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Population Structuring and Inter-river Movements of Northern Form Dolly Varden, *Salvelinus malma malma* (Walbaum 1792), Along the North Slope of Canada and Alaska

Structuration et mouvements entre les cours d'eau de la population de Dolly Varden – forme nordique (*Salvelinus malma malma*) (Walbaum, 1792) le long du versant nord du Canada et de l'Alaska

M.W. Kowalchuk, J.D. Reist, R. Bajno and C.D. Sawatzky

Fisheries and Oceans Canada / Pêches et des Océans Canada
Freshwater Institute / Institut des eaux douces
501 University Crescent / 501 Université Crescent
Winnipeg, MB
R3T 2N6

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ABSTRACT

Northern form Dolly Varden represent a unique part of the Canadian fish fauna, occurring in only six to eight rivers in Arctic Canada. The fish in each river system represent distinct populations based upon genetic and morphological data presented within this research document. Anadromous fish from each population display a strong sense of homing to their natal rivers, although a small percentage of non-spawning fish do stray between non-natal rivers for overwintering.

RÉSUMÉ

La forme nordique du Dolly Varden est un composant unique de l'ichtyofaune canadienne puisqu'on ne trouve l'espèce que dans six à huit cours d'eau de l'Arctique canadien. Les poissons de chaque réseau hydrographique forment des populations distinctes, selon les données génétiques et morphologiques exposées dans le présent document de recherche. Les individus anadromes de chaque population retournent souvent dans les cours d'eau où ils sont nés, même si un petit pourcentage de poissons non reproducteurs vont dans d'autres cours d'eau pour passer l'hiver.

1.0. INTRODUCTION

Dolly Varden (*Salvelinus malma* (Walbaum 1792)) are distributed coastally in North America from Washington State northward along the coasts of western British Columbia, Alaska, and the north coasts of the Yukon and Northwest Territories west of the Mackenzie River (Bajno and Reist 2002). Classification of Dolly Varden into a northern and southern form, *Salvelinus malma malma* (Walbaum 1792) and *Salvelinus malma lordi* (Günther 1866) respectively, has occurred based on differences in morphology, geographic range, and genetic makeup between the two (Armstrong and Morrow 1980; Behnke 1980, 1984; Craig 1989; Reist 1997; Kowalchuk *et al.* 2010). These two forms can be further divided based on one of four life history types. Anadromous fish migrate to sea annually to feed following smoltification, returning to freshwater to spawn and overwinter (Morrow 1980). Riverine (residual) fish (predominantly males) spend their entire lives in freshwater rivers co-occurring with spawning/overwintering anadromous fish, while stream-resident (isolated) fish are similar to residual fish but are separated from anadromous and residual fish by an impassable barrier (e.g., waterfall) or distance (Morrow 1980). Lacustrine fish which live the majority of their lives within a lake system are common in the southern form, though only a small number of such lacustrine populations have been found within the northern form, primarily within the Peel River basin (Morrow 1980; Anderton 2006 and references within; Reid and Skinner 2008; Sawatzky and Reist in prep.). Anadromous Dolly Varden from the North Slope of Alaska and Canada show a strong ability to home to their natal river system for both spawning and overwintering, although straying into non-natal systems has been observed in overwintering fish (McCart 1980; Crane *et al.* 2005). Variation in migration patterns of anadromous Dolly Varden has been exhibited in timing of migration as well as degree of homing.

Along the North Slope of Canada and Alaska anadromous northern form Dolly Varden are found in coastal streams between the Colville and Mackenzie rivers, which they use for both spawning and overwintering (Crane *et al.* 2005). Residual and isolated Dolly Varden occur primarily in interior streams in the Yukon and Northwest Territories as far inland as the Gayna River (Reist and Sawatzky 2010). Northern form Dolly Varden represent a unique part of the northern Canadian fish fauna, and occur in only eight river systems in Arctic Canada, namely, the Firth River and its main tributary Joe Creek, Babbage, Big Fish, Rat, Vittrekwa, Gayna, Fish and Peel rivers and possibly some rivers in the Coronation Gulf (e.g., Tree River) (Bryan 1973; McCart *et al.* 1974; Reist 2001; Mochnacz and Reist 2007; Reist unpubl. data) (Figure 1). Residual fish are confirmed from three of these systems - the Firth River and Joe Creek, as well as the Babbage and Big Fish rivers (Reist 2001). As well, Dolly Varden from the upper Peel watershed (e.g., the Blackstone, Bonnet Plume, and Wind rivers and their tributaries) are suspected to be residual and/or isolated fish. This is primarily because of the physical barriers and/or long distances from sea, which likely impede their ability to migrate to and from sea, although exactly which life history these populations exhibit has not been confirmed (Anderton 2006; Reid and Skinner 2008). Questions have arisen about population structuring within and between river systems because of the different life history types and apparent philopatry (i.e., homing to natal systems) exhibited by anadromous Dolly Varden (Rhydderch 2001). The objectives of this report are to: a) review all available literature and summarize population structuring of northern form Dolly Varden within and between North Slope rivers, and b) to describe the inter-river movements of northern form Dolly Varden (primarily the anadromous life history type) between rivers and coastal areas of Canada and Alaska.

2.0. POPULATION STRUCTURING

2.1. EVIDENCE OF DISTINCT POPULATIONS

In the context of this document a distinct population refers to a group of potentially interbreeding individuals within a given river system. One or more populations may occur within the same river system given differences in: a) spawning locations, b) spawning time (summer vs fall spawners), and c) genetic diversity.

