

Life History Types and Stages of Northern Form Dolly Varden, *Salvelinus malma malma* (Walbaum, 1792)

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by

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TABLE OF CONTENTS

PREFACE	v
ABSTRACT	vi
RÉSUMÉ	vii
INTRODUCTION	1
NORTHERN & SOUTHERN FORMS OF DOLLY VARDEN	1
NOTES ON TERMINOLOGY	2
LIFE HISTORY TYPES OF NORTHERN FORM DOLLY VARDEN	2
NOTES ON DISTRIBUTION	4
Firth River and Joe Creek	7
Babbage River	10
Big Fish River.....	12
Rat River	15
SPAWNING BEHAVIOUR	17
LIFE HISTORY TYPE – FACULTATIVE OR GENETIC AND ASSOCIATED CONSEQUENCES	18
GENERAL LIFE CYCLE OF NORTHERN DOLLY VARDEN	19
LIFE HISTORY STAGES	23
Mixed Types and Stages and Criteria Used for Identification	25
Data Required in the Field to Work the Key	27
Notes on Colouration and Secondary Sexual Characteristics of Dolly Varden.....	28
Key for the Determination of Life History Type and Stage of Northern Dolly Varden	29
ACKNOWLEDGEMENTS	31
LITERATURE CITED	32

LIST OF FIGURES

Figure 1. General North American distribution of southern, northern and possible intermediate Bering Sea form Dolly Varden, <i>S. malma malma</i>	3
Figure 2. Major Canadian rivers in which northern form Dolly Varden occur	7
Figure 3. Upper Firth River system with spawning and over-wintering sites indicated.....	9
Figure 4. Upper Babbage River system with spawning and over-wintering sites indicated.....	11

Figure 5. Upper Big Fish River system with spawning and over-wintering sites indicated.....	14
Figure 6. Upper Rat River system with spawning and over-wintering sites indicated.....	16
Figure 7. Diagrammatic representation of the linkage between anadromous and residual life history types of northern form Dolly Varden	24
Figure 8. Photos of northern form Dolly Varden identified by life history type	30

LIST OF TABLES

Table 1. Life history types of northern form Dolly Varden, <i>S. malma malma</i> , occurring in rivers of northern Canada	6
Table 2. General timing of key events in the life cycle of northern form Dolly Varden, <i>S. malma malma</i> , summarized by river system	22
Table 3. Description of life history acronyms used for northern form Dolly Varden, <i>S. malma malma</i>	26
Table 4. Codes for the determination of maturity stages of northern fishes	27

PREFACE

This report was written and intended for publication in 2014 and has not been updated to reflect information past that date. Prior to publication online in 2021, it was previously cited as follows:

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ABSTRACT

Sawatzky, C. D., and Reist, J. D. 2021. Life history types and stages of northern form Dolly Varden, *Salvelinus malma malma* (Walbaum, 1792). Can. Manuscr. Rep. Fish. Aquat. Sci. 3215: vii + 39 p.

Two forms of Dolly Varden, *Salvelinus malma* (Walbaum, 1972), have been formally recognized as subspecies in North America – northern (*S. malma malma* (Walbaum, 1792)) and southern (*S. malma lordi* (Günther, 1866)). The northern form is distributed from the north side of the Alaskan Peninsula to the Mackenzie River, Northwest Territories and the southern form occurs from Washington State to the Gulf of Alaska. Anadromous (sea-run), riverine (residual), stream-resident (isolated) and lacustrine (lake dwelling; rare) northern form Dolly Varden occur in waters of northern Canada west of the Mackenzie River. Six genetically distinct populations have been identified in this region. An overview of the life histories of each Canadian northern form Dolly Varden population, summaries of the general life cycle, and a key for field and laboratory identification to life history type and life stage are presented.

Key words: Babbage River; Big Fish River; Dolly Varden; Firth River; Joe Creek; key; life cycle; life history; Northwest Territories; Rat River; *Salvelinus malma*; spawning behaviour; Yukon North Slope

RÉSUMÉ

Sawatzky, C. D., and Reist, J. D. 2021. Life history types and stages of northern form Dolly Varden, *Salvelinus malma malma* (Walbaum, 1792). Can. Manuscr. Rep. Fish. Aquat. Sci. 3215: vii + 39 p.

Deux formes de Dolly Varden, *Salvelinus malma* (Walbaum, 1972) ont été officiellement reconnues comme des sous-espèces en Amérique du Nord – la forme nordique (*S. malma malma* [Walbaum, 1792]) et la forme méridionale (*S. malma lordi* [Günther, 1866]). La forme nordique se trouve du côté nord de la péninsule de l'Alaska jusqu'au fleuve Mackenzie, dans les Territoires du Nord-Ouest, et la forme méridionale se trouve dans l'État de Washington jusqu'au golfe de l'Alaska. La forme nordique anadrome (de mer), fluviale (résiduelle), résidente (de ruisseau, isolée) et lacustre (de lac; rare) de Dolly Varden se trouve dans les eaux du nord du Canada à l'ouest du fleuve Mackenzie. Six populations distinctes sur le plan génétique ont été identifiées dans cette région. Une vue d'ensemble du cycle biologique de chaque forme nordique canadienne de la population de Dolly Varden, des résumés du cycle de vie, et une clé pour l'identification sur le terrain et en laboratoire du type de cycle biologique et du stade biologique sont présentés.

