change; and the effects of hunting, both in Canada and Greenland (COSEWIC 2004); thus, narwhal must be carefully managed. Predators fill influential roles in marine ecosystems worldwide (Heithaus et al. 2008). Killer whale occurrence in the Canadian Arctic is on the rise (Higdon and Ferguson 2009) and it is likely that use of the region will only increase. In this chapter, I demonstrate the scope for killer whale predation to influence narwhal populations in the eastern Canadian Arctic. It is unknown how far across the Canadian Arctic marine ecosystem the influence of increased killer whale occurrence could cascade. These findings illustrate the possible magnitude of effects on narwhal populations caused by a climate-change related killer whale range expansion into Canadian Arctic waters.

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## CHAPTER 4. GENERAL CONCLUSIONS

In this thesis, I use Canadian Arctic killer whales (*Orcinus orca*) as a case study to explore the consequences of climate change-related predator range expansions. Killer whale occurrence in Canadian Arctic waters is ice-restricted and it has been suggested that climate change-related sea-ice declines have led to increased killer whale occurrence during the open-water season (Higdon and Ferguson 2009). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has designated Canadian Arctic killer whales as Special Concern due to the population's small size; the species' life history; and threats from hunting, acoustical and physical disturbance, and contaminants (COSEWIC 2008). Despite increased research efforts during the last decade (see Higdon and Ferguson 2009, 2014; Matthews et al. 2011, 2019, 2020a, 2020b; Young et al. 2011, 2020; Ferguson et al. 2012a, 2012b; Higdon et al. 2012, 2014; Reinhart et al. 2013; Westdal et al. 2013, 2016, 2017; Matthews and Ferguson 2014; Breed et al. 2017) many questions concerning killer whales and their influence on the Canadian Arctic marine ecosystem remain unanswered.

In chapter one, I review our knowledge of Canadian Arctic killer whale ecology and identify killer whale research priorities in the Canadian Arctic. These include furthering our understanding of the population's structure, demographics, spatial ecology, and feeding ecology. Two of these research priorities are addressed in chapters two and three. In chapter two, I explore killer whale population structure in the western North Atlantic using whole-genome sequenced samples. I describe two genetically distinct populations: one among Canadian High Arctic and Newfoundland killer whales, and a second among Canadian Low Arctic and Greenlandic killer whales.



$F_{ST}$  between these populations suggests limited gene flow. Comparison with previously published genomes suggests Canadian High Arctic killer whales are related to an ancestral Atlantic population, whereas Canadian Low Arctic killer whales are related to a population that diverged from the ancestral Atlantic population and expanded into the eastern North Atlantic (Greenland, Iceland, Norway) post-Last Glacial Maximum (Foote et al. 2019). Canadian High Arctic and Canadian Low Arctic killer whale co-occurrence is thus secondary contact between these two populations. These findings provide insight into the origins of western North Atlantic killer whales. In chapter three, I generate the first estimates of killer whale abundance and explore this population's possible influence on narwhal (*Monodon monoceros*) in the Canadian Arctic. I use photographs of sixty-three individually identifiable killer whales to estimate abundance in a capture-mark-recapture framework. The best-fitting model produced an estimate of  $163 \pm 27$ . This number of animals, given our region-specific understanding of killer whale bioenergetics and feeding, could consume  $>1000$  narwhal during their seasonal residency in Arctic waters; thus, demonstrating the scope for killer whale predation to influence narwhal populations in the Canadian Arctic. It is unknown how far across the Canadian Arctic marine ecosystem the influence of increased killer whale occurrence could cascade, although killer whale-mediated prey population declines have been recorded elsewhere (see Estes et al. 1998). These findings illustrating the magnitude of ecosystem-level modifications that can occur with climate change-related shifts in predator distributions.

Collectively, these findings contribute to an improved understanding of the consequences of climate change-related range expansions and the influence predators

impose on marine ecosystems. Continued climate warming will promote shifting distributions as species track suitable conditions. This is particularly true in polar regions where climate warming has led to substantial ecosystem-level change (Stroeve et al. 2014). Killer whale occurrence in the Canadian Arctic is on the rise (Higdon and Ferguson 2009) and it is likely that use of the region will only increase. Understanding how species are responding to climate change is required to predict and mitigate the effects of future change. Furthermore, a detailed understanding of killer whale ecology in Canadian Arctic waters is necessary for the effective conservation of this Arctic cetacean.

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