2.1.1. Genetic Evidence

In the Arctic, low biodiversity at the species level is replaced by high biodiversity below the species level, allowing diverse sub-specific forms to adapt more readily to the extreme variability exhibited in Arctic habitats (Reist *et al.* 2001). This is especially true for *S. m. malma* occurring along the north slope of Canada and Alaska.

Reist (1989) examined electrophoretic variation for 13 enzyme systems and at least 20 presumptive genetic loci to genetically differentiate between life history stages and types of Dolly Varden populations from Joe Creek, Firth River, Upper Babbage River, Canoe River, Little Fish Creek (often incorrectly identified as Cache Creek in the literature) and the Rat River (Figure 1). Of the 13, two were polymorphic enzymes (superoxide dismutase (SOD), and glucose phosphate isomerase-3 (GPI-3)) within the populations studied. Analyses of these two enzymes indicated there were no differences in allele frequencies between fish of different life histories (anadromous or residual) or life stages (spawning vs resting anadromous fish), however isolated fish in the Babbage River were different (at one enzyme) from anadromous fish in the same drainage basin (Reist 1989). Meristic data, specifically numbers of pyloric caeca and gill rakers, corroborate these findings. With the exception of the Babbage River, fish from each river studied had no significant genetic differences from other fish within the same river, although some genetic variation was observed within the Firth River system. There was significant variation between fish from the Firth River and one of its tributaries, Joe Creek when analysis was done using data from anadromous and residual life history types combined. The frequency of GPI-3 for combined data from Joe Creek was 0.709, while it was 0.841 for combined data from the Firth River. This suggests the presence of two populations in the Firth River system (Figure 1) (Reist 1989).

Significant genetic variation was also found among all populations from the four river systems studied, with the frequency of the common allele for SOD varying between 0.720 and 1.0, and that of GPI-3 between 0.474 and 0.841 for anadromous spawning adults. When all life history types were included there was little change in frequencies. For both enzymes, each spatially adjacent pair of samples of anadromous spawning adults from different river systems was significantly different ($P<0.05$ to $P<0.01$) (Figure 2) (Reist 1989). For the six possible pairwise comparisons of non-adjacent systems, only the Joe Creek and Canoe River populations were similar for both enzymes (Figure 2) (Reist 1989). Everett *et al.* (1997) found similar results in a genetic study which examined 49 loci that encoded for 22 enzymes in Dolly Varden populations from 11 drainages along the Beaufort Sea in Alaska and Canada. Twenty-one of the 49 loci examined were found to be variable, with polymorphisms occurring throughout all populations with an average of 19%. This showed that, similar to Reist's (1989) results, each river system studied supported a genetically distinct population, along with evidence for separate populations occurring within a single drainage in three of the river systems studied (the Babbage River, Hulahula River, and Sagavanirktok River). Unlike Reist (1989), Everett *et al.* (1997) reported little genetic variation among fish from the Firth River, although the sample sites were different from those used by Reist (1989). Everett *et al.* (1997) also found no genetic differences between fish of different life history types (anadromous vs residual) in the same drainage.

Rhydderch (2001) used mitochondrial (mtDNA) and nuclear DNA markers to determine the genetic relationships of Dolly Varden from Little Fish Creek (identified as Cache Creek), Canoe River, Rat River, Joe Creek, two locations on the Firth River, as well as isolated populations from Little Fish Creek and the Babbage River (Figures 1 and 3). His mtDNA sequencing revealed the presence of 20 haplotypes, which were further subdivided into two major phenetic clusters. Diversity in these two haplotype clusters decreased from west to east with the exception of Little Fish Creek (Figure 3), suggesting that they may be phylogeographically informative (Rhydderch 2001) (see below). Genetic variation occurred between populations of *S. m. malma* from all the sampled drainages at both mitochondrial and nuclear markers. One exception was that the two samples from the Firth River, which, similar to the findings of Everett *et al.* (1997), showed little genetic variation suggesting that substantial gene flow occurs between fish within the Firth River (Figure 3) (Rhydderch 2001). Similar to the mtDNA results, nuclear DNA results indicated that the populations from the most westerly drainage (Firth River and Joe Creek) had the highest allelic diversity, while the remaining populations had no unique alleles, containing only a subset of the alleles found in the Firth drainage. These findings further support those of previous studies, which found that North Slope rivers support genetically distinct populations of Dolly Varden. Similar to the findings of Reist (1989) and Everett *et al.* (1997), Rhydderch (2001) found no significant differences in the genetic compositions among different life history types or stages, with the exception of isolated fish differing from anadromous/residual fish from the same river system. With the use of mtDNA and nuclear DNA, Rhydderch (2001) was able to reassign individuals to their original natal site with varying success. Isolated populations were reassigned most successfully with the Little Fish Creek samples showing 100%, and the Babbage River samples showing 96% reassignment. Anadromous populations were more difficult to reassign with the most easterly drainages reassigning most successfully – Little Fish Creek 96%, Rat River 92%, Canoe River 86%, and the Firth River 59% reassignment, again highlighting the high diversity found in the Firth River.

Both mitochondrial and nuclear markers displayed a reduction in allelic diversity from west to east, which Rhydderch (2001) attributed to the effects of the most recent glaciation. He hypothesized that as the Wisconsinan ice sheet advanced, populations from the most easterly drainages were extirpated or severely bottlenecked, while the Firth River, being the farthest from the glacial margin, was not (or minimally) influenced and therefore acted as a refugium (Figure 4). Once the ice sheet retreated, colonization occurred from the Firth River to the other more easterly drainages (Rhydderch 2001).