Mots clés: rivière Babbage; rivière Big Fish; Dolly Varden; rivière Firth; ruisseau Joe; clé; cycle de vie; cycle biologique; Territoires du Nord-Ouest; rivière Rat; *Salvelinus malma*; comportement de fraye; Versant nord du Yukon

INTRODUCTION

Two forms of Dolly Varden have been recognized as occurring in North America: southern form Dolly Varden, *Salvelinus malma lordi* (Günther, 1866), and northern form Dolly Varden, *Salvelinus malma malma* (Walbaum, 1792) (Behnke 1980). Northern form Dolly Varden occur primarily in north-draining coastal waters west of the Mackenzie River, Canada and in coastal regions of north-western Alaska. Historically, all char occurring in this area were classified as western form Arctic char, *S. alpinus*. Morphological and genetic studies subsequently showed that these char were more similar to Dolly Varden and thus were re-classified as northern form Dolly Varden (Morrow 1980; Reist et al. 1997; see Reist and Sawatzky 2010). Thus, caution should be taken when reading older literature. Dolly Varden of four life history types are found in northern North America: anadromous (sea-run), lacustrine (lake dwelling; rare), riverine (residual), and stream-resident (isolated). Hereafter the latter two types are referred to as residual and isolated, respectively. Six confirmed populations of northern form Dolly Varden have been identified in Canada and there is evidence for additional populations. A summary of the life history types and life stages of the six confirmed Canadian populations is presented as well as an identification key to enable field or laboratory studies within the region.

NORTHERN & SOUTHERN FORMS OF DOLLY VARDEN

North American Dolly Varden sub-species can be differentiated by vertebral number (62-64 for the southern form and 66-68 for the northern), and gill raker counts (16-18 for the southern form and 21-23 for the northern) (Behnke 1980). Genetic studies confirmed the existence of these two distinct sub-species (Phillips et al. 1999) and Kowalchuk et al. (2010a) summarize additional supporting evidence. Southern Dolly Varden are distributed from Washington State to the Gulf of Alaska whereas, northern Dolly Varden are distributed from the north side of the Alaskan Peninsula and the Aleutian Islands north and east to the Mackenzie River, Canada (DeCicco and Reist 1999). Moreover, the northern sub-species may further be split into two additional sub-species (northern and intermediate Bering Sea) based on life history and biological and geological associations, raising the possibility that three distinct sub-species of Dolly Varden are present in North America (DeCicco and Reist 1999). However, scepticism by scientists has been expressed in the primary literature based on allozyme data showing a weak level of genetic divergence among northern populations (Osinov 2001). Ongoing studies are investigating this issue.

The general distributions of northern, southern, and the potential intermediate Bering Sea sub-species of Dolly Varden represented in Figure 1 is the current working hypothesis but will change as new information becomes available. For example, inland boundaries will likely change between sub-

species. Although indicated as continuous, the interior distribution depends upon the existence of suitable habitat. Offshore distributions are coastal and approximate, but occasional records exist for more distant occurrences (not shown on the map). Infrequent occurrences of a Dolly Varden-like char have been recorded east of the distribution shown for northern form Dolly Varden and are thought to represent vagrants (not shown on the map) (e.g., along the Tuktoyaktuk Peninsula and the head of Prince Albert Sound, Victoria Island). Rivers in the Coronation Gulf region exhibit a Dolly Varden-like char population that is currently under study. However, it is unclear whether this population (not shown on the map) is representative of an “outlying” disjunct population of northern Dolly Varden co-occurring with Arctic char, a riverine life history form of Arctic char which converges upon Dolly Varden morphology, or an introgressed group of chars exhibiting genetic and morphological characters of both species. McPhail (1961) suggested that a distinct inland sub-species is present in central Alaskan drainages (not differentiated on the map, Fig. 1) (see Reist and Sawatzky 2010).

NOTES ON TERMINOLOGY

1. As noted previously, the terms residual and isolated are used to refer to riverine and stream-resident life history types respectively. These terms are defined in the text.
2. The terms population and genetic stock as used here should be understood as the group of potentially interbreeding individuals within a given river system. Individual river systems may contain one population/genetic stock or several based on documented evidence such as two or more possible spawning locations, the potential for early and late spawners, and/or high levels of genetic diversity.

