Chapter

Migration, Dispersal, and Gene Flow of Harvested Aquatic Species in the Canadian Arctic

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Abstract

Migration occurs when key aspects of the life cycle such as growth, reproduction, or maintenance cannot all be completed in one location. The Arctic habitats are variable and Arctic species are often migratory. The predictable nature of migrations in both space and time allow Arctic people to harvest fishes and marine mammals. We describe migratory/dispersal behavior in four types of taxa from the Canadian Arctic: anadromous and freshwater fishes, marine fishes, marine invertebrates, and marine mammals. Patterns of migration are remarkably different between these groups, in particular between distances migrated, seasonal timing of migrations, and the degree of reproductive isolation. Migratory anadromous and freshwater fishes become adapted to specific locations resulting in complex life histories and intra- and inter-population variation. Marine mammals not only migrate longer distances but also appear to have distinct demographic populations over large scales. Marine fishes tend to be panmictic, probably due to the absence of barriers that would restrict gene flow. Migratory patterns also reflect feeding or rearing areas and/or winter refugia. Migratory patterns of harvested aquatic organisms in the Canadian north are extremely variable and have shaped the north in terms of harvest, communities, and culture.

Keywords: migration, genetics, harvest, ecology, Arctic, fish, marine mammal, invertebrate, distribution

1. Introduction

To grow, reproduce, and survive, organisms must find environments where they can successfully complete all aspects of their life cycle. In most taxa, the life cycle needs (e.g., foraging and reproduction) cannot be met in a single habitat. In such cases, the fitness of individuals benefits from movement to an alternate habitat [1]. If reproductive, rearing, foraging, or refugial environments are not all sympatric, then migrations are required [2]. As a result, many animals have evolved life history strategies that include coordinated movement from one habitat to another during specific life stages. This synchronous, directed movement of part or all of a population between discrete habitats is called "migration." In the Canadian Arctic, habitats can be relatively barren but some regions have great productivity (**Figure 1**). The "patchiness" of the Canadian Arctic encourages the evolution of migrations and the majority of endemic species are migratory to some degree.

Where resources are patchy in space and time, such as the Arctic, species must evolve migratory life histories for survival [3]. The evolution of migration can be interpreted in terms of a balance between benefits gained from migration and costs of migration [4]. Migration confers an advantage for finding the most suitable spawning habitat, more productive feeding areas, and/or finding refuge from inclement conditions [5, 6]. On the other hand, migration is costly in terms of mortality to both juveniles and adults and the energy used to migrate [7]. For the Arctic charr migrating downstream to the ocean, the cost occurs before the benefit of a richer food source. Phenotypes that can reduce the cost of migration will be favored [7]. For example, species have evolved adaptations in their morphology to facilitate more efficient swimming as well as osmoregulatory adaptations for moving between fresh and saltwater.

Among both plants and animals, dispersal usually takes place at the time of reproduction. Dispersal is defined as the movement of individual organisms from their birthplace to other locations for breeding [8]. Arctic aquatic organisms must

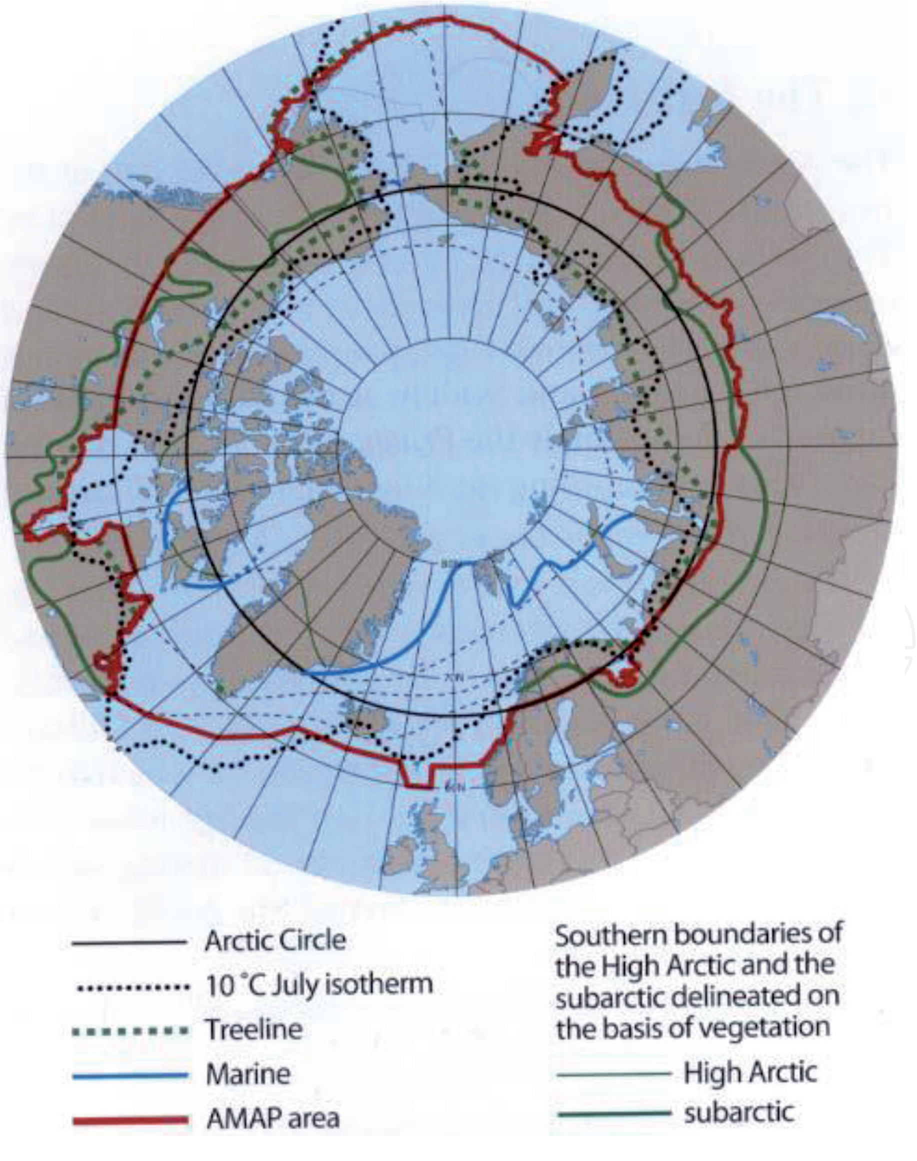

Figure 1.
Definitions of the Arctic region (source AMAP [122]). Comparisons between different definitions of the Arctic region are shown. The AMAP area is considered the most encompassing biologically for aquatic systems.

also be exceptional colonizers, and dispersal plays a critical role in the expansion of species in a post-glacial environment.