Reist (unpubl. data) expanded on Rhydderch's (2001) mtDNA analyses by conducting a more comprehensive (i.e., additional sites sampled, see Bajno and Reist 2002) study of Dolly Varden from the Yukon North Slope, and Norton Sound, western Alaska. Eleven haplotypes were distinguished and trends similar to those reported by Rhydderch (2001), in which haplotype variability decreased from west to east, were observed. The previous findings of Reist (1989) and Everett *et al.* (1997) that isolated populations and populations from different drainages are genetically divergent was also reinforced (Bajno and Reist 2002). Further mtDNA sequencing analyses by Reist (2001) also supported the genetic discreteness of fish in five North Slope river systems. In a comparison of the number of haplotypes in each population Reist (2001) initially found that the Rat River had the greatest diversity (six haplotypes), and that fish from the Rat River were distinct from other North Slope rivers. However recent analyses revealed that only one haplotype exists within the Rat River population (R. Bajno, Fisheries and Oceans Canada, pers comm.)

On a wider geographic scale similarities between populations in distant drainages proved problematic in terms of classifying distinct genetic populations. Everett *et al.* (1997) and Krueger *et al.* (1999) found that while geographically close populations were genetically different, there were considerable similarities between distant and non-adjacent populations. These similarities could be accredited to the migratory behavior exhibited by anadromous Dolly Varden (Bajno and Reist 2002).

Despite significant effort, no individual genetic study included samples from all of the known populations of northern Dolly Varden found from the Colville River of Alaska east to the lower Mackenzie River. Thus, the understanding of population structuring within northern Dolly Varden is presently incomplete. However, based on the studies summarized above, northern Dolly Varden are highly likely to be structured into individual, distinct biological populations (genetic stocks) on the basis of their river of origin. This is particularly true for the migratory anadromous life history type, and implies a high degree of philopatry by migratory fish to their natal systems. Further structuring within systems (i.e., sub-populations based on multiple tributaries or spawning locations) may be possible but results to date are inconclusive. Moreover, due to the incomplete coverage of all populations in these various studies, the ability to classify individuals from putative mixed-stocks to their respective stock-of-origin is compromised (see below). Current research is directed to redressing these issues.

2.1.2. Morphological Evidence

In addition to genetic analyses, Reist (1989) considered meristics as further evidence for population structuring among Dolly Varden from Joe Creek, Firth River, Upper Babbage River, Canoe River, Little Fish Creek (identified as Cache Creek) and the Rat River. There were significant differences between all locations for the number of pyloric caeca, as well as for upper and lower gill rakers present. Pairwise comparisons indicate this is primarily due to differences between Rat River fish and the remaining locations, and between fish from Joe Creek, Canoe River and Little Fish Creek (Figure 2) (Reist 1989). Meristic differences also occurred between isolated and anadromous life history types within the Babbage River system (Babbage River vs Canoe River) indicating that when considered with the corresponding genetic evidence, these fish represent distinct populations (Reist 1989).

Johnson (1996, unpubl. data) used statistical analyses of meristic and morphometric data from adult anadromous fish to distinguish within-drainage, and between-drainage population structuring of Dolly Varden from eight locations along the North Slope of Arctic Canada. Discriminant analysis (DA) clearly showed significant differences in the morphology of fish from the Firth, Babbage, and Big Fish rivers (Figure 5) suggesting distinct populations in each, while analysis of the meristic data did not differentiate among fish from within these river systems (Johnson 1996, unpubl. data). Because spawning fish exhibit strong sexual dimorphism the analyses were repeated on a “by sex” basis (males and females separated into 2 groups and re-analyzed) to account for morphological differences in spawning and non-spawning fish. This improved the discrimination of fish from each river into separate groups in the male group, but made no difference from the original analysis for the female group. This shows that between-river variation in morphology is stronger in males than in females likely because spawning males develop strong secondary sexual characteristics while females do not (Johnson, 1996 unpubl. data). Fish from the Rat River were also found to represent a distinct population based on morphological characteristics.

Distribution of discriminant scores for fish from the Firth River and Joe Creek show that there is an apparent difference morphologically between fish from these locations (Johnson 1996, unpubl. data), augmenting the previous findings of Reist (1989) that fish from these two tributaries represent separate populations. Re-analysis of the data separately by gender revealed an even stronger discrimination between these two samples of fish, especially for males (Johnson 1996, unpubl. data). Using principal component analysis, there were no differences between fish within the Babbage, Big Fish and Rat rivers indicating that each system contains only one population (Johnson 1996, unpubl. data).

2.1.3. Otolith Microchemistry

Babaluk *et al.* (1998) examined otolith cores (within the first annulus) using micro-proton induced X-ray emission (micro-PIXE) analysis to look at concentrations of trace elements (Sr – Strontium in particular) to discriminate stocks of fish from different river systems within Ivvavik National Park, Yukon Territory. The core of the otolith in fish from different river systems may contain different concentrations of trace elements laid down during early development. Because each river studied possessed unique water chemistry, the amount of each trace element in the otolith can theoretically be used to distinguish among systems and possibly determine the system of origin of migratory fish (Babaluk *et al.* 1998). When the otoliths of fish from rivers within the study area were examined, Babaluk *et al.* (1998) found a direct relationship between Sr in the otolith core and the water where the fish lived when the otolith was formed and were able to differentiate among fish from different river systems, as well as among fish from tributaries within these river systems (e.g., Canoe River of the Babbage River system). Similar to previous studies (Campbell *et al.* 2002; Outridge *et al.* 2002), Babaluk *et al.* (1998) found that there were no differences in Sr concentrations between fish of different life history types (anadromous vs residual) from the same river, while isolated fish displayed different concentrations of Sr. This further supports the separation of Dolly Varden into separate populations based on their river of origin, as shown earlier in genetic and morphological studies.