LIFE HISTORY TYPES OF NORTHERN FORM DOLLY VARDEN

Four life history types of northern form Dolly Varden are found in waters of the North Slope, west of the Mackenzie River (Reist 1989): 1) anadromous or sea-run fish; 2) residual fish that are almost exclusively males, associated with anadromous fish, but which mature without going to sea; 3) isolated fish that are cut off from other populations by impassable barriers to migration such as waterfalls and/or distance; and 4) lacustrine fish. The lacustrine type is rare and not well documented but may be present in some Alaskan North Slope lakes (unconfirmed) (Mecklenburg et al. 2002). Putative northern form Dolly Varden have also been documented in lakes of the Peel River basin (Anderton 2006). Lacustrine life history types of southern form Dolly Varden are known from Alaska (Palmisano 1971; Schmidt and Robards 1976; Armstrong and Morrow 1980; Mecklenburg et al. 2002;

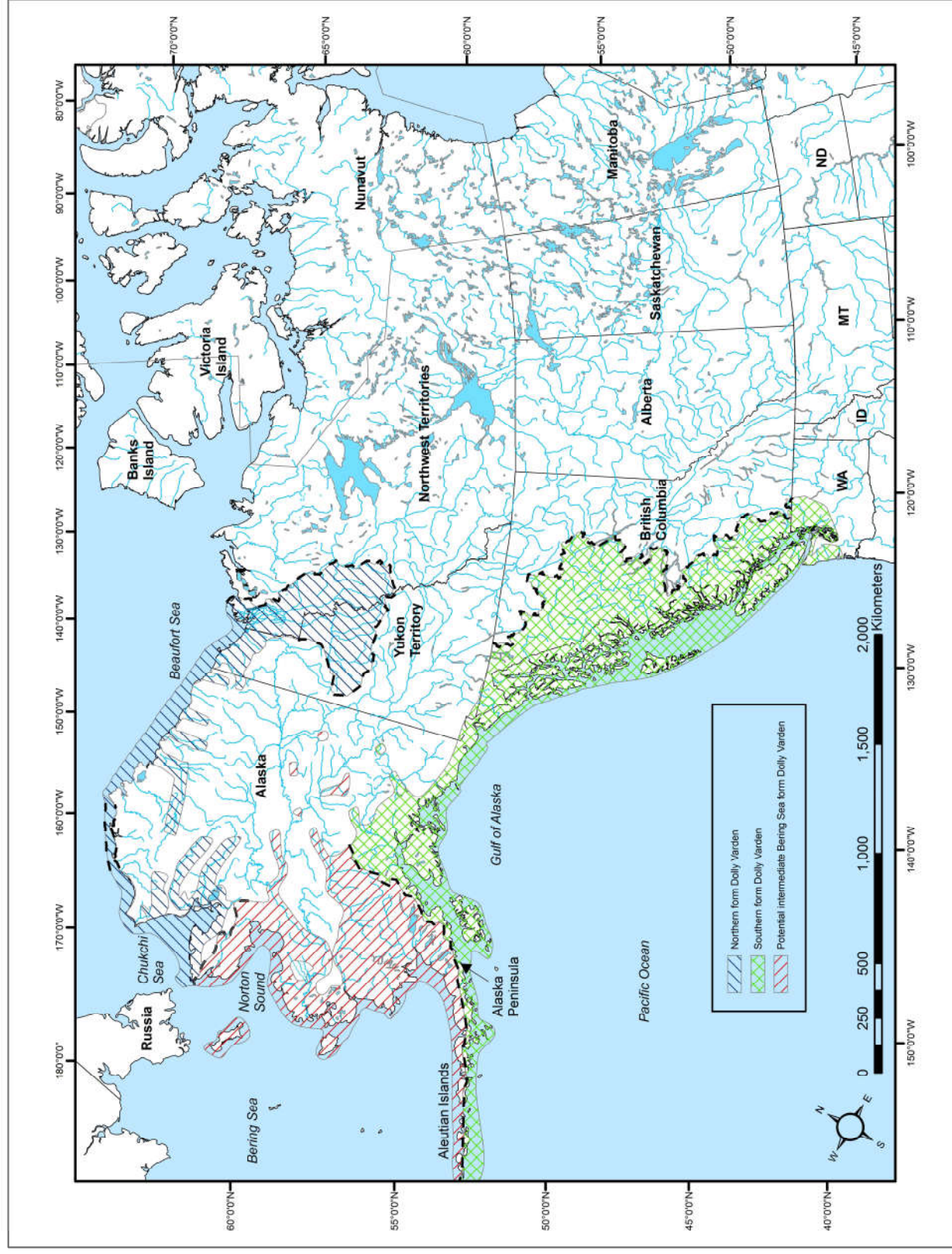


Figure 1. General North American distribution of southern, northern, and possible intermediate Bering Sea forms of *Dolly Varden*, *S. malma*. Dashed lines indicate uncertainty in extent of distribution boundary. Northwest Territories/Yukon Territory distribution follows Sawatzky et al. (2007), Alaskan distribution is modified from DeCicco (1997) (does not distinguish between forms), British Columbia distribution follows Wydoski and Whitney (2003). Approximate McPhail (2007) and drainage basin boundaries, and Washington distribution follows Wydoski and Whitney (2003). Approximate boundaries between the northern, southern, and potential intermediate Bering Sea forms are the result of work completed by Reist (1989, unpubl. data) and DeCicco and Reist (1999). Although classified as potential Bering Sea intermediate form, the inland distribution regions in the Yukon River drainage basin of Alaska may represent a distinct inland form (McPhail 1961).