Until the last 100 years, the survival of humans in the Arctic was entirely dependent on the fauna of the region as evidenced by the strong hunting cultures that persist to this day. Understanding the movement patterns of aquatic species allowed exploitation of migratory species by the aboriginal societies. Migrations consistently brought the desired species in concentrations to particular locations. Currently, a variety of aquatic species from invertebrates to marine mammals are utilized by the Inuit and other Arctic people for subsistence and commercial purposes.

The Arctic represents a relatively untouched region for fishery exploitation, given its remote and logistically challenging location and inaccessibility due to land-fast ice [9]. The region is therefore considered promising for fishery development, especially with receding ice cover as a result of global climate change [9]. Given this potential, there are mounting concerns over fishery development related to the glaring lack of basic biological data for the majority of species and populations and our understanding of the ecosystem as a whole [9, 10].

2. What are the harvested species in the Canadian Arctic?

The Canadian Arctic is challenging to define and there are many possibilities. For this chapter, we use the definition provided by Arctic monitoring and assessment program (AMAP) (see **Figure 1**). The AMAP definition is a composite that reflects biological, geographical, and political definitions of the Arctic. The place names mentioned in the text are in **Figure 2**.

The list of harvested aquatic species in the Canadian Arctic is long and diverse and would require an exhaustive review to cover them all and we will only discuss a few key ones in this chapter. Freshwater fishes such as lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), and landlocked forms of Arctic charr (*S. alpinus*) are extremely important and are harvested throughout Arctic Canada by indigenous people of the region. The freshwater fishery in sub-Arctic Great Slave Lake, comprised of lake whitefish, lake trout, and inconnu (*Stenodus leucichthys*), is the largest commercial freshwater fishery north of 60 N latitude. At a community level, anadromous fishes comprise a large portion of the subsistence harvest across the Canadian Arctic. In Nunavut, anadromous Arctic charr are harvested commercially by most communities. Anadromous (those that migrate between fresh water where they spawn and/or overwinter to marine habitats where they feed) coregonines such as broad whitefish (*C. nasus*), inconnu, lake whitefish, least, and Arctic cisco (*C. sardinella* and *C. autumnalis*) are harvested during their fall spawning migrations along western Arctic coastal rivers and especially in the Mackenzie River where a fishery estimated at 150,000 kg/year is taken for subsistence purposes [11]. Northern anadromous Dolly Varden Char (*Salvelinus malma*) are mainly subsistence fished in the Beaufort Sea coastal waters [12] and along the Mackenzie River system on their return migration from the coast (e.g., Aklavik and Fort MacPherson). Anadromous Arctic charr are harvested throughout the territory of Nunavut in all coastal communities as well as in the communities of Paulatuk, Ulukhaktok, and Sachs Harbour in the Northwest Territories.

Marine fishes are harvested when available by many communities in the North. There are large industrial fisheries for northern shrimp (*Pandalus montagui* and *Pandalus borealis*) in Davis Strait and Hudson Strait, and for Greenland halibut (*Reinhardtius hippoglossoides*) in Baffin Bay and Davis Strait and in Cumberland Sound, Nunavut. The shrimp fishery harvests up to 35,000 metric tonnes annually.

Figure 2.
Map of Canada with northern place names relevant to the text. Communities are marked by a black dot. The Mackenzie River system is in blue.

Greenland halibut are widespread, live deep (200–2000 m) and are long-lived [13–19]. The Baffin Bay fishery is now the largest groundfish fishery on the east coast of Canada. The total harvest regularly exceeds 10,000 metric tonnes. The Cumberland Sound fishery is a community-based winter fishery (500 metric tonnes quota) executed by setting longlines from the flow edge of the winter ice pack or through holes cut in the landfast ice. Commercial fisheries on this species operate at Baffin Bay and Davis Strait [20, 21].

Marine mammals are an important harvested resource for coastal communities in the Arctic not only for subsistence purposes but also for commercial sale of Narwhal (*Monodon monoceros*) tusks and other derived products. Ringed seal (*Pusa hispida*), narwhal, beluga whale (*Delphinapterus leucas*), bowhead whale (*Balaena mysticetus*), and walrus (*Odobenus rosmarus*) are all important species that are harvested throughout Arctic Canada.

3. Why is understanding migration so important for harvesting and management?

Migratory pathways of Arctic animals bring them into vulnerable situations pathways bring them into vulnerable situations in time and space where humans can access them in a predictable manner. Because of this, the management is generally tied to the migration patterns and is frequently done on a community by community basis. As well, most harvesters are aboriginal and harvests are for both economic gain and food security. The exception is the offshore marine fisheries which are comparable to other large industrial fisheries around the world.

As well, migrating exposes the animals to an accumulation of stressors such as shipping, pollution, and blocked migration routes (e.g., streams drying up due to global warming) which all can dramatically reduce their fitness. Additionally, climate change is anticipated to affect the Canadian Arctic most severely causing a major change, principally an increase in extent and duration of the open-water season. The region has been heavily characterized by the presence of long seasonal ice cover and multiyear sea ice. In the future, the ice-free season will be much longer and areas of multiyear ice will diminish. The change will not only affect migration but may also allow the movement of non-Arctic species into the region, which may be competitors, predators, or forage items. Therefore, to manage fisheries, a thorough understanding of migration patterns of the harvested species is required. Migration patterns of harvested Canadian Arctic species have been under study for the last 20 years and considerable progress has been made in the last 5 years. Although remarkable strides have been made in the understanding of migration, there is still much to understand.