2.1.4. Biological Evidence

Sandstrom and Harwood (2002) examined data from the Big Fish River from 1972-1994 to observe trends in stock size, morphology, life history, and growth. They found that fish from the Big Fish River matured earlier than those from other North Slope rivers, in particular the Babbage River. This early age of maturation was attributed to the Big Fish River fish being in a recovery phase due to recent over fishing (Sandstrom and Harwood 2002; Stephenson 2003). In growing populations, such as one recovering from decreased stock abundance, natural selection will push the age-of-first maturation to the physiological minimum (Sandstrom and Harwood 2002). They also determined that mature female fish in the Big Fish River spawned every year, as opposed to every second or third year as seen in the fish from the Rat and Babbage rivers (Sandstrom and Harwood 2002). Also, spawning female Dolly Varden from the Big Fish River exhibited higher fecundity and larger average egg diameter than fish from the Rat and Babbage rivers (Sandstrom and Harwood 2002).

Migrating current-year spawners can be divided into two groups in some rivers, summer and fall spawners, based upon timing of migrations and spawning (DeCicco 1989, 1997). Summer spawners spawn from late August to early September, while fall spawners spawn from mid-September through early October (DeCicco 1997). Most current year summer spawners do not migrate to sea in the spring, but instead move upstream from overwintering sites to potential spawning grounds in late June and remain there until spawning is complete. They then move downstream and join non-spawning fish to overwinter, spending up to 20 months in freshwater, though some may spawn earlier in the summer and migrate to sea before returning to overwinter in freshwater. Because of inter-river straying of non-spawning Dolly Varden (see below) some summer spawners are not in their natal rivers at the beginning of their spawning season and must first migrate to sea in the spring before ascending their natal river to spawning grounds in late July, where they join other summer spawners (DeCicco 1997). Fall spawners spend the summer at sea feeding before entering freshwater in August. Fall spawners then travel directly up-river to spawning areas, which differ from those used by summer spawners. Most fall spawners will remain in or near spawning areas to overwinter (DeCicco 1997).

Although not conclusive evidence of population structuring, biological differences such as these are consistent with, and further support, other lines of evidence of structuring.

2.2. EVIDENCE OF MIXING IN NEARSHORE AREAS

Once at sea, anadromous Dolly Varden migrate along the shore and distribute themselves in near-shore habitats along the entire Beaufort Sea coast, at which time there is probably considerable mixing of stocks from different drainages (Craig and McCart 1976; McCart 1980 and references therein; Stewart *et al.* 2009). Krueger *et al.* (1999) investigated the variation in population composition of suspected mixed-stocks of Dolly Varden at separate collection sites along the coast of the Beaufort Sea in Alaska (three sites) and Canada (one site) (Figure 6, A-D). They used data from Everett *et al.* (1997) to develop three broad geographic stock groups; two separate groups composed of fish from Alaskan rivers, and one group from Canada including fish from the Firth and Babbage rivers. Using a mixed-stock analysis to estimate stock composition at each site, it was determined that each site contained fish primarily from local groups, however, there was significant contribution from the other, distant non-local groups (Krueger *et al.* 1999). Fish from the Canadian group contributed significantly to fish from the Alaskan sites (20-25%). Additionally, fish from the Alaskan groups contributed significantly to the mixed group of fish at the Canadian site (up to 65%). Furthermore, significant differences were observed in composition from month-to-month, and year-to-year suggesting substantial movements along the Beaufort Sea coast by Dolly Varden away from their natal rivers. The results of Krueger *et al.* (1999) indicate that Dolly Varden from both Canadian and Alaskan rivers mix to varying degrees along the coasts of both countries (Krueger *et al.* 1999; Bajno and Reist 2002). This mixing during the summer marine migrations of Dolly Varden (Stewart *et al.* 2009) forms the basis for local coastal fisheries in both Canada and Alaska (Krueger *et al.* 1999). Presumably individual fish return with high fidelity to their natal systems during fall migrations to freshwater for overwintering and spawning.

Griffiths *et al.* (1977) conducted surveys in the Kaktovik Lagoon, Alaska near Barter Island, and found that char (referred to as Arctic Char *Salvelinus alpinus*, but now known to be northern form Dolly Varden *S .m. malma* (Reist 1989; Kowalchuk *et al.* 2010)) undergo widespread coastal movements during their summer spent at sea. Based on tag-return data it was found that fish captured in the study area had originated in North Slope streams to the east and west of Barter Island (Figure 6), again demonstrating the tendency of Dolly Varden to occur as mixed stocks when at sea.

3.0. INTER-RIVER MOVEMENTS

Northern form Dolly Varden have been termed facultatively anadromous by Craig (1989) because of the variation in life history that they exhibit, as opposed to obligate anadromous fish which *must* go to sea to complete their life history (e.g., Pink Salmon) (Reist *et al.* 2001). Fish from the same population may be anadromous and migrate to sea annually or may live out their entire life in freshwater (residual and isolated forms) (McCart 1980). Anadromous northern form Dolly Varden display variation in timing and location of migrations to and from freshwater depending on maturity.

3.1. LONG DISTANCE MOVEMENTS

In tagging studies in northwest Alaska, DeCicco (1989, 1992) showed that Dolly Varden are capable of long distance migrations once at sea, recovering tagged fish at distances of 530 km, 750 km, 1560 km, and 1690 km away from the river in which they were originally tagged (Figure 7). These tag recoveries were made in southern Alaska and eastern Chukotka, illustrating the ability of Dolly Varden to undergo long distance, trans-boundary (between country) migrations.