Reist, unpubl. data) and British Columbia (Andrusak and Northcote 1971; Schutz and Northcote 1972; Armstrong and Morrow 1980; McPhail 2007), and Dolly Varden/Arctic char hybrids may occur in Becharof Lake (57.95°N, 156.38°W) on the Alaska Peninsula (Reist, unpubl. data; see Reist and Sawatzky 2010).

Anadromous Dolly Varden are generally large at maturity (>70 cm fork length), lose parr marks during smoltification, display typical spawning colouration, and migrate between freshwater and marine environments (Reist 1989). Residual Dolly Varden are non-anadromous stream residents that have a small body size at maturity (~ 30 cm in length and never exceeding 40 cm). They retain parr marks throughout life, exhibit year-round spawning colouration, and remain associated with natal streams fed by groundwater (Reist 1989). Residuals are almost always male and co-occur with the anadromous form during early life history and spawning, and possibly during over-wintering (McCart 1980). Residual northern form Dolly Varden reach maturity as early as age 2; their anadromous counterparts reach maturity at age 7-9 (Armstrong and Morrow 1980).

Isolated Dolly Varden exhibit the same general characteristics as the residual form, but are isolated in headwaters of rivers by barriers, such as waterfalls, that are impassable to anadromous migrants (Reist 1989). They may also be isolated by distance or intervening unsuitable habitat. Isolated fish may, however, immigrate into the downstream anadromous population introducing the possibility for unidirectional gene flow (Reist 1989). Both sexes are present in isolated populations indicating self-sustainability.

NOTES ON DISTRIBUTION

Six confirmed populations of Dolly Varden have been found in river basins of Arctic Canada, primarily on the Yukon North Slope (J. Reist unpubl. data cited in Reist 2001): (1) the Firth River and its major tributary Joe Creek (may be distinct populations), (2) the Babbage River, and (3) the Big Fish River on the Yukon North Slope, (4) the Rat River of the western Mackenzie Delta, and (5) the Vittrekwa and (6) Blackstone rivers of the Peel River basin. Additional populations, assumed to represent isolated life history types, also occur inland in the Mackenzie and Peel river basins.

Dolly Varden are common in tributaries of the upper Peel River (e.g., Blackstone, Snake, and Bonnet Plume rivers) where suitable habitat exists (Anderton 2006; Millar 2006; Reid and Skinner 2008; A. VonFinster, Fisheries and Oceans Canada, pers. comm.) and are isolated from those occurring in tributaries of the lower Peel River by Aberdeen Falls (~ 65.87°N, 135.74°W). Dolly Varden have also been documented in at least four lakes of the upper Peel River basin: Elliott Lake (64.48°N, 135.56°W), unnamed (Horn) lake (64.45°N, 138.64°W), an unnamed lake in the Bonnet Plume River Drainage (64.21°N, 132.09°W), and an unnamed lake in the East Blackstone River Drainage (64.81°N, 138.23°W), all of which are suspected or confirmed (unnamed lake, East Blackstone River

Drainage) to provide over-wintering habitat with the exception of the small unnamed lake at the mouth of Bonnet Plume River, of which little is known (Bodaly and Lindsey 1977; Mann and Tsui 1977; Yukon Department of Environment 2000 unpubl.; Yukon Department of Environment 2004 unpubl. cited in Anderton 2006; Reid and Skinner 2008). Fisheries and Oceans Canada captured putative small Dolly Varden in minnow traps at the Rackla River/Beaver River confluence (64.114°N, 134.379°W) on the upper Stewart River (tributary of the Yukon River) in 1997 or 1998, however, the specimens were not preserved thus identification cannot be confirmed (A. VonFinster, pers. comm.). Dolly Varden may also be widespread in the the upper Stewart River (above Fraser Falls (63.51°N, 135.15°W)), but this is unconfirmed (A. VonFinster, pers. comm.). Those in the Peel Basin may be the northern sub-speices or may belong to a distinct interior form which has been hypothesized to occur in the upstream Yukon River basin of Alaska (McPhail 1961; Reist and Sawatzky 2010). Evidence for additional populations in the Gayna River, lower Mackenzie River basin (Mochnacz and Reist 2007), and Fish River in the extreme western area of Ivvavik National Park has been put forth (Bryan 1973; Craig and McCart 1974; McCart 1974). An outlying population may be present in Tree River (67.68°N, 111.88°W) (Reist unpubl. data) and similar rivers in the Coronation Gulf region far to the east. These regions may contain outlying populations of Dolly Varden co-occurring with Arctic char, a hybridized/introgressed group of both species, or a riverine morphotype of Arctic char converging on Dolly Varden morphology (Reist unpubl. data; see Reist and Sawatzky 2010). Field work and genetic studies are ongoing to distinguish among these.

An overview of the life history types and structures of the populations of northern form Dolly Varden in Canada with the exception of the lesser known populations of the Peel Basin and the Fish, Gayna and Tree rivers is presented in Table 1 and Figure 2. Kowalchuk et al. (2010b) summarises population structure of northern form Dolly Varden in greater detail.

Table 1. Life history types of northern form Dolly Varden, *S. malma malma*, occurring in rivers of northern Canada. Uncertainties are indicated by question marks and related footnotes; isolation may be due to a barrier or distance.