4. Migratory patterns

4.1 Freshwater and anadromous species

4.1.1 Coregonines

4.1.1.1 Inconnu (Stenodus leucichthys)

Inconnu have a partially circumpolar distribution. They mainly inhabit rivers flowing into the Arctic Ocean. They range from the Anderson River, NWT at latitude 128 W westward to 35 E on the edge of Finland. They are harvested throughout their range for subsistence and commercial purposes. Howland et al. [22–24] undertook a radio-telemetry, otolith microchemistry, and long-term seasonal gillnetting study which, along with a synthesis of existing historical data, revealed that both freshwater (those defined as only using riverine habitats and never migrating to the ocean) and anadromous Inconnu (*Stenodus leucichthys*) in the Mackenzie River, NT system are migratory. However, their feeding/overwintering habitats and the timing and distance of their spawning migrations differ substantially between life history types (**Figure 3**). Two factors, seasonal temperatures and distance of the migration, probably played a role in the timing of migration as the freshwater population migrated and spawned later by 2–2.5 months and 3 weeks, respectively, than did the anadromous population. There is little mixing between the anadromous forms in the lower Mackenzie River and freshwater Inconnu in the Great Slave Lake area. Tagging studies, however, have provided evidence for long distance movement in this species (~1800 km) suggesting the potential movement and mixing between the two forms [25]. Some fish seem to use only the upper river for their life cycle suggesting that a third riverine form occurs. In the lower Mackenzie River, Inconnu travel more broadly using coastal and the Mackenzie Delta for nourishment and as a winter refugium, whereas Inconnu in the Great Slave Lake area eat and survive the winter in the lake and migrate less distance to spawn. These results were reflected in differences in mitochondrial (Howland DFO unpublished) and microsatellite (Weins DFO unpublished) DNA analysis.

4.1.1.2 Broad whitefish (Coregonus nasus)

Broad whitefish have a partially circumpolar distribution. They mainly inhabit rivers flowing into the Arctic Ocean. They range from latitude 105 W westward to 50 E. They are harvested throughout their range for subsistence and commercial

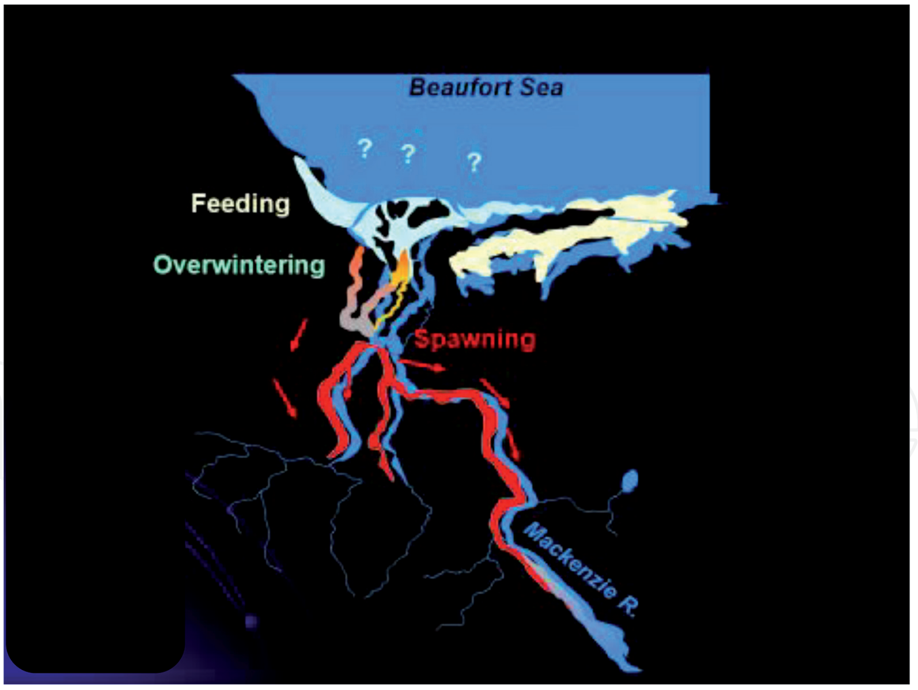

Figure 3.
The lower Mackenzie River showing spawning, overwintering, and feeding areas used by migratory Coregonids. The pale yellow or cream colored area is the suspected feeding area. The off-white area in the Mackenzie Delta is a proposed over-wintering area. The red shows the migration to spawning grounds. Blue is the water.

purposes in the lower Mackenzie River system of Canada's NWT. Broad whitefish exhibit three presumed life history strategies including anadromous, riverine, and lacustrine (complete their life cycles entirely within a lake) forms [26, 27]. One anadromous population of Broad whitefish is known to spawn in the Arctic Red River at Weldon Creek, about 160 miles upriver from the mouth [28]. The minimum total distance that Arctic Red River anadromous Broad whitefish migrate from their over-wintering grounds to spawning beds is 350–450 km. First-time spawners, arriving from rearing grounds on the Tuktoyaktuk Peninsula, migrate considerably farther [29] (**Figure 3**). Spawning locations for anadromous fishes have also been suggested in the Peel River and the mainstem Mackenzie River near the town of Fort Good Hope [29, 30]. Recently, Harris et al. [25] examined migratory strategies in this species using otolith microchemistry and documented at riverine form that undertakes migrations solely within the Peel River in the region.

A lacustrine form of Broad whitefish occurs in Travaillant Lake, a deep lake about 31km^2 in surface area [31]. Broad whitefish use the lake for rearing and overwintering. Reproduction occurs in two locations, in the outlet of Travaillant Lake above Andre Lake to the south and in a major inlet to Travaillant Lake, directly to the north [31, 32]. The migration distance to spawning grounds is short, only 5–12 km.