3.2. LOCAL NORTH COAST MOVEMENTS

Similar movements have been observed in northern form Dolly Varden along the North Slope of Canada and Alaska (Glova and McCart 1974; Furniss 1975; McCart 1980; Crane *et al.* 2005) (Figure 8). Tagging studies that focused on inter-river movements of northern form Dolly Varden along the North Slope of Canada and Alaska (Table 1) have revealed that homing to natal rivers is strong among anadromous spawning and most non-spawning overwintering fish, however, a limited number of non-spawning fish have displayed the proclivity to wander into non-natal streams to overwinter (Furniss 1975; Craig and McCart 1976; McCart 1980; Sandstrom and Harwood 2002; Crane *et al.* 2005). These fish sometimes wander over great distances or between countries (McCart 1980; Crane *et al.* 2005). Furniss (1975) examined char populations (again referred to as *S. alpinus*, but now known to be *S. m. malma*) from the Sagavanirktok River system and found that while individual fish spawn in their natal rivers, large aggregations of mixed-stock fish overwintered together at only one site in the main stem of the Ivishak River (Figure 8). Between-river straying of non-spawning fish was observed, but was limited to only two fish - one had traveled from the Ivishak River to the Canning River, and the other had traveled from the Canning River to the Ivishak River (Furniss 1975). Crane *et al.* (2005) results showed that the majority of mature fish overwintering at the Ivishak site had originated from that system, demonstrating the strong philopatry common in spawning fish. However up to 15% of immature fish captured had originated from other Alaskan North Slope systems, primarily the Canning and Anaktuvuk rivers (Figure 8). Glova and McCart (1974) also reported long distance movements of Dolly Varden in this area, two fish that had been originally tagged in the Firth River (Canada) were captured in the Canning and Kongakut rivers (Alaska) respectively, again displaying trans-boundary straying (Figure 9).

Reist (1989) reported that little or no straying by anadromous Dolly Varden occurred within the Rat River or Little Fish Creek (referred to as Cache Creek), regardless of spawning condition. This is in contrast to previous studies (see above) where a small percentage of anadromous, non-spawning fish were shown to wander between systems to overwinter. The lack of straying may result from the long distance between these two rivers and all other North Slope rivers (Reist 1989). Regardless, a consequence of this is that Dolly Varden populations in the Rat and Big Fish systems are essentially “self-contained” with very little or no input from outside immigrants. They must rely on internal population processes (e.g., survival, growth, reproduction) for persistence and population growth. Although most documented “strays” among other populations are non-spawners, the possibility exists for them to supplement depressed populations.

4.0. SUMMARY

The northern form Dolly Varden occupying the North Slope of Alaska and Canada are divided into separate biological populations reflecting their stream of origin, as established by genetic, morphological, and biological data. Further work will clarify the issue of within-river population structuring, although data from otolith core analyses appears to distinguish between populations of fish from specific tributaries and their corresponding river. There is evidence that isolated fish may differ from anadromous/residual fish from the same river system.

Some Dolly Varden exhibit long distance and trans-boundary (between country) migrations. Mixing of fish from different populations occurs at sea, but there is strong homing to natal streams especially for spawners. Minimal straying between river systems does occur, primarily in the non-spawning anadromous fish, which overwinter in these non-natal waters. These distinct populations represent a unique situation for fisheries managers given that each population must be managed separately while in their respective river system, yet managed as mixed-populations while at sea.

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Table 1. *Tagging and recapture locations of six fish along the North Slope of Alaska and Canada as seen in McCart (1980.*

Tagging Location	Recapture Location
Sagavanirktok River	**Colville River**
Sagavanirktok River	**Canning River**
Canning River	**Sagavanirktok River**
Firth River	**Canning River**
Firth River	**Kongakut River**
Rat River	**Big Fish River**

Figure 1. *Major Canadian rivers (bolded river course) in which northern form Dolly Varden are known or reported to occur (Sawatzky and Reist in prep.).*