	North Slope Populations						Upper Mackenzie Populations		Peel Basin Populations			Eastern Population
Life History Type	Fish River	Firth River	Joe Creek	Big Fish River	Babbage River	Rat River	Gayna River	Other Upper Mackenzie	Vittrekwa River	Blackstone River	Other Upper Peel	Tree River
Anadromous	?	✓	✓	✓	✓	✓ (Early? Late?)	-	-	✓	-	-	?
Residual	?	✓	✓	✓	✓	✓ (?) ²	-	-	✓ (mostly male)	-	-	?
Isolated	?	-	-(?) ¹	✓ (Barrier)	✓ (Barrier)	-(?) ²	✓ (Barrier)	?	? (Distance) ³	✓ (Distance)	✓ (Barrier)	?

1. Uncertain (but unlikely) whether an extreme headwater population is present.

2. Uncertain whether recent findings of small putatively non-anadromous fish in upper reaches represent residual males or an isolated population.

3. The exact nature of the Vittrekwa population is uncertain – some anadromy occurs, most resident individuals are males but a population partially isolated by distance may be present.



Figure 2. Major Canadian rivers (bolded river course) in which populations of northern form Dolly Varden, *S. malma malma*, are known or reported to occur.

Firth River and Joe Creek

The Firth River (Fig. 3) originates in the Davidson Mountains of Alaska and flows over 160 km northeast to the Beaufort Sea (DFO 2003a). This system contains anadromous and residual (only males observed) Dolly Varden in both major tributaries: the upper Firth River and Joe Creek (Reist 1989). There are no reliable estimates of stock size for this population (DFO 2003a). Harvesting on the Firth River occurs for sport purposes only (DFO 2003a), however, the anadromous segment of this population is vulnerable to mixed-stock subsistence fisheries in Yukon and Alaskan coastal waters

(Krueger et al. 1998, 1999). Similar to all North Slope Dolly Varden populations, spawning occurs in the fall. Current-year anadromous spawners return to freshwater approximately one month earlier than non-spawners, indicating a shorter time at sea or a reduced seaward migration (Glova and McCart 1974). All spawning and most over-wintering occur in the headwaters of the Firth River, and in Joe Creek (Baker 1987; DFO 2003a). An unnamed spring (69.45°N, 139.7°W) that flows into the delta of the Firth River provides important over-wintering and potential spawning habitat (Craig and McCart 1974). Potential over-wintering sites have also been identified on the Firth River main-stem near the confluence with Boulevard Creek, and in the Firth Delta. Anadromous char arrive later to upper Joe Creek than to the upper Firth River. Spawning in upper Joe Creek starts at a later date likely due to higher spring water temperatures at the Joe Creek spawning site (Table 2) (Glova and McCart 1974; Mutch and McCart 1974).

Genetic and meristic differences between anadromous adult spawners from Joe Creek and Firth River are not significant, however, when residual fish are pooled with the anadromous fish from Joe Creek a significant difference between the two locations is apparent and indicative of the potential presence of very fine-scale structuring of genetic stocks in the Firth River system (Reist 1989). Strontium concentrations in otolith cores were found to be effective for distinguishing anadromous Dolly Varden in Joe Creek from those in Firth River (Babaluk et al. 1998).

Genetic differences have not been found between anadromous and residual Dolly Varden in the Firth River (Reist 1989; Everett et al. 1997, 1998; Rhydderch 2001) nor between those in Joe Creek (Reist 1989; Rhydderch 2001). All residuals are male suggesting that both life history types belong to the same genetic population and thus represent a polymorphism in life history strategy (Reist 1989). The basis for this polymorphism (i.e., genetic or facultative) is not known. Dolly Varden in Joe Creek and Firth River had the highest allelic diversity and were found to be the most closely related when compared to the populations in the Babbage, Big Fish, and Rat River drainages (Rhydderch 2001).

Rhydderch (2001) had variable success identifying the river of origin for Dolly Varden from North Slope populations using mitochondrial DNA (mtDNA) and microsatellite data. Fish from the eastern populations (Babbage, Big Fish, and Rat rivers) were often correctly assigned. Those from the Firth River drainage were often incorrectly assigned to other drainages, likely due to the high allelic diversity, whereas each of the other populations had a subset of this diversity. Glaciation may have caused extirpation or bottlenecks in the populations of the three eastern drainages. The Firth drainage, furthest from the glacial margin, was least affected by glaciation and the likely source of Dolly Varden for recolonization of eastern areas post-glaciation (Rhydderch 2001). The high level of genetic diversity in the Firth drainage makes the populations of great importance for preservation (Rhydderch 2001).

