A review of anadromous Arctic char (*Salvelinus alpinus*) migratory behavior: implications for genetic population structure and fisheries management

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ABSTRACT

Existing data on the migratory behavior of anadromous Arctic Char (*Salvelinus alpinus*) from the Canadian Arctic is here summarized with the goal of making recommendations for fisheries management. Like other salmonids, Arctic char home to their natal habitats to spawn, but evidence suggests that straying is more common than in other anadromous salmonids. A distinction is made between two types of straying events that have very different biological and management implications: breeding dispersal occurs when an individual fish moves to a non-natal habitat to spawn; and overwintering dispersal occurs when an individual fish moves to a non-natal habitat during the years when it is not spawning. The former has the potential to lead to gene flow and therefore has important consequences for the demography and genetic integrity of Arctic char populations. The latter leads to mixing of stocks targeted by fisheries, but does not lead to genetic or demographic exchange between populations. Estimates of straying rates for Arctic Char from Canadian populations are first reviewed and they do appear higher than in other salmonids, although they vary tremendously among years and geographical locations. Second, considerable evidence is available to suggest that Arctic char that are not current year spawners are more likely to stray than current-year spawners. It is argued that this behaviour creates a paradox for management. On the one hand, it leads to mixing of stocks, which should favor a more regionally-integrated approach to management. On the other hand, it allows the maintenance of genetic differentiation among populations, which should favor a river-by-river management approach. It is therefore recommended that the river-by-river management approach continue to be applied to healthy stocks, and that in cases where a single stock suffers declines, nearby fisheries should also be closed or reduced to avoid the capture of migrant fish from the affected stock.

RESUME

Les données disponibles sur le comportement migratoire de l'omble chevalier (*Salvelinus alpinus*) anadrome de l'arctique canadien sont ici synthétisées dans le but d'emmètre des recommandations pour la gestion des pêches. Comme les autres salmonidés, l'omble chevalier retourne à son habitat natal pour se reproduire, mais les données suggèrent que la dispersion vers les habitats non-nataux est plus commune que chez les autres salmonidés. Une distinction est apportée entre deux types d'évènements de dispersion qui ont des implications différentes autant au point de vue biologique qu'au point de vue de la gestion. La dispersion reproductive se produit lorsqu'un individu se déplace vers un habitat non-natal dans le but de se reproduire, alors que la dispersion d'hivernage se produit lorsqu'un individu se déplace vers un habitat non-natal durant une année où il ne se reproduira pas. Dans le premier cas, ce comportement peut se traduire en flux de gène entre populations avec d'importantes implications pour la démographie et l'intégrité génétique des populations d'omble chevalier. Dans le second cas, un mélange de différents stocks se produit lors de la pêche, mais sans échange démographique ou génétique entre les populations. Une compilation d'estimés de taux de dispersion provenant de populations canadiennes confirme que les taux sont généralement plus élevés que pour les autres salmonidés, mais démontre aussi beaucoup de variation interannuelle et interrégionale. De plus, une quantité considérable d'études suggèrent que les ombles chevaliers qui ne vont pas se reproduire dans la prochaine année sont plus susceptibles d'utiliser un habitat non-natal que les individus qui vont se reproduire. Nous suggérons que ce comportement créé un paradoxe pour la gestion des pêches. D'une part, ce comportement résulte en un mélange de stocks, suggérant ainsi une approche de gestion à échelle régionale. D'autre part, ce mélange d'individus ne se traduit pas en échange génétique, ce qui contribue au maintient de la différentiation génétique des stocks, et qui suggère donc une approche de gestion 'rivière-par-rivière'. Nous recommandons donc que l'approche 'rivière-par-rivière' soit maintenue dans les cas où les stocks sont en bon état. Si par contre un stock est en déclin, la fermeture ou la réduction de la pêche sur les stocks voisins devrait être considéré afin d'éviter la capture d'individus migrants du stock affecté.

BACKGROUND AND RATIONALE

The goal of the present document is to summarize the available data on the migratory behaviour of anadromous Arctic Char (*Salvelinus alpinus* (L.)), in order to provide advice for the management of fisheries targeting this species. The focus is on populations from Arctic Canada, and the emphasis is placed on aspects of the migratory behaviour that will have important implications for stock structure and delineation. Specifically, evidence for homing behavior (or philopatry) is discussed because it has important consequences for the management of the species. Homing is the behavior of salmonids by which individuals tend to return to their natal habitat (i.e., where they were hatched) to spawn (Quinn 1993). It is an important aspect to consider in management because it reduces the exchange of individuals between populations and thus the potential for gene flow, which leads to varying degrees of demographic independence among stocks, defined as “semi-discrete groups of fish with some definable attributes of interest to managers” (Begg et al. 1999). Furthermore, homing reduces genetic interactions (i.e., gene flow) among local populations, which increases genetic differentiation and promotes the evolution of local adaptation (Taylor 1991; Fraser et al. 2011). The maintenance of a variety of genetically independent stocks with variable life-history characteristics has been shown to have positive economic impact on fisheries by buffering the influence of temporal variation in environmental quality (the so-called portfolio effect, Schindler et al. 2010). We contend that the maintenance of this genetic diversity should be a priority for managers.

The definitions of some of the key terms used throughout the present document can vary in the literature and should therefore be clarified here. Dispersal is usually defined as the “…the movement the animal makes from its point of origin to the place where it would have reproduced if it had survived and found a mate” (Howard 1960). This definition, however, is somewhat restrictive when it comes to the complex life cycle of Arctic Char, and we also use the term dispersal when discussing the behavior of Arctic Char that utilize a non-natal system to overwinter (see next section for details). A term closely associated to dispersal and widely used in the salmon literature is straying, which refers to the use of non-natal freshwater habitat by an individual returning from its marine migration (Quinn 1983; Hendry et al. 2004). The inverse of straying and dispersal is homing, or philopatry, which refers to the behavior of an individual which returns to its natal freshwater habitat. Dispersal and straying, if it involves spawning individuals, has the potential to result in gene flow, which refers to the exchange of genetic material among populations (Allendorf and Luikart 2007). Not all dispersal or straying events, however, necessarily result in gene flow. Finally, we use the term migration to refer to the “relatively long-distance movements made by large numbers of individuals in approximately the same direction at approximately the same time … usually followed by a regular return migration”

(Endler 1977). In the case of Arctic Char, migration therefore refers to the seasonal movement of individuals between freshwater and marine environments.

ANADROMOUS ARCTIC CHAR LIFE-CYCLE

We here briefly review the life-cycle of Arctic Char as it pertains to straying and genetic stock. We focus on anadromous Arctic Char because (1) they are the primary targets of commercial fisheries for this species in Nunavut, and (2) this life-history type has the potential for demographic and genetic exchange between stocks, whereas land-locked and resident forms do not.