4.1.1.3 Arctic cisco (C. autumnalis) and least cisco (C. sardinella)

Least and Arctic cisco have a partially circumpolar distribution. They mainly inhabit rivers flowing into the Arctic Ocean. Least cisco range from latitude 100 W westward to 50 E. They are harvested throughout their range for subsistence purposes, but to our knowledge, they have not been fished commercially. Arctic cisco range from latitude 105 W westward to 40 E. They are harvested throughout their range for subsistence purposes and historically supported a large commercial fishery in Alaska [33, 34]. These species follow similar life styles with eggs hatching in spring and young-of-the-year are carried downstream with increased water flow from spring melt to coastal, brackish environments [33]. Least cisco distribute themselves in coastal brackish and fresh waters to feed in the summer months, but unlike Arctic cisco they do not migrate 400 km that separates Colville River, Alaska, and the Mackenzie Delta [33]. Young-of-the-year Least cisco and eastward Arctic cisco over-winter within areas of the Mackenzie Delta where there is a stable layer of freshwater under the sea ice [35]. Migration to natal streams occurs with the onset of sexual maturity. The age of sexual maturity in Siberian populations varies between 5 and 10 years but there are no studies in Canadian waters [35]. In contrast to Least cisco, Arctic cisco are distributed more widely within the coastal marine environment as a result of their ability to tolerate and acclimate to higher salinity [36]. A strong eastern wind facilitates the migration of Arctic cisco young-of-the-year to Alaska from the Mackenzie River system by wind-driven coastal currents that force the movement of warm, less saline water to Alaska [34]. Young-of-the-year that reach Alaskan waters reside in the area to forage and utilize the Colville River to over-winter. Upon reaching sexual maturity, Arctic cisco return to natal tributaries within the Mackenzie River system to spawn [37] (**Figure 3**).

Arctic cisco are thought to only spawn within four tributaries (Peel River, Arctic Red River, Liard River, and Great Bear River) in North America, which are part of the greater Mackenzie River system [38, 39]. There is strong evidence indicating that Arctic cisco have relatively long oceanic migrations of approximately 600–700 km, whereas Least cisco have shorter oceanic migrations of approximately 200–300 km [35, 40]. Presently, both species co-occur in the Arctic Red River, but little scientific research has been undertaken to understand their life history strategies.

4.1.1.4 Lake whitefish (C. clupeaformis)

Lake whitefish are located throughout most of Canada and Alaska. They are harvested throughout their range for subsistence and commercial purposes and form the largest freshwater fishery north of the 60 N in Great Slave Lake. Lake whitefish are considered relatively sedentary with migrations occurring within lakes over relatively short distances between feeding and spawning areas. Surprisingly, there is little information on the migration of Lake whitefish in Arctic or sub-Arctic regions. However, this little information shows a marked departure from the patterns in the southern part of their range. Lake whitefish in the Mackenzie River are considered unusual because they migrate along the river to coastal areas. Lake whitefish from the Mackenzie River estuary are believed to overwinter there and in the river's delta [41], and to spawn in various tributaries of the Mackenzie, such as the Rat, Peel, and Arctic Red rivers [42]. Lange and Tallman [43] noted that the number of ripe lake whitefish increased within the Arctic Red River in the months of September and October. Limited radio-tracking information suggest that they migrate similar distances to broad whitefish [35] (**Figure 3**).

4.1.2 Salmonines (Salvelinus spp.)

4.1.2.1 Dolly varden (Salvelinus malma)

The northern form of Dolly varden (*S.m. lordi*) is found in northwestern North America and northeastern Eurasia. In North America, populations range from Bristol Bay along the north slope of Alaska and the Yukon Territory, and east to the Mackenzie River [44]. Approximately 5–10% of the global population exists within Canadian waters. Population sizes are largely unknown.

Anadromous Dolly varden char (*Salvelinus malma*) are mainly fished for subsistence using gillnets in Beaufort Sea coastal waters of both Canada (Northwest Territories and Yukon) and Alaska [12]. They are also harvested in Inuvialuit and Gwich'in communities along the Mackenzie River system (e.g., Aklavik and Fort McPherson) on the return migration to headwater spawning/overwintering areas. Dolly varden have variable migration strategies [45–49]. For example, anadromous individuals may migrate to sea or part of the same population will stay in fresh water throughout its life; this behavior appears to be facultative and may be linked to early growth history [49] with residents being genetically indistinguishable from their anadromous counterparts [45]. There are also genetically distinct isolated freshwater populations above waterfalls in several river systems [50, 51]. Residents do not migrate to the sea, but remain in fresh water year-round. The majority of these are small males that adopt a 'sneak spawn' strategy (taking on a freshwater "resident" lifestyle) in order to fertilize eggs of depositing anadromous females [39]. While rare, a few cases of female residents have been documented in Canadian Arctic systems [46]. Residents are characterized by their small size, dark color, visible parr marks, and early maturation. Spawning of Dolly varden in Canadian rivers occurs from early September to late October just before freeze-up, with fry emerging from the gravel in May and June [39]. Anadromous juveniles remain in fresh water from 1 to 5 years before beginning annual migrations to feed in productive marine waters of the Beaufort Sea [49, 52, 53]. Downstream migration to the sea begins during spring freshet, which is typically in early to mid-June and may be linked with ice conditions in the Beaufort Sea [39, 47]. Upstream migration can begin as early as July and last until mid to October in some systems [43, 49]. Dolly varden of all life history stages show high fidelity to spawning/overwintering areas as evidenced by their distinct genetic structuring by river systems as well as tag return information [45, 51, 52, 54, 55]. Mature spawning adults tend to return to natal streams first, while smolts are usually the last fish to return [56]. Dolly varden are iteroparous, with populations/individuals typically migrating and spawning either annually or biennially [57, 58]; however, some populations are known to skip both migration and spawning in some years [54].

Gallagher et al. [59] used otolith strontium and multi-year mark-recapture information to characterize associations between migration patterns and spawning frequencies in an anadromous Dolly varden. They observed that fish either migrated annually after smoltification or periodically skipped an annual ocean migration to remain in fresh water and spawn. Annually migrating fish had lower longevity (≤9 years vs. ≤13 years). They also observed that some fish returned from the sea considerably earlier than the majority of other current-year migrants.

Based on recent studies involving the use of satellite tagging, migration in the marine environment can involve movements well offshore at least in the region of the Mackenzie estuary (Gallagher and Howland, unpublished) as well as off the coast of Alaska [48]. In general, Dolly varden have been noted to migrate longer distances than Arctic charr, for example, DeCicco [55, 60] recorded a migration from Alaska to Russia.