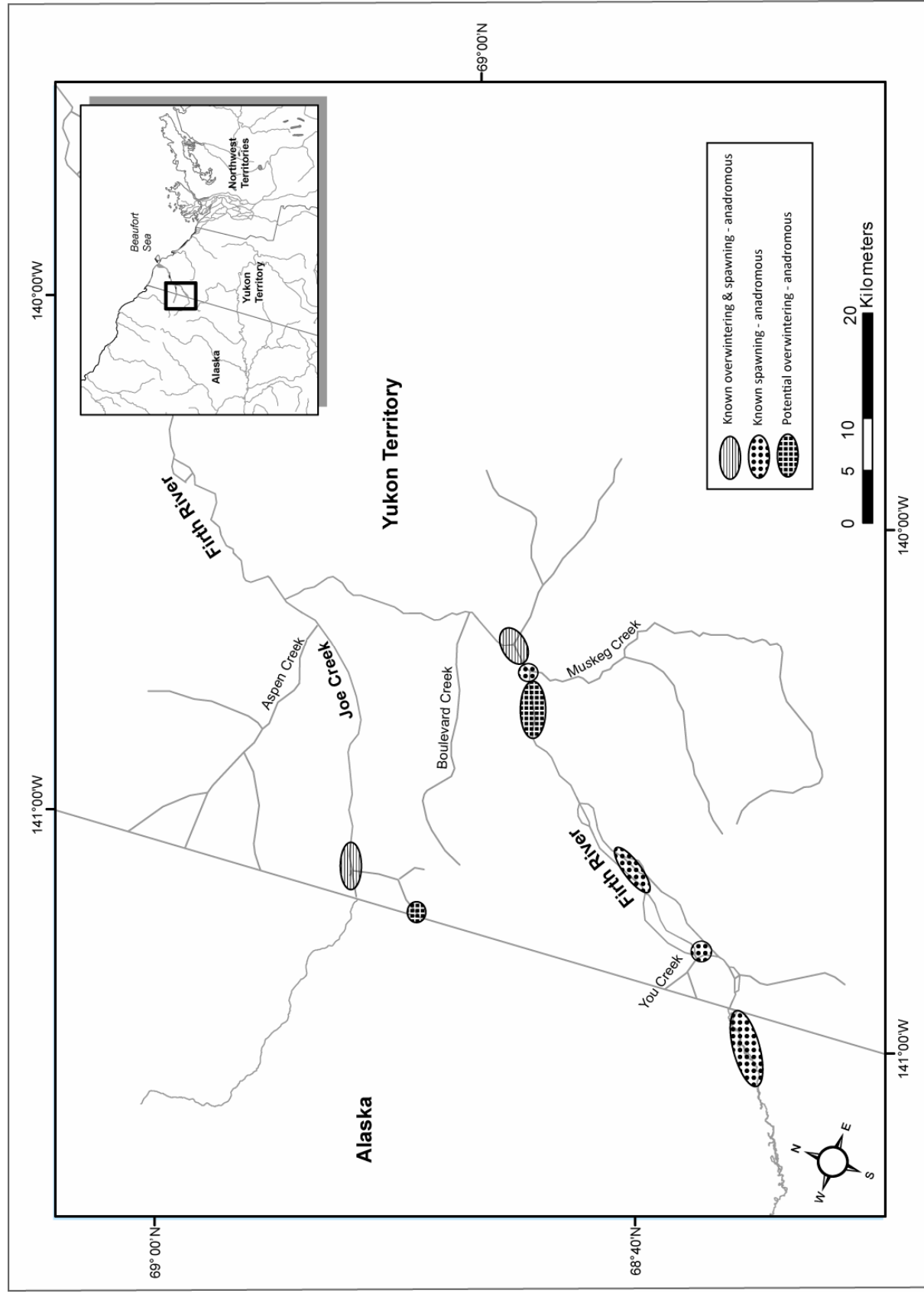


Figure 3. Upper Firth River system with spawning and over-wintering sites indicated. Note: spawning and over-wintering sites are shown for reference purposes only, they are not to scale, also, additional sites may exist further upstream in Alaska (see Bryan 1973; Harden et al. 1977). Seasonal use of side tributaries may also occur but is undocumented. (after Mochnacz et al. 2010)

Babbage River

The Babbage River (Fig. 4) originates in the British Mountains, Yukon Territory and flows 137 km north to the Beaufort Sea (DFO 2003b). This system contains anadromous (most common), residual (mostly male), and isolated stream resident (above the falls in the headwaters of the Babbage River) Dolly Varden (Bain 1974; Kristofferson and Baker 1988; DFO 2003b). In 1991 the anadromous stock size was estimated at 13,600 fish (95% Confidence Interval (CI): 7600 – 19,700) (Bailey's estimate) (Sandstrom et al. 1997; DFO 2003b). Based on data from the 1990's it was concluded that the stock was not being overexploited, but that the mixed-stock coastal fishery may result in over harvest in some years (DFO 2003b). Isolated Dolly Varden over-winter in the open-water area directly above the falls whereas anadromous and residual fish spawn and over-winter at "Fish Hole", a spring-fed area in Fish Hole Creek, a tributary of the Canoe River (Bain 1974; Craig and McCart 1974; Sandstrom et al. 1997). Over-wintering may also occur in the deep plunge pool at the base of the falls (Craig and McCart 1974), however this is not confirmed at this time. It is likely (but not certain) that this area is used for spawning. If over-wintering does occur in this area the following life history types may be present: a) anadromous/residual life history types of the Babbage River/Canoe River population; b) over-wintering anadromous fish from other systems; c) strays from the upper Babbage isolates; or d) a mix of all of the above. Residual males were found to be common in Fish Hole Creek and Bain (1974) suggested their presence was maintained by persistent selection, whereby residual males spawning with anadromous females may ensure that the gene(s) suppressing anadromy remain stable within the gene pool. However, this assumes anadromy is genetically determined, which has not been confirmed to date.