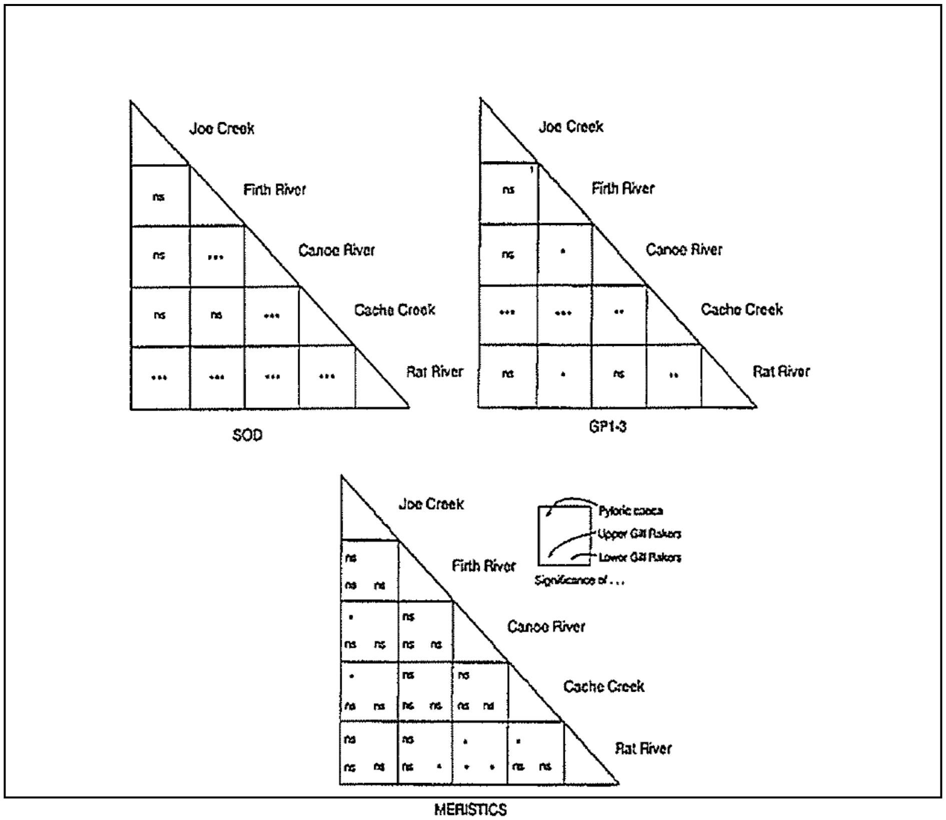

Figure 2*.Significance of pair wise comparisons of adult anadromous spawners. Locations are ordered from the west (top) to east, thus the diagonal represents tests for spatially adjacent river systems. Enzyme acronyms explained in text. Significance levels are: ns = not significant, * = P<0.05, ** = P<0.01, and *** = P<0.001 (after Reist 1989).*