4.1.2.2 Arctic charr (S. alpinus)

Arctic charr (*Salvelinus alpinus*) have an unbroken circumpolar distribution. They are found in north flowing streams, rivers, and lakes around the Arctic Ocean. Arctic charr are important as an iconic symbol of the North, important for food security of aboriginal people, and form the basis for valued commercial fisheries. Most stocks are prosecuted using gillnets or weirs. Arctic charr have been recently studied for both dispersal patterns and for migrations. Dispersal can influence the process of local adaptation, when the dispersers successfully breed (i.e., gene flow occurs) in the non-natal habitat [61]. Fiords might be an important influence on gene flow and also may be a major barrier across Cumberland Sound, NU [62]. Arctic charr showed isolation by distance and it is thought that dispersal in Arctic charr follows a stepping stone pattern [62]. Anadromous Arctic charr display a complex migratory behavior throughout a large portion of their range. Breeding and nonbreeding individuals have very different movements, and for genetic analysis, it is important to distinguish them. As well, individuals do not necessarily reproduce every year, but to survive the winter, they must return to fresh water. Moore et al. [61] used a genetic assignment approach to study dispersal of charr from Cumberland Sound on Baffin Island, Canada. Dispersal estimates ranged from 15.8 to 25.5%, which is higher than recorded for other salmonids. Those returning to fresh water solely for overwintering and not spawning purposes were more likely to use non-natal habitats than breeding individuals, thus resulting in estimates of dispersal that overestimate the potential for gene flow among populations. Moore et al. [61] also parameterized a population genetic model showing that gene flow is probably sufficiently low to allow for local adaptation among populations. It is hypothesized that that Arctic charr home to their natal river to spawn, but may overwinter in rivers with the shortest migratory route to minimize the costs of migration in nonbreeding years [63]. Several studies in the Canadian Arctic have also suggested that dispersal is often asymmetrical among discrete stocks [61, 64] and that gene flow often conforms to a stepping-stone-pattern [55, 57]. These results underscore the importance of understanding patterns of dispersal for appropriately evaluating potential consequences for local adaptation and management.

In general, Arctic charr are not suspected to migrate long distances while summer foraging in the marine environment and that they tend to remain close to the shore [65–68]. More recently, Moore et al. [69] used an array of fixed acoustic receivers (N = 42) to track the summer marine movements of 121 anadromous Arctic charr equipped with acoustic transmitters at three locations in the Cambridge Bay region, where the largest commercial fishery for this species exists. They found that the seasonal time of movement between salt and fresh water depended on the river of origin rather than size or sex. The sexes differed in the distance they moved with the males moving further from where they were tagged. The fish remained in brackish estuarine environments for the most part and curiously travelled mainly westward from their river of origin. They appeared to be moving to the water in Wellington Bay that was the warmest and freshest. The pattern of movement was to rest in the estuaries of rivers and then move rapidly through the more marine areas. Charr preferred near-shore habitats based on the increased numbers of detections on receivers located less than 1.5 km from the coast. Finally, they noted an implication for fishery management because they observed evidence of extensive stock mixing throughout the summer, including at known fishing locations and periods (**Figure 4**). Mixed-stock migrations in marine habits appear to be a common phenomenon in this species [64, 70].

4.1.2.3 Lake trout (S. namaycush)

Lake trout are widespread in North America from the Arctic coast and near islands to the northern United States. They are harvested for subsistence, and sport throughout the north and commercially in Great Slave Lake.

Lake trout migrations are mainly limited to within lakes although since they inhabit some lakes such as Great Bear Lake that are freshwater oceans, these migrations may cover quite a distance (e.g., upwards of 60 km). Recently, Swanson et al. [71] noted that Lake trout could undertake limited migrations to the sea to take advantage of the lipid reaching prey sources present in marine habitats. Using

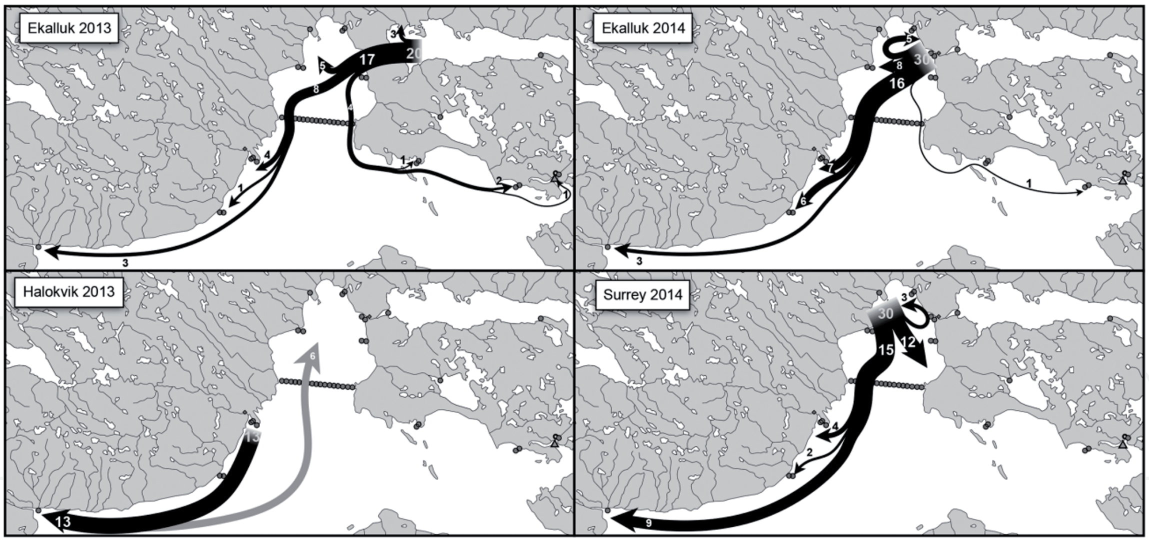

Figure 4.
General patterns of movements of Arctic charr tagged in the Cambridge Bay area, Nunavut, at three tagging locations in 2013 and 2014 and detected in summer 2014. Black arrows indicate movement from tagging location for fish tagged in 2014 or from fresh water for returning migrants tagged in 2013. The thickness of the arrows is proportional to the number of individuals observed performing a specific movement pattern (also indicated by numbers). From Howland et al. [12].

a genetic assignment-based approach combined with otolith microchemistry [72] also documented anadromous migrations in Lake trout and also noted substantial inter-lake movements in this species in the Husky Lake drainage basin, Northwest Territories, where freshwater resident, semi-anadromous, and brackish-water resident lake trout life history types are documented. Kissinger et al. [73] documented that anadromous migrations in this species can sometimes be unexpectedly longer than previously assumed.