The Babbage River Dolly Varden population is morphologically and genetically distinct from surrounding populations (Reist 1989; Everett et al. 1997, 1998; Rhydderch 2001). Analysis of otolith strontium concentrations has been used successfully to distinguish between anadromous Dolly Varden from the Canoe River and the Firth River system (Babaluk et al. 1998). Isolated fish from the upper Babbage River and anadromous spawners from the Canoe River are significantly different, in both genetic (Reist 1989; Everett et al. 1997, 1998) and meristic characteristics (Bain 1974; Reist 1989), and thus appear to constitute distinct populations (Reist 1989). They likely differ in key population parameters such as reproductive and growth rates, and in their ability to withstand exploitation over time (Reist 1989). The isolated Dolly Varden in the upper Babbage River are also genetically distinct from the non-isolated fish below the falls, but this difference is less pronounced than that between the isolated fish and the anadromous fish from the Canoe River (Everett et al. 1997, 1998). Meristic characteristics of residual Dolly Varden sampled immediately below the falls do not differ significantly from the isolated fish above the falls, but are significantly different from the anadromous and residual Dolly Varden in Fish Hole Creek (Canoe River tributary) (Bain 1974).

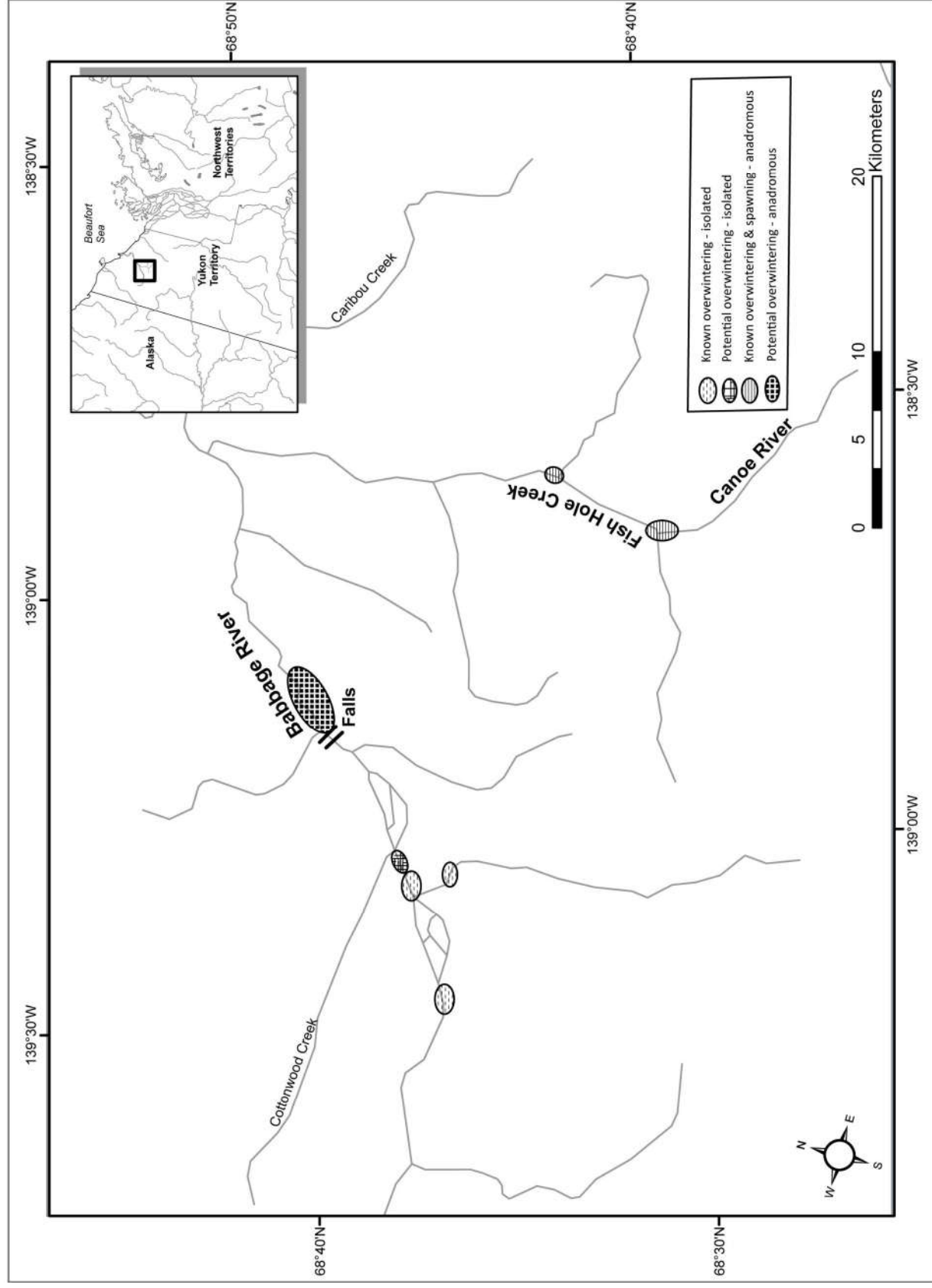


Figure 4. Upper Babbage River system with spawning and over-wintering sites indicated. Note: spawning and over-wintering sites are shown for reference purposes only, they are not to scale. Seasonal use of side tributaries (e.g., Caribou Creek (Sandstrom et al. 1994) may also occur). (after Mochnacz et al. 2010)