During the freshwater phase of its life cycle, Arctic Char occupy primarily lacustrine habitats. Spawning typically occurs in the fall in the gravel bottom of lakes and after an incubation period that ends the following spring, hatched juveniles will rear from three to nine years in fresh water before attempting their first ocean migration (Johnson 1980). Downstream migration of juveniles and adults occurs at ice break-up in the spring or early summer (Bégout-Anras et al. 1999). This marine phase of the Arctic Char life cycle typically lasts 30 to 60 days, a period during which most of the feeding and growth takes place. Before rivers freeze, all individuals, including non-mature individuals (juveniles and mature adults that are not spawning in the current year) must migrate back to fresh water to overwinter. In some locations, individuals spend an entire year in freshwater before spawning events (e.g., Gyselman 1994). In most other salmonid species (i.e., all Pacific and Atlantic Salmon), only current-year spawners migrate upstream, while non-mature fish remain in the ocean for one or multiple winters until reaching sexual maturity. Arctic Char, however, are believed to be unable to survive the winter at sea, perhaps because of a lower salinity tolerance than other salmonids, or because of their inability to survive sub-zero temperatures in salt waters. This forces Arctic Char to return to fresh water every winter (Johnson 1980). Upstream migrations back to fresh water invariably occur in the fall, sometimes starting as early as the end of July. Evidence indicates that most individuals home to their natal system to spawn and, but to a lesser degree, overwinter. Straying, however, appears more common in Arctic Char than in other salmonids and mixing of stocks could therefore be important (see later sections). Furthermore, there is some evidence that adult fish not spawning in the current-year (i.e., resting) have an increased propensity to stray than spawning fish (Moore et al. 2013). Evidence for homing and for overwintering straying is discussed at length in a later section.

Spawning occurs between September and November (Johnson 1980). Arctic Char are iteroparous (i.e., they reproduce more than once, as opposed to Pacific salmon) and it is suggested they have the highest rate of iteroparity of all anadromous salmonids, with up to 50% of adults spawning at least twice during their lifetime in some populations (Fleming 1998). The spawning events, however, are separated by two to four years (Dutil 1986). It is inferred that this occurs because the short marine phase of the life-cycle, when most of the feeding takes place, is not long enough to allow the time necessary to re-build energy reserves for gonadal development (Dutil 1986). Such skipped-spawning is not unique to Arctic Char and occurs in other iteroparous salmonids (Sandstrom et al. 2009; Rideout & Tomkiewiscz 2011), although other anadromous salmonids typically do not migrate back to fresh water in the years where they do not spawn (but see Larsen *et al*. 2008 for an example in Brown Trout, *Salmo trutta*).

Regardless of the complexity of the migratory life-cycle and of the unique features of specific systems, we refer to overwintering dispersal as the movement of non-spawning char to non-natal habitats. This behavior is to be distinguished from breeding dispersal, which is the movement of spawning individuals to non-natal habitats. The important distinguishing feature here is that the former does not lead to genetic exchange between populations. Thus, it also does not allow for the demographic rescue (i.e., a population that escapes extinction or severe bottleneck via the supplementation of individuals immigrating from elsewhere; Brown and Kodric-Brown 1977) of the populations in these non-natal habitats because the strays are not reproducing in these systems. The distinction is therefore critical to make for management because while overwintering dispersal may lead to stock mixing and mixed-stock fisheries, it will not necessarily affect the genetic and demographic integrity and independence of the stock. The management implications of this behavior are discussed in detail below.

COMMERCIAL HARVEST OF ARCTIC CHAR IN NUNAVUT

Arctic Char in Nunavut is extensively harvested by the Inuit both for subsistence and commercial purposes. Subsistence fisheries are managed locally by hunters and trappers organizations, whereas Fisheries and Oceans Canada is responsible for the management of the commercial harvest. The present document aims to provide advice for management of commercial fisheries and so we focus exclusively on summarizing elements of the commercial harvest for which the present review is relevant.

Commercial harvest of char has been ongoing in several communities since the 1960s (Roux et al. 2011). Territory-wide combined commercial harvests between 2001 and 2008 ranged between 74,124 kg and 95,558 kg (round mass) out of a total quota that varied between 281,500 kg and 409,800 kg during these same years (Roux et al. 2011). Quotas are usually assigned to each river separately (the ‘river-by-river’ approach) and are often set in the absence of abundance estimates. To minimize the chances of over-exploitation, a system of exploratory licenses was set in place where a conservative quota is assigned to a river, which is then fished for five consecutive years when biological information on the harvested catch is gathered (fork length, round mass, otolith age, sex, maturity). This data is then used to assess the sustainability of the current harvest level. Some mark-recapture or weir enumeration estimates of abundance have been attempted in certain locations, but the highly complicated migratory behaviour of char violates many assumptions of these methods (Roux et al. 2011).

Two important commercial fisheries that operate in Nunavut are contrasted below to provide an overview of the diversity of harvest methods, environments where harvests take place, and the life-history variety of the stocks harvested.

The Cambridge Bay fishery

A commercial fishery targeting various stocks of Arctic Char has been operating in the Cambridge Bay region since 1960 (Day and Harris 2013). Historically, eight fishing sites were harvested (Fig. 1) for a total yearly harvest averaging 41,290 kg round weight. The methods of capture include gill nets (usually 140 mm mesh size) and weirs. The gill nets can either be set close to the mouths of rivers in the ocean or wholly in freshwater. In the former case, fishing in the ocean can occur soon after ice break-up (presumably targeting fish migrating downstream for the summer) or in the fall during the upstream run (presumably targeting fish migrating upstream to overwinter). In the latter case, nets are usually set at the outlet of lakes and intercept fish migrating upstream in the fall. The weir harvest takes place in two different river systems (Halokvik and Jayco; Fig. 1) and blocks the entire width of the river for a few days in the fall during the upstream run. Fish are collected in a box in the center of the weir and pushed into a modified seine net. The absence of gill marks and the high quality of the fish harvested with this method commands a higher price. Quotas in the region vary between 2,400 kg and 20,000 kg per river per year (Day and Harris 2013), making them some of the largest in Nunavut (Roux et al. 2011). The fishery is currently managed on a river-by-river basis, but an area quota was experimented with in the 1960s. This area quota resulted in a rapid decline in the fishery at Ekalluk River where most of the fishing took place due to its proximity to the town of Cambridge Bay (Day and Harris 2013). This decline probably indicates a certain degree of natal homing.

The topography of the region around Cambridge Bay is flat and watersheds are geographically extensive and complex (Fig.1), with each drainage basin usually comprised of numerous connected lakes. For example, the Ekalluk River, an important fishing site, drains an area of approximately 5,835 km^2 with at least four lakes where Arctic Char have been observed to spawn (Kristofferson 2002). The largest of those lakes is the 75km long Ferguson Lake, which has a surface area of 740 km^2. Evidence suggests that the Char utilizing different spawning locations within this complex watershed are morphologically distinct (Kristofferson 2002). A weir enumeration conducted on the Ekalluk River in the fall of 1979 counted 183,203 individuals migrating upstream. A majority of the harvested rivers in the Cambridge Bay region empty themselves in Wellington Bay and are relatively close to each other. This could in part explain the high rates of stock mixing documented in this region by Dempson and Kristofferson (1987). Whether stock mixing occurs more frequently during the spring or fall harvest is currently unknown, but preliminary data from a telemetry study suggest that stock mixing may be higher during the spring fishery (J.-S. Moore and L.N. Harris, unpublished data).

The Cumberland Sound fishery

Commercial fisheries targeting anadromous Arctic Char are operated on 17 stocks in the Cumberland Sound region (Roux et al. 2011). All these fisheries take place in the fall during the upstream migration and utilize gill nets with 140 mm mesh size. Commercial quotas are set for each river, and tend to be smaller than in the Cambridge Bay area with none being greater than 5,000 kg (Roux et al. 2011). The smaller size of the freshwater systems in this area means that each river probably supports smaller populations. However, no abundance estimates exist for these stocks, and many of the fisheries are still at an exploratory phase.

The region surrounding Cumberland Sound is mountainous and characterized by long glacial fjords. Most watersheds sustaining Arctic char fisheries are fairly small and simple and are usually found at the head of long fjords with a small number of headwater lakes. The topography of the region means that the average distance between fish-bearing freshwater systems is comparatively larger than in the Cambridge Bay region. Still, genetic data indicates that stock mixing could be important (Moore et al. 2013).