4.2 Marine fish

4.2.1 Greenland halibut (Reinhardtius hippoglossoides)

Greenland halibut has a circumpolar distribution in the Northern Hemisphere in the North Atlantic, North Pacific, and Arctic oceans. It is an important commercial species supporting fisheries in these zones. Floy tagging between 1994 and 2000 indicated that Greenland halibut located in the northern winter fishing grounds were resident, while fish tagged near the mouth of Cumberland Sound were migratory to offshore waters of Baffin Bay and Davis Strait [19]. Western Greenland fiords have similar inshore populations of Greenland halibut that are sink populations with origins offshore but settling into the inshore [20]. It is likely that the same circumstance exists in Cumberland Sound. The existing inshore allocation or total allowable catch (TAC) of Greenland halibut was assigned to a new management area that encompasses northern Cumberland Sound. Subsequently, the question arose whether the inshore stock in Cumberland Sound was distinct from the offshore. Through acoustic telemetry monitoring of fishes at depths between 400 and 1200 m, combined with environmental and fishery data, Hussey et al. [13] examined the movement patterns of Greenland halibut in Cumberland Sound, Nunavut. They noted biotic and abiotic factors that were driving fish movements. Greenland halibut undertook clear seasonal movements between the southern and northern regions of the sound driven by temperature, dissolved oxygen, and sea ice cover, with most tagged fish using the entire sound over the course of the year.

Barkley et al. [74] used acoustic transmitters to track Greenland halibut in Scott Inlet, coastal Baffin Island, Canada, over a 1-year period. Their aim was to determine if fish could be vulnerable to both the inshore and offshore fisheries in the area.

Barkley et al. [74] described a dual pattern of movement in Greenland halibut. Most fish moved between the inshore in the summer and offshore during the winter months. A few fish moved offshore with the others but returned inshore during the main winter months. Greenland halibut seemed to avoid ice-cover in the inshore and likely moved offshore as the sea-ice formed in November.

It was thought that Greenland halibut remained within the coastal environment of Baffin Bay during the year. The recent data show that this is not the case in all areas. In the coastal regions such as Scott Inlet, inshore-offshore connectivity occurs. This implies that many of the Halibut are from a single population and vulnerable to harvest in both the inshore and the offshore fisheries. To avoid over-harvesting, fishery management must take this into account.

Further studies have noted that adult Greenland halibut may make longer migrations over wide areas for the purposes of spawning and growth (A. Fisk, University of Windsor, pers. comm.)

4.3 Marine invertebrates

4.3.1 Zooplankton

Northern shrimp are distributed patchily throughout the circumpolar region. In Canadian waters, they form important fisheries in Davis and Hudson straits and in Cumberland Sound. Webster et al. [75] noted that macrozooplankton (e.g., krill, amphipods, and jellyfish) and nekton (e.g., decapod shrimp, squid, and fish) are integral parts of pelagic ecosystems, but knowledge of their vertical distributions and migrations during winter at high latitudes is lacking. Webster et al. [75] quantified macrozooplankton and nekton distributions during the polar night in a partially ice-covered high Arctic fjord. Most nekton occurred under the 100 m thermocline both during the day and night. The nekton biomass was dominated by a varied fish community (10 species present) with shrimp and squid being the other main components. Large *Calanus* spp. copepods and gelatinous zooplankton of the macroplankton occurred all along the water column. In contrast to the nekton, the majority were above the thermocline day and night. Biomass could be predicted with a general additive model with depth, time, and moonlight. The model predicted that biomass increased with depth for both macrozooplankton (over the top 100 m) and nekton, but revealed no patterns in biomass over time.

4.3.2 Northern and striped shrimp (Pandalus borealis and P. montagui)

While the extent of large scale adult pandalid migration remains unknown due to difficulties associated with tagging and tracking of such small organisms, it is known that pelagic larvae settle in shallow waters where they reside until reaching approximately 2 years of age [76]. At that time, juvenile males migrate to deeper waters where they spend a short period of time (~1 year) before transitioning into females. Following metamorphosis, ovigerous females return to shallow waters where larvae are released. The pelagic life stage can last up to 3 months [77] and is highly influenced by oceanographic currents while settlement patterns are heavily influenced by the release location as well as the vertical migration behavior [78]. However, discrepancies still exist in our understanding of life-stage specific habitat preferences between northern and striped shrimp but there is a general agreement that *Pandalus montagui* are found in shallower (200–500 m) and cooler (−1 to 2°C) waters throughout their development [79]. Nonetheless, both species have been shown to perform diel vertical migrations to facilitate the feeding on zooplankton organisms during the night time [76, 80].

4.4 Marine mammals

4.4.1 Pinnipeds

4.4.1.1 Ringed seal (Phoca hispida)

Ringed seals are distributed throughout the Arctic Ocean. Ringed seals have a circumpolar distribution from approximately 35°N to the North Pole, occurring in all seas of the Arctic Ocean. They are hunted for food by indigenous peoples of the Canadian north and are critical to food security.

Ringed seals travel great distances during their life. Harwood et al. [81] deployed satellite-linked time-depth recorders on 17 Ringed seals in early summer in 1999, 2000, and 2010, near the Inuvialuit community of Ulukhaktok, Northwest Territories, Canada. During the open water period, mature and immature Ringed seals moved large distances (mean distance travelled = 5844 km; range of distance travelled = 1232–9473 km). Ringed Seals maintain big home ranges averaging 122,854 km^2 for immature, 76,658 and 21,649 km^2 for mature females and males, respectively, while mature seals spent the bulk of their time in a foraging/resident mode (69.5%) but also spent a lot of time moving (22.8%). Ringed seals spent three-quarters of their time in either Prince Albert Sound or eastern Amundsen Gulf. At some point, most Ringed seals did move outside the area into Prince of Wales Strait, Viscount Melville Sound, Minto Inlet, and western Amundsen Gulf. Immatures spent more time moving (36.8%) and less time foraging (51.4%) than adults. Most Ringed seals wintered in either Prince Albert Sound or Amundsen Gulf.