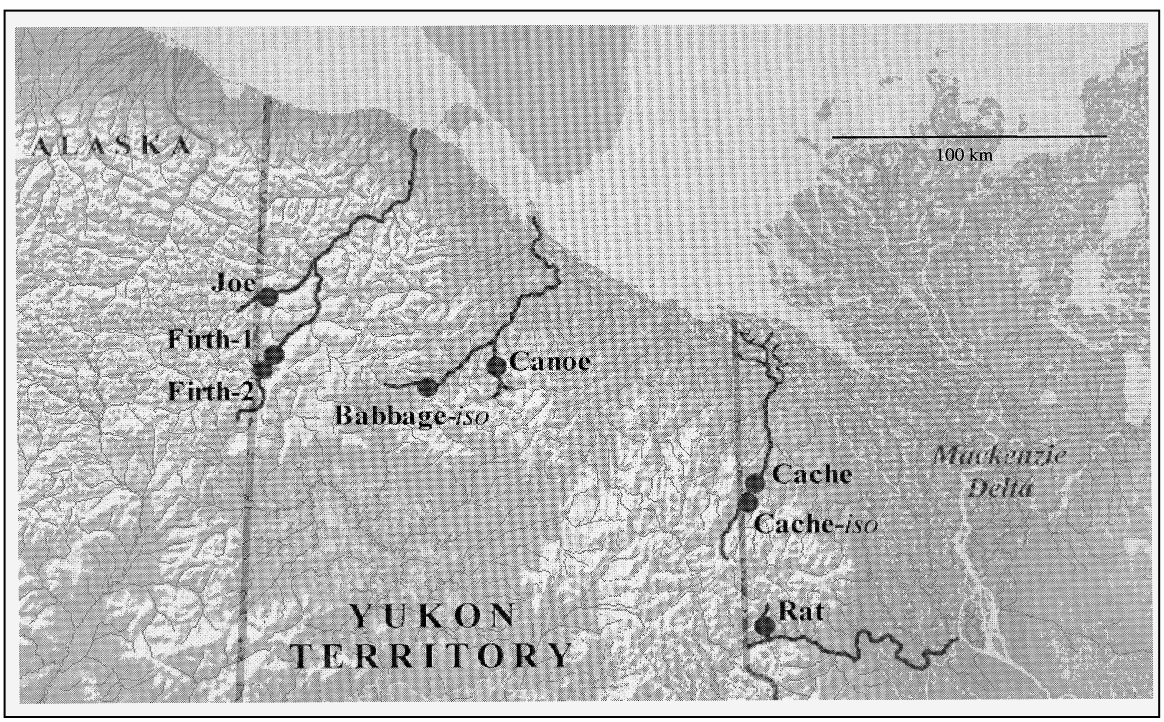

Figure 3*. Yukon North Slope, including sampling sites of Rhydderch (2001).*

***Figure 4**. Approximate glacial margins of the Yukon North Slope (Dyke* et al. *2003).*

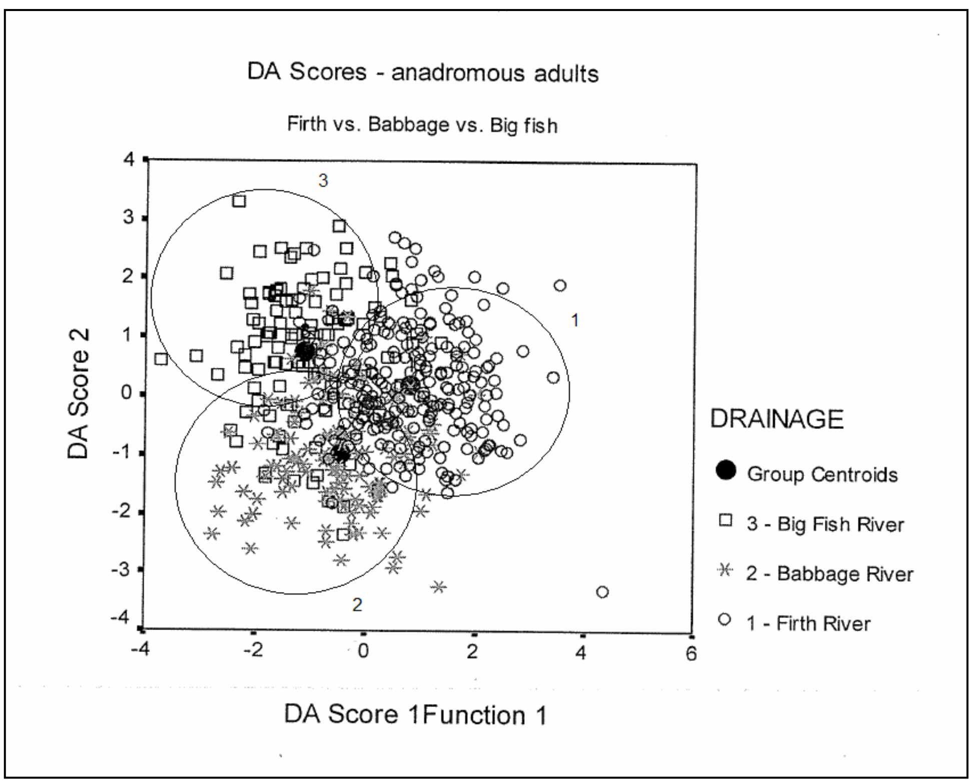

***Figure 5**. Discriminant analysis of morphometric characteristics for fish from the Firth, Babbage, and Big Fish rivers (Johnson 1996 unpubl. data).*