APPROACHES TO THE STUDY OF MIGRATORY BEHAVIOR

Here, we briefly review available methodologies for the study of migration in fishes. The list of possible methods is not exhaustive, but is rather limited to methods that have been applied specifically to Arctic Char. The rationale, advantages, and limitations of each method are briefly discussed, with an emphasis on their importance for the specific topics we address in this review.

Capture-mark-recapture

In capture-mark-recapture (CMR) approaches, external (e.g., t-bar tags, Carlin tags) are attached to individual fish. Movement behavior is inferred from the distance between the release location of the tagged fish, and the location where it was recaptured. The advantage of this approach is that it is possible to mark a large number of individuals at low costs. A large number of marked individuals, however, are often required to generate enough data for statistical appraisal of movement patterns, because only a very small proportion of tagged fish are usually recaptured. Furthermore, in many studies (reviewed below), recapture events are often dependent on fisheries (i.e., a reward is provided to fishers for tag returns or for information pertaining to recapture location). This does not provide an unbiased assessment of movement because fishers do not recapture fish using any specific sampling design (i.e., effort may not be distributed equally throughout the study region – although this is not necessarily a problem for studies of straying). Additionally, the natal system of an individual fish may also not be known because the fish may not necessarily be tagged in their river/system of origin. This has important implications for species like Arctic Char that are hypothesized to have a high propensity for dispersal. Finally, tag loss and tag-associated mortality can bias results if not taken in consideration. For instance, Berg and Berg (1990) estimated a 28.8% reduction in sea survival rate of tagged first-time migrants and reported important tag loss. Tagging, however, did not influence the survival rate of migrating older-char (Berg and Berg 1990).

Telemetry

Broadly speaking, telemetry is defined as the remote measurement of data (Cooke et al. 2004), and, in the present context, applies to the remote tracking of the location of individual animals. We further focus on animal-born transmitters that permit the tracking of free-ranging animals. The studies of Arctic Char using telemetry technology reviewed here only include designs where acoustic or radio transmitters are surgically implanted into fish (or in one case, externally attached), and movement is tracked through fixed arrays of receiving stations or using hand-held receiving devices (or a combination of the two in some cases). Although satellite tracking technology and archival data loggers that record GPS coordinates of individuals are available, no reviewed study used such technologies.

The main advantage of telemetry studies over capture-mark-recapture is that they can provide detailed data on fine-scale movements. Telemetry studies can also track the movement of individual fish over a long period of time and can allow researchers to discern daily or annual variation in movement behavior (e.g., Spares et al. 2012). This is often impossible with capture-mark-recapture studies of the kind described above because recapture is often lethal (at least in the case of fishery-dependent recaptures). One disadvantage of telemetry approaches employing fixed-station monitoring receivers is that detection of individual fish is limited to the location of receivers, and that important movement may be missed if appropriate receivers are not present. Consequently, careful design for passive, fixed-receiver locations that use available information on migratory behavior, or the incorporation of hand held receiver devices for actively tracking individual fish, is crucial. Furthermore, as described above for capture-mark-recapture studies, the tagging or transmitter implantation location may not be the system of origin of the marked fish. Finally, the surgical implantation of telemetry transmitters can also lead to adverse effects on the fish, which can change the physiology and behavior and lead to increased mortality (Jepsen et al. 2002). Here, a distinction has to be made between acoustic and radio telemetry because the latter involves an externally trailing antenna. It has been suggested that the antenna could reduce swimming ability by increasing drag, but evidence for this remains scarce (Jepsen et al. 2002). Biofouling of the antenna has also been reported, as has inflammation, infection and tissue necrosis at the antennae exit wound (Jepsen et al. 2002). Acoustic tags, on the other hand, are generally fully contained in the body cavity. They have been shown to have adverse effects on swimming ability and spawning success in some species with elongated and flat body shapes, but appear to have minimal negative impacts on salmonid fishes (Jepsen et al. 2002).

Genetic approaches

When mixing among populations is sufficiently low, genetic differences tend to accumulate at a rate that is proportional to: (1) the amount of genetic exchange among populations (i.e., gene flow); (2) the size of the populations (the smaller the populations, the faster the differences accumulate by a stochastic sampling process referred to as random genetic drift); (3) the time since the populations split or were established; and (4) the rate of mutation at a particular genetic locus (Allendorf and Luikart 2007). The ensuing genetic population structure (e.g., variation in allele frequencies and genetic differences) observed among populations can then be informative regarding the interconnectedness or the differentiation of various stocks and several statistical methods are now available for inferring gene flow and dispersal among populations. Another application of genetic markers is that they can be used to perform population assignment of individuals (Manel et al. 2005; Paetkau et al. 2004). This approach is similar to a discriminant function analysis, where the multi-locus genotypes of individuals are used to maximize the variation among populations or stocks. Using reference samples (samples known to come from a specific location/population), it is then possible to assign individual fish to their putative population of origin on the basis of their multi-locus genotype. The genetic assignment approach, which has traditionally relied mainly on fast-evolving microsatellite markers, has had considerable success being applied to fishery management problems (Hansen et al. 2001). In salmonids, the approach is often applied in mixed-stock fishery analyses aimed at resolving which populations are being harvested, and to what extent (e.g., Harris and Taylor 2010, Beacham et al. 2012). More recently, single nucleotide polymorphisms (SNPs) markers have started being used more heavily as well. These markers are less variable than microsatellites, and thus provide less information per marker. But they are more amenable to high throughput data generation, and more markers can easily be developed and used in a single study. They can thus equal, and even surpass the resolution of microsatellite markers when several hundreds to thousands of markers are used. They also have the added advantage of being more easily standardized across laboratories. SNPs are heavily used for mixed-stock fishery analysis in Pacific Salmon species (e.g. Smith et al. 2005).

The advantages of genetics methods are that (1) they are relatively inexpensive once the samples have been collected because long periods in the field are not required, and (2) unlike all the other methods presented above, the population of origin of an individual can be determined, provided that appropriate baselines are available (i.e., reference samples of known origin – this requirement can be relaxed in some situations) and population structure is significant. This last advantage is particularly important for the study of straying behaviour, information that we argue is crucial to the management of Arctic Char. Genetic methods, however, are not without some important disadvantages. In order to have sufficient power to assign individuals to their population of origin, genetic differences among populations must be sufficient (Cornuet et al. 1999). Lack of sufficient power can lead to high levels of uncertainty and potential error in assignment. The accumulation of genetic differences being contingent on a suite of evolutionary forces acting at both historical and contemporary timescales, researchers must rely on available genetic variation and cannot influence it beyond the choice of appropriate markers and study design. This can be particularly problematic for northern fishes like Arctic Char that only very recently recolonized their current distribution following the last glaciation (Brunner et al. 2001), and thus had little time to accumulate genetic differences through mutation and drift. Additionally, assignment power is also dependent on the number of loci employed and the variability at these loci (Cornet et al. 1999). Therefore, increasing the number of genetic markers sampled, in the case of microsatellite loci for example, can alleviate some of these limitations. New, more powerful, genomic tools are also becoming increasingly available for non-model organisms at rapidly decreasing costs and offer the promise to greatly increase our power of assignment for populations with minimal genetic divergence. These new tools will be discussed in greater detail in the 'Future work' section. Finally, all of the potential source populations need to have baseline samples included in the analysis to get accurate estimates, and fish in the baseline sample need to be sampled at the appropriate life-history stage to ensure they are local fish (i.e. spawners or pre-smolt juveniles).