4.4.1.2 Walrus (Odobenus rosmarus)

Atlantic Walruses range across the Canadian Arctic, to Greenland, Svalbard, and the western part of Arctic Russia. They are occasionally harvested by Inuit for food and the tusks.

Two subspecies of Walrus occur in the Canadian Arctic: the Atlantic Walrus (*Odobenus rosmarus rosmarus*) and the Pacific Walrus (*O. r. divergens*), although the latter ranges into Canadian waters from Alaska only occasionally. The Atlantic Walrus is widely distributed throughout the eastern Canadian Arctic, where the high Arctic population occupies the waterways of the central Archipelago and northern Baffin Bay as far east as Greenland, and the central/low Arctic population occurs in northern Hudson Bay, Foxe Basin, Hudson Strait, and Davis Strait. The degree to which these populations undertake seasonal movements or migrations is not well understood, although studies in recent years have indicated both localized movements and large-scale migrations in response to seasonal variation in ice conditions [82, 83].

Walrus require large areas of open water overlying shallow (<80 m) bivalve beds, their preferred prey, with nearby ice or land for hauling out [84]. In areas where polynyas and dynamic leads in pack ice persist throughout winter, Walrus occur year-round and undertake only localized movements between wintering areas and onshore haul-out sites during summer. Walrus occur year-round in Foxe Basin, northern Hudson Bay, and western Hudson Strait [85, 86]. Although Walrus move seasonally within Foxe Basin, there is no evidence of concerted movements between Foxe Basin and Hudson Strait [87]. There is similarly no evidence of seasonal movements into or out of southeastern Hudson Bay, where Walrus move from the floe edge in winter to terrestrial haul-out sites in summer [88]. There is, however, evidence of seasonal movements between Hudson Bay and Hudson Strait, with general westward movement in summer, and return movements north and eastward in fall [89].

Historically, Walrus were known to migrate northward along West Greenland in spring and to return southward along the east coast of Baffin Island in fall (Freuchen 1921 and Vibe 1950, as cited in [89]). Although no longer observed on that scale, recent studies have confirmed seasonal Walrus migrations between Greenland and Canada. 50 Walruses from the high Arctic population, instrumented with satellite transmitters, departed their feeding banks along the Greenland coast in June–July at the onset of ice melt, swimming west into the Canadian Arctic Archipelago [83]. Tags on three of the animals transmitted long enough to document their return migration from Ellesmere Island to their original tagging locations off the Greenland coast in October [83]. Similarly, Dietz et al. [82] showed that eight of 23 Walruses from the central/low Arctic population satellite tagged at their winter grounds off central West Greenland migrated to southeast Baffin Island during April–May. Individual Walruses took on average 7 days to make the crossing, and generally followed a similar 400-km long migration path over the shallowest and narrowest part of Davis Strait [82]. As with Walrus migrations further north, the westward spring migration coincided with the seasonal retreat of the pack ice edge. Satellite transmissions did not last long enough to document a return migration, although an animal flipper-tagged off southeast Baffin Island and subsequently shot 2 years later off West Greenland provides evidence of such [82]. Telemetry results are also supported by genetics analysis that showed no differences between Walruses from West Greenland and southeast Baffin Island [90]. The seasonal movement of this species between Greenland and Canada is relevant to Walrus hunt management in both countries.

4.4.2 Cetaceans

4.4.2.1 Beluga (Delphinapterus leucas)

Beluga whale are distributed through out the Arctic Ocean and are one of two species adapted to living with pack ice. They are hunted for food by Inuit in Canada. Most Arctic populations are healthy but the population in Cumberland Sound is of concern.

Belugas take part in a yearly cycle of migration from their summering grounds to their wintering grounds. Belugas tend to frequent river estuaries and coastal water during the summer. Belugas spend the winter next to the ice edge, and in an area of open water [91]. Then, Beluga migrate back to their summering grounds. The migrations vary widely in the distance travelled but the same seasonal pattern is found in all the Arctic Beluga populations.

Beluga of the Cumberland Sound population stay within the Cumberland Sound area all year round. Their summer distribution is restricted fjords and more than half the population can be found in August in a small area of less than 150 km^2 [92]. They migrate from fjords to the open water at the mouth of Cumberland Sound in the winter [93], a migration that is only a couple hundred kilometers.

The Eastern Beaufort Sea (EBS) beluga population has a much larger summer range with the core area covering more than 50,000 km^2 [94]. Sexual segregation has been reported during the summer. Males tended to have a large home range than females [94] and they also selected areas with higher ice concentrations during July-August [95]. Females preferred areas close to the shore (<200 km) [95]. Belugas of the EBS population tended to leave their summering ground in September [94] for their fall migration westward to the Bering Sea [96]. This migration was more than 3000 km long [96].

There are two main recognized beluga populations in Hudson Bay: the Western Hudson Bay (WHB) and the Eastern Hudson Bay (EHB) [97]. Belugas in Hudson Bay spent their summer in the estuaries and river mouths. Belugas of the WHB population started their migration around mid-October [98]. EHB belugas migrated in groups of related individuals and their migration route seemed to be learned and shared by related individuals [99]. As they migrated in the spring and fall along Hudson Strait [100], both WHB and EHB belugas were susceptible to harvest by coastal aboriginal communities along their migration route [101].

4.4.2.2 Narwhal (Monodon monoceros)

Narwhal are found in Canadian, Greenlandic, and Russian Arctic waters. They are the other species adapted to exist under ice packs. They are hunted for food and their tusks by the Canadian Inuit. A tusk can be worth up to $10,000CAN.