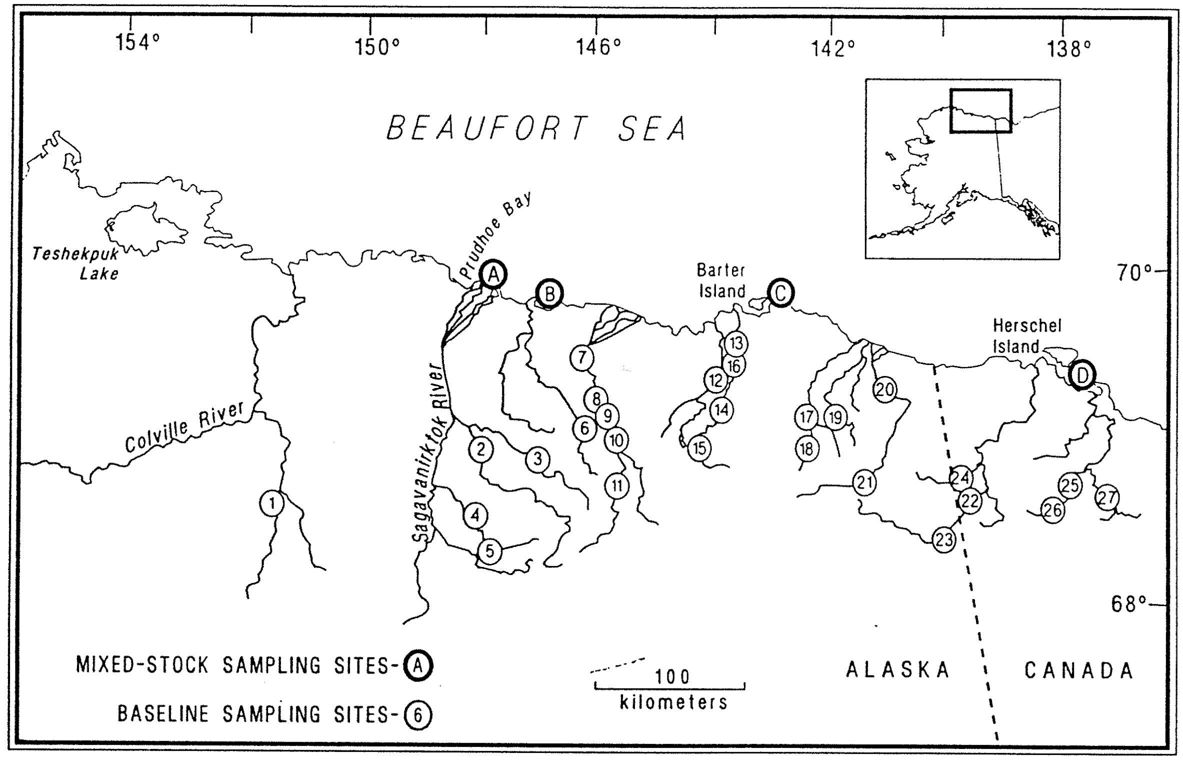

***Figure 6**. Alaskan North Slope, including sampling sites (A-D) (Krueger* et al. *1999).*

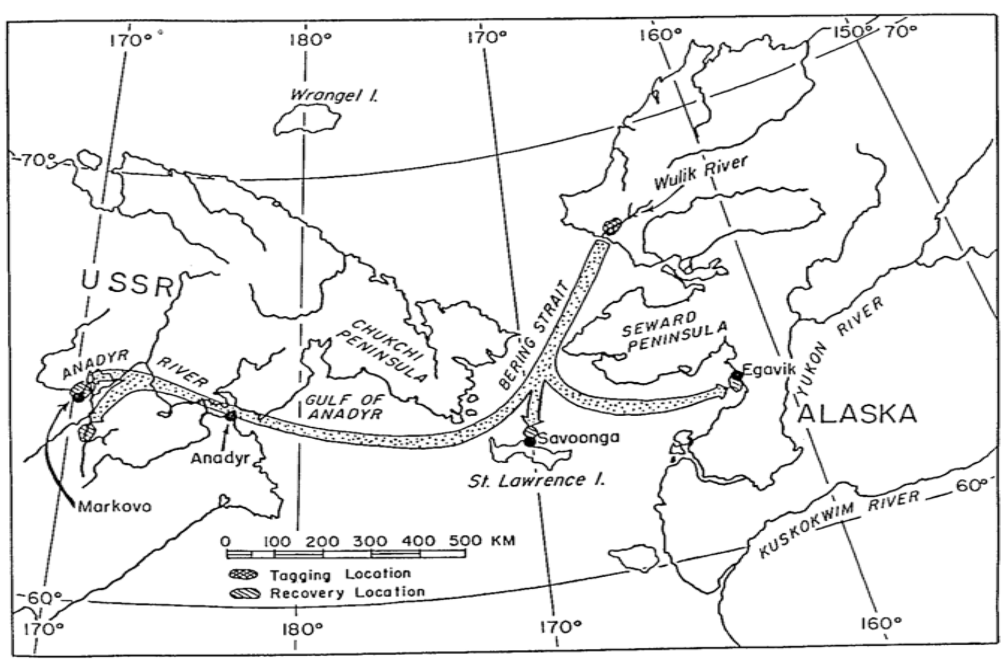

***Figure 7**. Documented long distance movements of Dolly Varden (DeCicco 1992).*

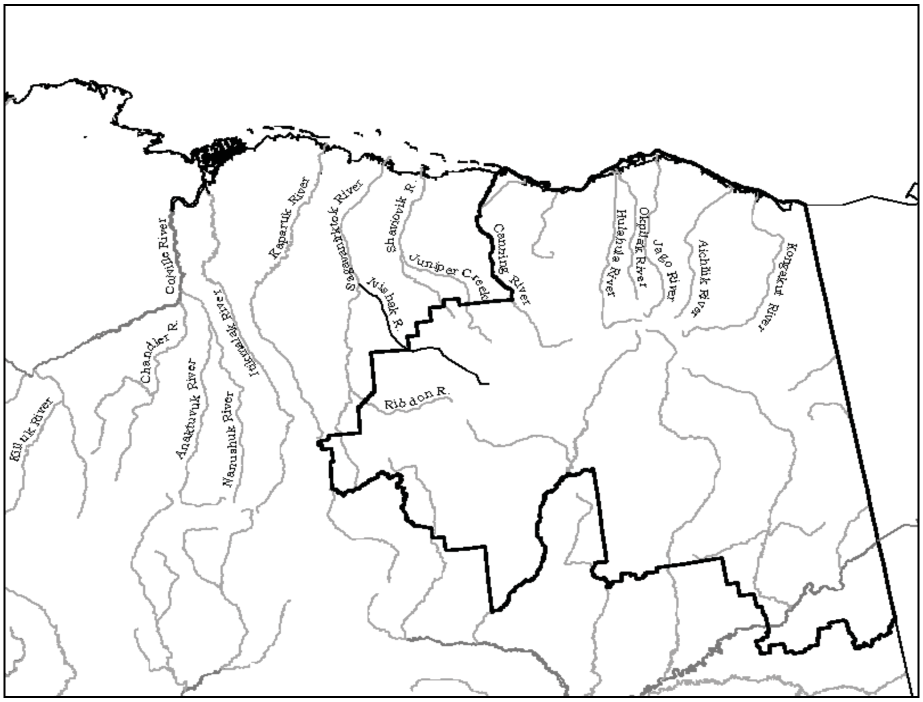

***Figure 8**. Alaskan North Slope (Crane* et al. *2005)*

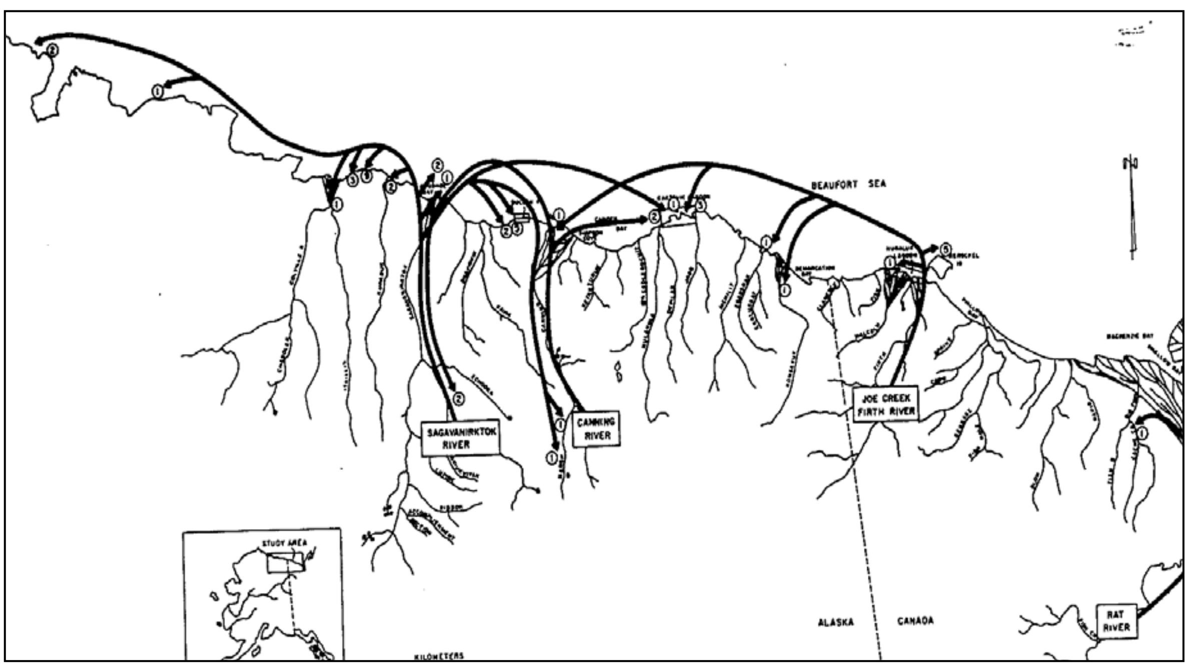

***Figure 9**. Movements of fish between drainages as seen in McCart (1980).*