Other approaches

Other approaches, used to a lesser degree in Arctic Char, for inferring movements and migration are also available. Two older studies relying largely on observations are worth mentioning here, although their conclusions will not be discussed further given the unreliability of the methods used. Grainger (1953) acted as an observer on a fishing vessel near the Sylvia Grinnell River, Frobisher Bay, Baffin Island, Nunavut, in 1948 and 1950. Additional observations were made from shore in 1951 by the author alone and not as part of the commercial harvest. Some observations regarding the movement and timing of migrations are made in this article, but because the fish observed were not tagged, it is difficult to interpret the individual patterns with confidence. Similarly, Moore (1975) visually observed Arctic Char migrations in two rivers in Cumberland Sound, Baffin Island, Nunavut. He inferred from his observations that there was minimal mixing between stocks from two adjacent rivers, despite a fairly extensive zone where the two stocks intermingled. His observations, however, do not exclude the possibility that fish stray among rivers.

Finally, analyses of the elemental signatures within the otoliths have also been used for inferring movements and population of origin in salmonids (e.g., Wells et al. 2003). For example, Strontium (Sr) varies markedly depending on the environment and this element is readily incorporated into the calcified structures of fishes. It is found at much higher concentrations in seawater than in freshwater (Secor and Rooker 2000) and therefore assessing Sr concentrations in fish otoliths can provide data on freshwater versus marine habitat use (Swanson et al.

2010). Incorporating additional elements (e.g., Barium, Calcium, Zinc) allows for much finer resolution of habitat use and system of origin (Wells et al. 2003). The main disadvantage of these microchemistry methods is that fish have to be sacrificed to obtain the otoliths. Such methods, however, may be promising for assessments of straying, especially when combined with some of the methods described above.

ARCTIC CHAR MIGRATORY BEHAVIOR

Homing and straying: evidence from Canadian populations

On an annual basis, a proportion of Arctic Char leave freshwater habitats in the spring to enter the marine system for feeding. These fish must then return to freshwater in the fall to overwinter and/or spawn. Given this life-history characteristic, a behavior of interest in studies of migration in anadromous salmonids is the propensity of individuals to stray from (i.e., not return to) natal streams/lakes to either spawn or overwinter. Estimates of straying would ideally measure the likelihood that any given individual strays from its natal river. In practice, however, most estimates are obtained by observing the number of fish migrating up-river that are identified as immigrants from other rivers (e.g., based on physical tagging or genetic results). While the proportion of immigrants can provide an indication of the importance of straying, it is not necessarily equivalent to the population-level straying rate (the word *rate* is defined as the proportion of individuals from a given population that utilize a non-natal habitat in any given year). For example, a large number of individuals from a large population may disperse to nearby populations even if the straying rate is low. This distinction should therefore be kept in mind when interpreting results of studies that merely document the number of strays without an estimate of population size. In addition, straying in other salmonids refers to individuals migrating for the sole purpose of reproducing (Fleming 1998; Klementsen et al. 2003; Quinn 2005). As discussed earlier, this is not the case for Arctic Char, which only spawn once every few years but must return to freshwater every year. We will discuss the difference and resulting implications of overwintering dispersal versus spawning dispersal in the next section.

Dempson and Kristofferson (1987) provided a detailed description of two extensive capture-mark-recapture studies conducted in Labrador and in the Cambridge Bay region. In the Labrador study, a total of 7566 fish were tagged with Carlin tags and these fish were subsequently recaptured in local commercial fisheries over a period of 7 years. The proportion of fish that were recaptured in rivers different from the river where they were tagged varied from 3 to 17% depending on the stock (a total of 5 ‘stocks’ were studied, with some stocks consisting of bays into which multiple rivers flowed). For instance, 97% of the fish tagged in the Nain area were recaptured in the same area, while only 83% of fish tagged in the Voisey Bay area were recaptured there (interestingly, the remaining 17% were captured in the Nain river, indicating asymmetric dispersal). There was also substantial variation in return rates among years. The capture-mark-recapture study conducted in the Cambridge Bay region uncovered considerably higher rates of straying. There, a total of 6195 char were tagged with Floy tags and recaptures were also fisheries-dependent. The proportion of fish that were recaptured in rivers different from where they were tagged again varied among river from 7 to 54%. The lowest number (7%) is from the most distant river (Jayco River) which was the only river fished in that region, which probably explains the lower number of straying fish recorded there. Again, asymmetries in dispersal were evident: 33% of the fish tagged in the Halovik River were recaptured in the Lauchlan River, but only 4% of the fish tagged in the Lauchlan River were recaptured in the Halovik River.

In the Nauyuk Lake system on the Kent Peninsula in Nunavut, Gyselman (1994) operated a fish weir between 1974 and 1979. He found that 30-50% of the tagged char that left the Nauyuk River in the spring never returned. The size of the fall upstream run, however, did not decrease between years. This suggests that it was supplemented by nearby systems and that fish that did not return one year were not mortalities, but that they apparently utilized other nearby systems for overwintering and/or spawning. While this particular design is obviously imperfect for the study of straying, especially given the absence of sampling at nearby rivers, this study provides evidence similar to that provided by Dempson and Kristofferson (1987) suggesting that straying among char stocks may be prevalent.

More recently, a small capture-mark-recapture study was conducted in Frobisher Bay, Nunavut, between 2009 and 2011. In this study, Arctic Char were tagged in two proximate rivers: the Sylvia Grinnell River and the Bay of Two Rivers (VanGerwen-Toyne et al. 2013). Although the small number of char recaptured in this study (83) makes drawing strong conclusions difficult, the results appear to show little movement of char between systems. Indeed, all of the recaptured fish marked in the Sylvia Grinnell River were recaptured either in the river itself, or in Frobisher Bay, but near the river. Three char marked in the Bay of Two Rivers, however, were collected close to the Sylvia Grinnell River, suggesting that movement may be asymmetric in this system. The fact that only a small number of char (N = 72) were tagged in the Bay of Two Rivers makes this even more plausible. Moreover, an acoustic telemetry study conducted on the same two rivers also found evidence of asymmetric movements from the Bay of Two Rivers to the Sylvia Grinnell area (Spares et al. 2012).

Moore et al. (2013) used a genetic assignment approach to identify strays in samples of fish collected, for the most part, during the fall upstream migration of char in the Cumberland Sound region of southeast Baffin Island. The power of their approach, however, was limited by small amounts of genetic differentiation among stocks. As a consequence, estimates of straying varied extensively depending on the analysis method used. The estimates, however, fell within the range of previously reported estimates from mark-recapture studies, with an estimated 15.8% to 46.5% of genotyped individuals being assigned to a river different than that from which they were caught. These authors, however, did find that the majority of individuals identified as strays were assigned to proximate rivers, suggesting that long-distance dispersal may be limited in this system.

Overwintering straying

It has long been hypothesized that Arctic Char may display a higher propensity to stray in the years when they are not spawning (Johnson 1980). Direct and strong evidence for this behaviour, however, has been elusive. Several studies only cite indirect evidence for the behavior (Dempson and Kristofferson 1987; Gyselman 1994; Bernatchez 1998), and these, combined with more recent direct evidence (e.g., Moore et al. 2013), suggest that this behavior is likely present in a wide variety of anadromous Arctic char populations.