There are five main Narwhal populations in the world: the Northern Hudson Bay, the Baffin Bay, the East Greenland, the Northeast Greenland, and the Svalbard-Russia populations. The Baffin Bay population is the largest with more than 150,000 individuals. Narwhals summer in known aggregations in bays and fjords in the high Arctic [102]. Although the location and occurrence of these summer aggregations are predictable, a proportion of narwhals seem to mix between summer aggregations [103].

Information about Narwhal migration comes from satellite telemetry and local knowledge. Narwhals started their fall migration before the ice started to form. During this critical period, they were susceptible to being trapped in ice if sudden changes in weather and wind conditions precipitated the formation of ice [104]. Narwhals from the Baffin Bay population overwintered in Baffin Bay and Davis Strait, in extreme ice coverage [105]. The total length of the migration route of Narwhal from summering to wintering ground could be more than 1000 km. Narwhals from the Northern Hudson Bay population undertook a migration of similar length between Repulse Bay, in the North West part of Hudson Bay in Canada, to the Labrador Sea [106]. Spring migrations back to the summering ground were often lead by groups of males [107]. Limited information from satellite telemetry suggests that some Narwhal returned back to the same summering ground [108]. However, satellite telemetry data also showed that Narwhal can change between summering ground [103].

4.4.2.3 Bowhead (Balaena mysticetus)

Bowhead whale live entirely in the Arctic and Sub-Arctic waters of the northern hemisphere. They complete their entire life cycle in the north. Hunting for bowhead whales commercially nearly extirpated populations but now is banned. Inuit in Nunavut are allocated up to three whales annually for subsistence harvest by communities. Hunts occur in different communities each time. Hunt planning and permits take several years and the hunt is closely monitored.

There are four bowhead whale populations around the circumpolar Arctic and the two largest spend the majority of their time in Canada—the Bering-Chukchi-Beaufort (BCB) Sea and Eastern Canada-West Greenland (ECWG) populations. Both populations migrate great distances, as would be expected for large-bodied marine mammals [109] and can cross paths within the Canadian Archipelago [95]. The main location of seasonally rich food supplies occurs in the polar summer and is spatially and temporally separated from environments used for mating, calving, and lactation [110]. There is an increased understanding of Bowhead migratory behavior because of the use of new satellite telemetry techniques to track marine mammal migration [111, 112]. In some cases, these migrations follow predictable routes but age, sex, and reproductive spatial segregation occurs [113].

The BCB population travels more directly from their winter range because the greater amount of clear water and a small amount of pack ice allow easier movements [114]. After the winter, the spring migration is to the north and east into the Beaufort Sea [115]. During summer, they live principally in the Canadian part of the Beaufort in the Amundsen Gulf and Viscount-Melville areas [116]. Finally, the fall migration takes the bowheads through the Alaskan Beaufort and Chukchi Seas, and then through the Bering Strait into the Bering Sea. Within Canadian waters, the total range of the Bering-Chukchi-Beaufort Sea population is approximately 207,000 km^2.

In contrast, the ECWG population circumnavigates Baffin Island with the extent of occurrence of roughly 1 million km^2 [58]. Wintering occurs in areas with unconsolidated pack ice, particularly in Hudson Strait and along the southeastern Baffin Bay coastline. A segment of the ECWG Bowhead whale population moves east to the West Greenland coast (Disko Bay) in late winter-early spring, likely mature adults involved in mating. Another segment of the population consisting mostly of females with calves and juveniles moves west and north into Foxe Basin [117]. In summer, the Greenland portion travels north and west into western Baffin Bay, whereas the portion in Foxe Basin travels through Fury and Hecla Strait into the Canadian High Arctic, particularly Gulf of Boothia and Prince Regent Inlet, where they are met by the Greenland portion of the population [118]. The fall migration occurs over 2–3 months starting in late August/September with whales either moving back through Fury and Hecla Strait into northern Hudson Bay or along the east coast of Baffin Island to winter areas in the south [119]. Peak feeding is thought to occur during the fall migration and areas such as Isabella Bay along the east coast of Baffin Island are considered key foraging habitat [120]. Bowhead whales appear to follow the waxing and waning of seasonal sea ice presumably because these areas provide access to food and shelter/protection from killer whale predation [111]. Large adults are likely able to defend against killer whales with access to coastlines and shallow water and therefore use open water areas along the Greenland and Baffin Island coastlines during summer and autumn [121]. Whales that are smaller and more at risk of killer whale predation stay.

5. Conclusions

The Canadian Arctic is a region of great ecological variability. The species that have evolved in this area make use of the variable opportunities presented by undertaking extensive migrations. These migratory activities have consequences to the population structure and to the availability of the biota to humans. For example, anadromous fishes perform precise long distance migrations for the purposes of reproduction travelling from marine feeding areas to freshwater spawning areas. They subsequently have a complex population structure with many unique populations or stocks. Inter-population genetic variability is high. It is likely that the genetic adaptability of the salmonidae is why they dominate in northern zones. Their travels also make them most available to human predators and the accessibility to harvest is frequently the reason for the location of communities in the Canadian Arctic. Accordingly, resource management must be stock-by-stock on relatively small geographical scales. In contrast, the main harvested marine fish species, Greenland halibut, appears to have little population structuring over vast areas. The migrations do not segregate them into distinct stocks. Probably, the use of planktonic larvae is related to this and that the profundal zones where they live as adults are not especially variable. Finally, marine mammals show a population structure but not to the same level as fishes. Their migratory abilities are the most pronounced but the segregation between them is more likely a result of learning than instinct.

Migratory patterns are highly variable among harvested aquatic organisms in the Arctic but the understanding of the patterns of migration is critical for successful harvesting and management. The patterns of migration in freshwater and anadromous fishes have often determined the location of indigenous communities, which may have started as simple fishing camps. It is likely that the patterns of migration in marine mammals also have had a large influence on northern development in Canada. Knowledge of the precise time and location of migrations was essential for survival in a harsh and unforgiving region. In contrast, the migrations and segregation of offshore marine resources are relatively imprecise. Development of fisheries has come with the induction of "western technologies" of large industrial scale ships and nets. The knowledge of migratory patterns is relevant to designating management zones but not to survival. The migratory patterns of aquatic organisms have shaped northern culture, communities, and the way of life for aboriginal populations.

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