Mark-recapture studies have provided the bulk of data supporting the hypothesis that Arctic Char returning to freshwater to overwinter have an increased propensity for straying from their natal system. Over the seven-year duration of their study in Labrador, Dempson and Kristofferson (1987) recaptured 21 tagged individuals more than once at counting fences. Of those 21, five had been absent two years before returning to their tagging location. Dempson and Kristofferson (1987) inferred from the topography of the study area that these absentees likely utilized other nearby rivers in the intervening years for overwintering. In his mark-recapture study of Nauyuk Lake, Gyselman (1994) found that 7.2% of recaptured fish were absent for one or two years before being recaptured again at the weir and over 35% of tagged fish in this study never returned to the river where they were tagged. Although the latter can be attributed at least to some degree to mortality, these data suggest that other nearby systems may be important (i.e., for overwintering and/or spawning). Finstad and Heggberget (1993) also observed a number of char returning to their tagging location after one or more years of absence, but did not provide numbers. All these studies, however, are unable to directly demonstrate increased propensity to stray in overwintering fish because (1) the reproductive status of tagged individuals is often unknown (it is difficult to assess without opening the body cavity and directly observing gonads); and (2) the actual river of origin for the tagged fish is unknown.

The genetic assignment approach used by Moore et al. (2013) was also used to investigate the question of dispersal solely for overwintering. This approach circumvents the shortcomings to mark-recapture studies because (1) the reproductive status of all genotyped fish was known (i.e., fish were dead-sampled), and (2) the population of origin of assigned fish was known. As indicated earlier, however, assignment power was low and large uncertainties remain regarding assignment. Despite these caveats, all analytical methods found evidence that overwintering individuals had an increased propensity to stray compared to individuals in breeding condition, and that only 24-31% of fish identified as dispersers were in breeding condition. These results indicate that overwintering Arctic Char, at least in this system, do have a considerably elevated propensity to stray compared to breeding individuals, but that straying is still present in breeding individuals.

The radio-telemetry study of Beddow et al. (1998) also provided evidence of individuals overwintering at a different location from their spawning site, but the situation described here is likely unique. In the Voisey Bay region of Labrador, two rivers flow to the ocean in very close proximity: the Ikadlivik Brook and the smaller Reid Brook. Fish tagged in the fall in Ikadlivik Brook stayed there for the entire duration of the study (1 Aug - 31 Oct). A large proportion (48%) of the fish tagged in the Reid Brook, however, were observed to move to Ikadlivik Brook starting in late August, although most of this movement between rivers occurred in October, presumably after spawning was concluded. Beddow et al. (1998) explain this exodus by the absence of suitable overwintering habitats in Reid Brook itself. A similar situation occurs in the Nauyuk Lake system, where fish have to overwinter in Nauyuk Lake before being able to access the spawning grounds in the upstream Willow Lake (Johnson 1980). This occurs because the creek connecting Willow and Nauyuk lakes only contains sufficient water to permit migration during the spring freshet (Johnson 1980). In both of these cases, overwintering dispersal is ‘imposed’ on Arctic Char by the local environment and topography. It is therefore a different behavior from that documented in the above studies, where individuals move among different available, suitable habitats in different years.

The biological, and hence management, implications of the increased propensity of overwintering individuals to stray are potentially profound. It means that the majority of straying events would then have no potential to lead to gene flow (i.e., the exchange of genetic material among stocks). This means that genetic differences among stocks could accumulate despite extensive mixing of individuals from different systems. This increased capacity for genetic differences to accumulate could also theoretically increase opportunity for local adaptation among stocks, a possibility that was formally explored with population genetic models by Moore et al. (2013). As will be discussed in greater detail in a later section, the preservation of locally-adapted stocks should be a management priority because it can increase the long-term stability of fisheries. It also means that dispersal does not necessarily lead to increased recruitment opportunities, and that dispersal from nearby stocks may not necessarily be effective in cases where conservation plans rely on natural re-colonization (although this is highly speculative as breeding dispersal may be density-dependent and increase in cases where ‘empty’ habitats exist). The management implications of the behavior are discussed in a later section.

Spatial extent of straying

The spatial extent of straying (i.e., how far from their natal rivers do individual fish stray), also has important biological consequences because it determines the geographical scale of population connectivity. This is, of course, a crucial consideration when determining the scale of appropriate conservation measures and management strategies. Some of the capture-mark-recapture and genetic studies presented above can inform this question.

In general, there is reasonable evidence that straying is most prevalent among proximate systems. Both capture-mark-recapture programs summarized by Dempson and Kristofferson (1987) found that most recapture events were recaptured close to the site where tagging occured: in the Labrador study, 95% of recaptures were within 70 km of the tagging site, while in Cambridge Bay 85% were within 60 km. The spatial extent of the Labrador study area was of over 250km and that in the Cambridge Bay region of more than 500km so these values are unlikely to be biased by limited sampling extent. Note also that these numbers include both philopatric and straying individuals. Still, strays were often observed to be from nearby rivers. In Cambridge Bay, for example, the Ekalluk, Halovik, and Lauchlan rivers, all emptying in the Wellington Bay, exchanged large numbers of migrants with each other, but almost none with the Jayco River draining into Albert Edward Inlet to the northeast of Cambridge Bay. In addition, no fish from Victoria Island were recaptured in rivers from the mainland despite the relatively short distance. Note, however, that fishing effort may have been lower on the mainland rivers. A long-term, mark-recapture study performed in northern Norway (Jensen and Berg 1977; Berg and Jonsson 1989) reached similar conclusions, showing that 54.9% of tag recoveries were from within three km of the marking site, and only 1.2% were from more than 80 km away. The study of Finstad and Heggberget (1993), also in Norway, was conducted on a smaller spatial scale, but also recovered 80% of its tags within 30 km of the tagging location. The acoustic telemetry study conducted by Spares et al. (2012) in the Frobisher Bay region also showed that most movement occurred close to river mouths. Indeed, most detections of acoustically-tracked char were made within 4 km of the river mouth in which they were tagged, and the farthest detected relocation was only 26.6 km from its tagging location. It should be noted, however, that the range of detection was limited by the fixed acoustic array in this study, so further movement may have gone undetected. Finally, the genetic assignment study of Moore et al. (2013) also suggests that dispersal is restricted to nearby rivers in the Cumberland Sound area, as evidenced by a rapidly declining frequency of dispersers assigned as distance from their capture sites increased. The general pattern of isolation by distance identified in the Cumberland Sound populations also lends support to this notion (Harris et al. *in press*).

Despite the general tendency of char to return to either natal or to nearby rivers, most studies above also identified a small number of long-distance migrants. Dempson and Kristofferson (1987) report that, in the Cambridge Bay region, an Arctic Char tagged in the Ekalluk River was subsequently recaptured 550 km from its tagging location (at Shephard Bay). Another Arctic Char tagged in the Ekalluk River was recaptured in the Jayco River, a coastal distance of almost 400 km. Similarly, a few fish from the Jayco River were recaptured in the Cambridge Bay area, 300 km from their tagging location. Jensen and Berg

(1977) reported a char recaptured 940 km away from its tagging location in northern Norway. It should also be noted that effort usually (but not always) decreases with distance from tagging location in such studies, such that there is a possible bias towards increased likelihood of capturing short-distance migrants. Thus, the fact that most char are recaptured close to their tagging location does not necessarily imply that char are limited in their abilities to cover large distances.

Genetic differences among stocks

One of the most important biological consequences of straying is that it has the potential to lead to gene flow among populations. Gene flow among stocks can slow the accumulation of genetic differences, and prevent the evolution of fine-scale population structure and local adaptation (Hendry et al. 2004). There now exist a handful of genetic studies relying on fast-evolving microsatellite markers for assessing population structure and addressing some of these questions in anadromous Arctic Char.

The first available study to assess fine-scale population structure in anadromous Arctic Char was performed on six populations from Labrador (Bernatchez et al. 1998). Despite using only six microsatellite markers (a small number by modern standards, which should result in lower statistical power) the study was able to identify significant genetic differentiation among stocks at the scale of the river, with an average F_{ST} (a measure of genetic differentiation among populations) among anadromous stocks of 0.039. Harris et al. (in press) also used microsatellite markers to assess fine-scale population differentiation among 14 sampling locations distributed throughout Cumberland Sound. The study used a larger number of microsatellite markers (15 informative markers) and was able to resolve significant genetic differences at the scale of the river system, with an average pairwise F_{ST} among rivers of 0.042. The study also identified the presence of hierarchical genetic structure, with stocks from the northern part of Cumberland Sound more genetically similar to each other than to stocks from the southern part of the Sound. Data on hierarchical genetic structure will be helpful in cases where area-specific management actions are required by providing important information on the spatial extent of connectivity among stocks. Finally, a small survey of genetic differences between the Sylvia Grinnell and the Bay of Two Rivers systems in Frobisher Bay was performed for a recent Regional Advisory Process (RAP) meeting on the status of the Sylvia Grinnell River Arctic Char stock (VanGerwen-Toyne et al. 2013). The genetic differences between these two sites was smaller than that observed in other studies (F_{ST} = 0.019). Lower genetic differentiation in this system may be the result of increased spawning dispersal and the tagging studies mentioned above have found this dispersal to be asymmetric (from Bay of Two River to the Sylvia Grinnell River).

In conclusion, genetic differences at the scale of the river are common in populations of anadromous Arctic Char. Those differences, however, tend to be small. It is currently difficult to interpret these genetic differences biologically because they could result from both high gene flow (the parameter of interest for management) or from the short amount of time elapsed since those areas were re-colonized following the last glaciation. Indeed, most extant populations of anadromous Arctic Char (and certainly all the above-mentioned populations) were only established less than 12,000 years ago following the retreat of the glaciers that covered their current range during the last glacial maximum (Brunner et al. 2001; Dyke et al. 2003). Recent data suggest that most of the Canadian Arctic was colonized from a single source population that appeared to have low amounts of genetic diversity (Moore et al. in prep). It is therefore possible that the small amount of genetic differentiation observed among Arctic Char stocks is at least in part due to the lack of sufficient time to accumulate differences through mutation, selection and genetic drift.

MANAGEMENT IMPLICATIONS OF ARCTIC CHAR MIGRATORY BEHAVIOR

Current management paradigm: the 'river-by-river' approach

Commercial fisheries for anadromous Arctic Char are currently managed on a 'river-by-river' basis, with each river (or system) receiving a quota independent of other rivers or system (e.g., Day and Harris 2013). This was initially based on the assumption that each system represented a discrete stock (Kristofferson et al. 1984). Although this may be true for Arctic Char systems to some degree, when fishing in coastal areas it is likely that several populations can be concurrently harvested, raising mixed-stock fishery concerns (i.e., when several populations are vulnerable to harvest at a discrete location). Thus, effort should be allocated for determining the proportional contribution of each population that is potentially being exploited (e.g., Harris and Taylor 2010). Further, given the vast size and complexity of some of the freshwater systems in the Canadian Arctic, it is reasonable to assume that there is an admixture of local stocks within many of the river systems (Kristofferson 2002). Thus, it is clear that the fishery is not likely targeting a homogenous stock at each location, which further complicates management (Kristofferson and Berkes 2005). Providing insights into these two concerns would undoubtedly be an expensive undertaking and one that would have to occur periodically to take into account temporal variation in stock contributions to the fishery. Thus, although there is undoubtedly dispersal and gene flow among proximate Arctic Char systems disputing the discrete stock hypothesis in the Canadian north, until a better understanding of the scale of population structuring is attained, the river-specific management approach is still viewed as the most effective strategy (Roux et al. 2011). Furthermore, the statistically significant genetic structure resolved between most systems using more advanced molecular methods, even rivers that are proximately situated, also suggests that a river-by-river management strategy is appropriate for the time being (Harris et al. 2014).

Straying without gene flow: a paradox for management
As mentioned earlier, important gaps remain in our understanding of straying and homing behavior in Arctic Char. The discussion below should therefore be interpreted with caution and most of the conclusions discussed are associated with a great deal of uncertainty.

Despite these important data gaps, a few general conclusions emerge from the review of Arctic Char migrations that have important implications for the management of Arctic Char fisheries. The first important point is that, while good estimates of straying 'rates' are still lacking, there appears to be enough evidence for migration to non-natal streams to conclude that it is a common feature of the Arctic Char life cycle. These data suggest that the current management approach of managing each river independently of other rivers may not be the most appropriate strategy, at least to a certain degree in some systems. The high rates of straying observed in most stocks where it was measured suggest that a more regionally-integrated approach should perhaps be considered.

There are several potential problems, however, with this approach. First, regional quotas have been applied to Arctic Char fisheries in the past and have met with minimal success, if not absolute failure. For example, in the Cambridge Bay region, a Wellington Bay area quota (which included the Ekalluk, Paliryuak (Surrey) and Halovik (30 Mile) rivers) was established in the late 1960s (Kristofferson and Berkes 2005). The majority of fishing effort, however, was concentrated on the Ekalluk River population given its closer proximity to the community of Cambridge Bay (Kristofferson and Berkes 2005). Fishing in this manner with higher than anticipated exploitation of Ekalluk River char continued for three years, and over this period, the average weight of Arctic Char in this system decreased by 50 % (from 3.0 to 1.4 kg, Cosens et al. 1990). Under this area quota, the fishery was viewed as collapsed and subsequently closed for several years (Cosens et al. 1990). Interestingly, the population recovered quickly, perhaps due to immigration of Arctic Char from nearby systems, and the fishery was reopened a few years later. Second, a regional approach to management ignores potential genetically based differences among stocks within a region. The few genetic studies of anadromous Arctic Char from Canada suggest that significant genetic differences at neutral loci exist between nearby stocks (Bernatchez et al. 1998, Moore et al. 2013; Harris et al. 2014). This is in line with behavioral data, which suggest that overwintering char are more likely to disperse than spawning char. This behavior results in a situation where gene flow among stocks remains limited despite extensive mixing of individuals. This presents an interesting paradox for management: should there be an emphasis on the fact that most stocks are genetically distinct due to low gene flow, and therefore be managed on a river-by-river basis; or should the emphasis be on the fact that pervasive straying leads to mixed-stock fisheries that would suggest a more regionally-integrated approach to management? We argue below that the optimal approach to take into account the complex migratory behavior of Arctic

Char in management is to adapt management approaches depending on the situation.

Recommendations
Based on the above discussion, we recommend that the current river-by-river management approach be maintained for Arctic Char stocks that are deemed stable and assumed to be harvested at sustainable levels. This conservative approach has a demonstrated record of success being applied to virtually all important commercial fisheries for Arctic Char in Canada, and it is the management approach that is best suited to the preservation of genetic variation among stocks.

The river-by-river approach, however, is likely to be problematic is cases where a single stock suffers from decline and requires management action. This is likely to occur in many parts of Nunavut where stocks located close to communities often sustain significant subsistence and recreational harvest in addition to commercial harvests. In cases where action is required for the conservation of a single stock, the 'river-by-river' approach may be ineffective because it ignores the fact that fish from the focal stock may move to nearby systems to overwinter and, to a lesser extent, spawn. When declines in specific stocks require management action such as fishery closures and/or decreased quotas, the high amount of straying observed would suggest that similar actions should be envisaged at nearby stocks as well. This is especially important in cases where large and small stocks are in close proximity, or in cases where dispersal is asymmetric. Effective application of such a strategy would thus require more information on patterns of migration than currently available for most stocks.

This recommendation, however, hinges on a few important hypotheses that remain largely untested. First, ignoring practical issues related to area quotas discussed above, the biological rationale for managing each stock independently despite widespread straying is that genetic differences among stocks are maintained. There is currently little available data on these questions. The available data from the Labrador, Cumberland Sound and Frobisher Bay suggest that small but significant genetic differences exist at neutral microsatellite markers, which provides an indication of some restricted gene flow in those systems. Additionally, the genetic differences among the Cumberland Sound populations were greater than those among Frobisher Bay populations, suggesting that important variation exists among regions. The hypothesis of genetic differentiation of stocks should therefore be tested rather than assumed in all regions where Arctic Char are commercially harvested. For some of the stocks currently commercially harvested (e.g., those around Cambridge Bay, or on the Kivalliq coast), no such data exist. Second, the spatial scale of genetic differences is often unknown, and the presence of hierarchical genetic structure can complicate decision-making. Identifying such hierarchical structure is crucial for appropriate management. For example, the study of genetic structure in the Cumberland Sound identified 14 genetically distinct populations that were hierarchically organized into two larger genetic groups: one in the northern part of the Sound and one from the southern part (Harris et al. 2014). Knowing the presence of such hierarchical structure is required to identify the appropriate geographical scale of management actions.

In addition, all available data are for neutral markers, typically microsatellites, which provides an indication of how much gene flow exist among stocks (i.e., how many fish successfully spawn in non-natal systems), but cannot answer the question of whether the genetic differences that accumulate among stocks are biologically meaningful. Indeed, the main biological rationale for preserving genetic variation among stocks assumes that this variation has functional significance in terms of local adaptation and evolutionary potential. For example, the ‘portfolio effect’ documented in Pacific salmon shows that the presence of genetically differentiated stocks in Alaska increases the economic value of the fishery, but this genetic variation needs to reflect differences in life-history traits and other biological characteristics to help buffer against temporal variation in environmental quality (Schindler et al. 2010). The question of whether stocks of Arctic Char are locally adapted to the conditions in their specific system remains unanswered. If the preservation of functionally important genetic diversity and of the evolutionary potential of Arctic Char is a priority, and we contend that it should be, more in-depth investigations of genetic variation and population structure among stocks should also be a priority. The documentation of life-history and other biologically important differences among stocks would help elucidate this question, as would the use of more sophisticated genomic techniques that now allow to survey the entire genome for signature of local adaptation (see next section). This is especially true for populations in the Canadian Arctic that are anticipated to be especially vulnerable to the impacts of climate change (Reist et al. 2006).

Finally, available evidence suggests that straying rates vary tremendously not only between years, but also among locations. Applying the above recommendation to all Arctic Char stocks without measuring specific rates of straying among rivers over several years therefore implies a considerable amount of risk (in terms of both conservation and/or lost harvest opportunities). Measuring this parameter for stocks of management concern should therefore be a priority.

FUTURE WORK

Projects currently under way aim to address some of the knowledge gaps identified in the present document and are therefore worth mentioning here. First, an opportunity arose for the department to collaborate with the Ocean Tracking Network (OTN), a large multi-institution NSERC-funded project that aims to study the migratory behavior and habitat use of dozens of species of marine animals in all three Canadian oceans. OTN plans to start acoustic tagging projects on anadromous Arctic Char in Nunavut, Nunavik and Nunatsiavut (Labrador), which will afford an opportunity to increase our knowledge of anadromous Arctic Char migratory behavior. The Nunavut component of the study will focus on the Cambridge Bay region, which is fortunate since this is the most important commercial fishing area in the territory. This work, which aims to quantify straying among rivers, will update the information collected in the 1970’s described by Dempson and Kristofferson (1987). Existing data will also allow interesting comparisons that may inform questions regarding temporal variability of straying estimates. The use of acoustic technology will, however, have several additional advantages compared to the tagging studies. First, the detailed movement data that is possible to collect with such technology will allow tracking fine-scale movement patterns and thus answer questions regarding the environmental determinants of movements. Second, the fixed acoustic arrays used in these studies will provide a somewhat less biased assessment of movement patterns than fishery-dependent tag recoveries, which can be heavily influenced by spatial variation in fishing pressures.

Combined with the acoustic telemetry work, a genetic project using modern genomic tools will also be conducted. The Cambridge Bay area has never been the focus of genetic work using microsatellite markers, but such work is currently proposed. It is therefore not currently known whether genetic differences among Cambridge Bay populations will be comparable to those observed in other areas (e.g., Cumberland Sound). Assuming they are, however, microsatellite markers may lack the power to assign individuals to their river of origin as in the Cumberland Sound (Moore et al. 2013), and will thus be of somewhat limited value in specifically quantifying straying rates among populations. Microsatellite markers, however, do afford the opportunity to resolve fine-scale population structuring in this system.

The rapidly decreasing costs of genomic technologies, and the expertise available through collaborations, offer an opportunity to apply much more powerful methods to this question. Next-generation technologies, used with the RAD-sequencing protocol, now allow the detection of thousands of informative SNP (single nucleotide polymorphisms) markers in a single experiment (Davey and Blaxter 2010). The use of a much greater number of marker loci (thousands compared to tens of microsatellite markers) should theoretically maximize the power of assignment despite low genetic differentiation. In particular, it is possible to identify loci that differ more than others between populations (outlier loci), which provide even more power of assignment. The identification and use of outlier loci in population assignment has led to vast improvements in assignment power in other salmonid populations (e.g. Freamo et al. 2011; Russello et al. 2012).

In addition to increasing the power of assignment of individuals and thus increasing the precision of genetic-based estimates of straying rates, the identification of outlier loci can also help identify genomic signatures of local adaptation among rivers that would go unnoticed using neutral markers such as microsatellites. Using thousands of loci increases the likelihood of finding markers that are located in, or close to, genes under selection. Identifying regions of the genome that vary across the landscape can thus provide insights into the existence of patterns of local adaptation, and also regarding the scale at which local adaptation is possible. As discussed at several points in this document, the preservation of genetically-isolated and locally-adapted stocks should be a priority for management, and genomic tools provide an unprecedented opportunity to address this question.

SUMMARY

- Straying appears prevalent in Arctic Char, with estimates of the proportion of returning Arctic Char from a non-natal system varying between 3% and 54%.
- Estimates of straying propensity vary tremendously among regions, and among years within region. It is currently difficult to evaluate whether this variation is biologically meaningful, or only the result of variation in study design.
- There is considerable evidence for the behaviour whereby individuals that are not in reproductive condition show an elevated propensity to stray. This has important consequences for the genetic distinctiveness of stocks, which may be considerable despite widespread mixing of stocks.
- Patterns of marine movement are still poorly understood. Available evidence suggests that most individuals remain close to the river from which they migrated downstream in the spring. Rare long-distance movements, however, has been detected with individuals travelling sometimes more than 500 km.
- Small but statistically significant amounts of genetic differences have been detected at the scale of river system whenever measured, suggesting that the river is the appropriate stock unit for fisheries management.
- The complex migratory behavior of Arctic Char creates a paradox for management: pervasive straying suggests that regionally-integrated management should be applied, while the observation of significant genetic differences among stocks (presumably because straying is mainly restricted to non-breeding individuals) suggests that the river-by-river management of char fishery continues to be applied.
- We recommend that the river-by-river management approach continues to be applied in cases where fisheries appear sustainable. A more regionally integrated management should only be applied in cases where specific stocks are in decline. In those cases, effective conservation would call for closures or reduction of fishing pressure on nearby stocks. Such measures would hopefully be based on movement data from those specific locations, since previous work has shown straying propensity to vary tremendously among regions.
- Despite these conclusions, our understanding of Arctic Char migrations remains incomplete, and most evidence discussed here is fragmentary,

inconclusive or limited to a short period of time or to small geographic regions. Accumulation of data on genetic population structure, straying and marine movements is crucial for fishery management. Gaining a better understanding of how these vary across regions and among years will allow managers to be proactive and to respond efficiently to future management challenges.

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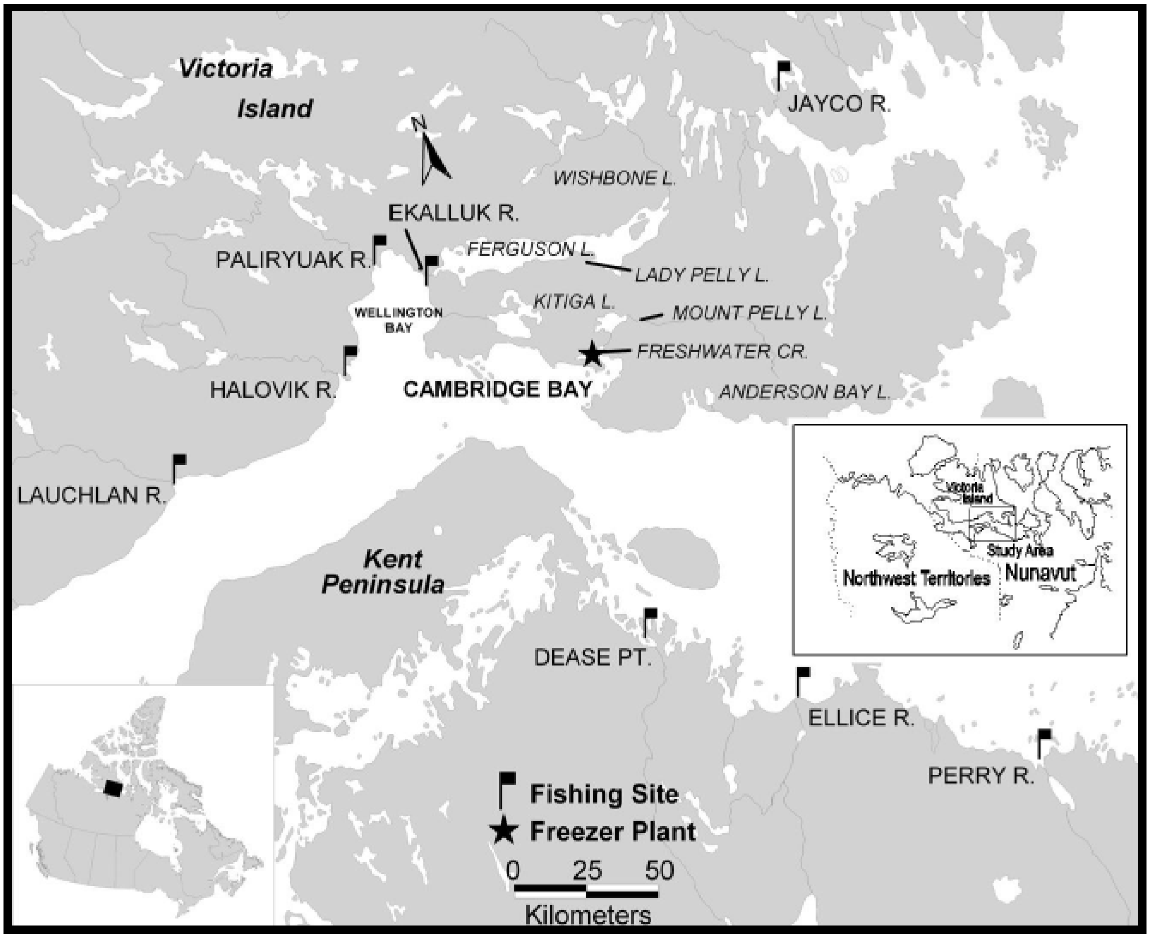

Figure 1. Map of the Cambridge Bay region showing the locations of fishing sites (adapted from Day and Harris 2013).

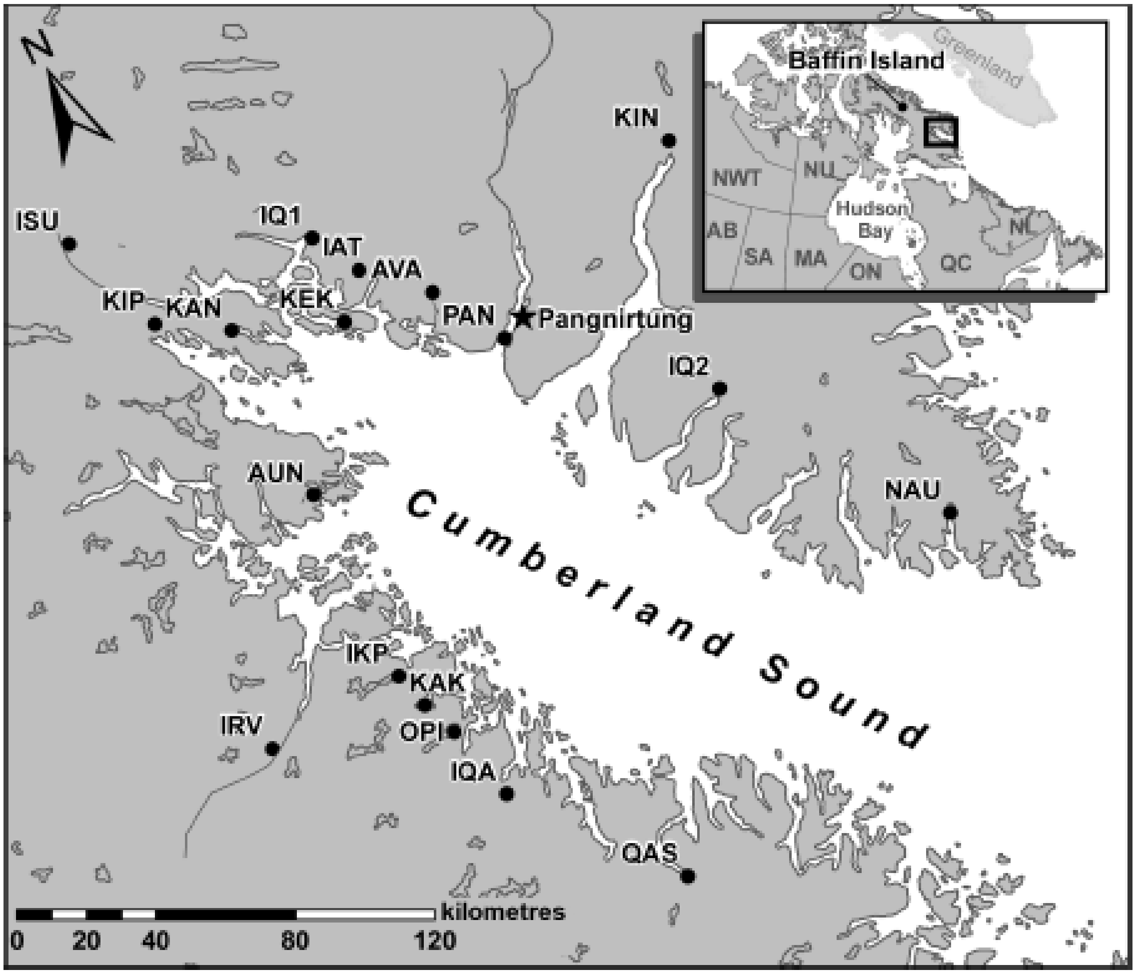

Figure 2. Map of the Cumberland Sound region showing the major commercial quotas (adapted from Moore et al. 2013).