The combination of the low number of mature residual char found directly below the falls and the lack of mature residual char further downstream in the Babbage River, led Bain (1974) to suggest that the char immediately below the falls are immigrants from the isolated population. Further research is needed to confirm this suggestion.

Big Fish River

The Big Fish River (Fig. 5) originates in the Richardson Mountains of the Yukon Territory and flows approximately 85 km to the Mackenzie Delta (Gillman et al. 1985). This system contains anadromous, residual, and isolated stream resident Dolly Varden (McCart and Bain 1974; DFO 2003c). The latter occur above the falls in Little Fish Creek which is often incorrectly identified as Cache Creek. In 1972, the stock size for the anadromous segment of the population was estimated at 13,500 (95% CI: 11,300 – 16,000) to 20,700 fish (95% CI: 15,800 – 27,600) (Petersen estimates). By 1985 this estimate had dropped to 9,300 (95% CI: 6,300 – 14,300) (Petersen estimate) (Kristofferson and Baker 1988; Sandstrom and Harwood 2002; DFO 2003c). From 1993 to 1998 the estimate decreased further to 4,026 (95% CI: 2,988 – 5,563) (Petersen estimate) (Stephenson 1999; DFO 2003c). The fishery was closed voluntarily in 1987 (Baker 1987) and re-opened in 1992 to limited subsistence harvests at the mouth of the river and at Fish Hole on Little Fish Creek (Stephenson 1999, 2003; DFO 2003c).

In spite of these management practices, the stock has not recovered, and habitat change is suspected to be a limiting factor (DFO 2003c). Records indicate that in the late 1970s and early 1980s, four seismic events occurred within 20 km of the spawning and over-wintering site. These geological events may have led to a decrease in the volume of groundwater discharge that limited available over-wintering habitat. In turn, a decrease in the number of anadromous Dolly Varden the site could sustain was observed (Sandstrom and Harwood 2002). Furthermore, Big Fish River Dolly Varden spawn approximately 2 km downstream from a groundwater discharge area, likely due to higher water temperatures at the discharge site. Spawning in other river systems such as the Babbage River, occurs on or very near to the discharge area, exposing the eggs to a relatively constant incubation temperature. In winter the water temperature drops as it flows downstream from the discharge area until eventually freezing. If the stream is more shallow presently than 20-30 years ago, or becomes so in the future, the temperature of water reaching the spawning bed would fluctuate with air temperature possibly decreasing hatching success (Sandstrom and Harwood 2002).

A second limiting factor is over-harvesting. The Little Fish Creek fishery has collapsed due, at least in part, to overexploitation of anadromous Dolly Varden (Reist 1989). Immigration from other populations is unlikely due to a general lack of wandering between systems, thus the residual males may represent an important genetic reservoir for the recovery of the population. The anadromous segment of the population also contributes to the mixed-stock fishery at Shingle Point, but the extent

of this is unknown (Sandstrom and Harwood 2002; DFO 2003c; Stephenson 2003). Dolly Varden in the Big Fish River drainage are genetically distinct from other populations on the North Slope (Reist 1989; Rhydderch 2001) and the isolated fish above the falls have been differentiated from their anadromous counterparts in the remainder of the system by both meristics (McCart and Bain 1974) and genetics, although genetic divergence was low (Rhydderch 2001).

Spawning and over-wintering occur at Fish Hole on Little Fish Creek (DFO 2003c). In contrast to those in nearby basins which typically spawn every second year, the low number of mature, non-spawning Dolly Varden in resting phase (silvers) observed in Little Fish Creek compared to surrounding systems suggests that many of the females spawn yearly once maturity is reached (Armstrong and Morrow 1980; Sandstrom 1995; DFO 2001; Sandstrom and Harwood 2002). Anadromous males made up an average of only 14% of the spawning Dolly Varden sampled in Little Fish Creek (6 females:1 male) in studies conducted between 1984 and 1994.

Large numbers of residual males are found at the spawning site in this basin. This suggests that the low numbers of anadromous males may be due to a higher incidence of early maturation in the Big Fish River males caused, partially by fishing pressure (Sandstrom and Harwood 2002). That is, fishing pressure may be the cause or a contributing factor to the shift in life strategy from anadromous to residual males. Generally, fishing targets anadromous males as kypes are easily caught in the nets. If life history has a genetic basis, fishing would tend to cause a shift to non-anadromy. It would also decrease population size resulting in decreased competition in over-wintering and early summer freshwater habitats (Sandstrom and Harwood 2002). This would increase the chance of survival for residual males and/or juveniles.

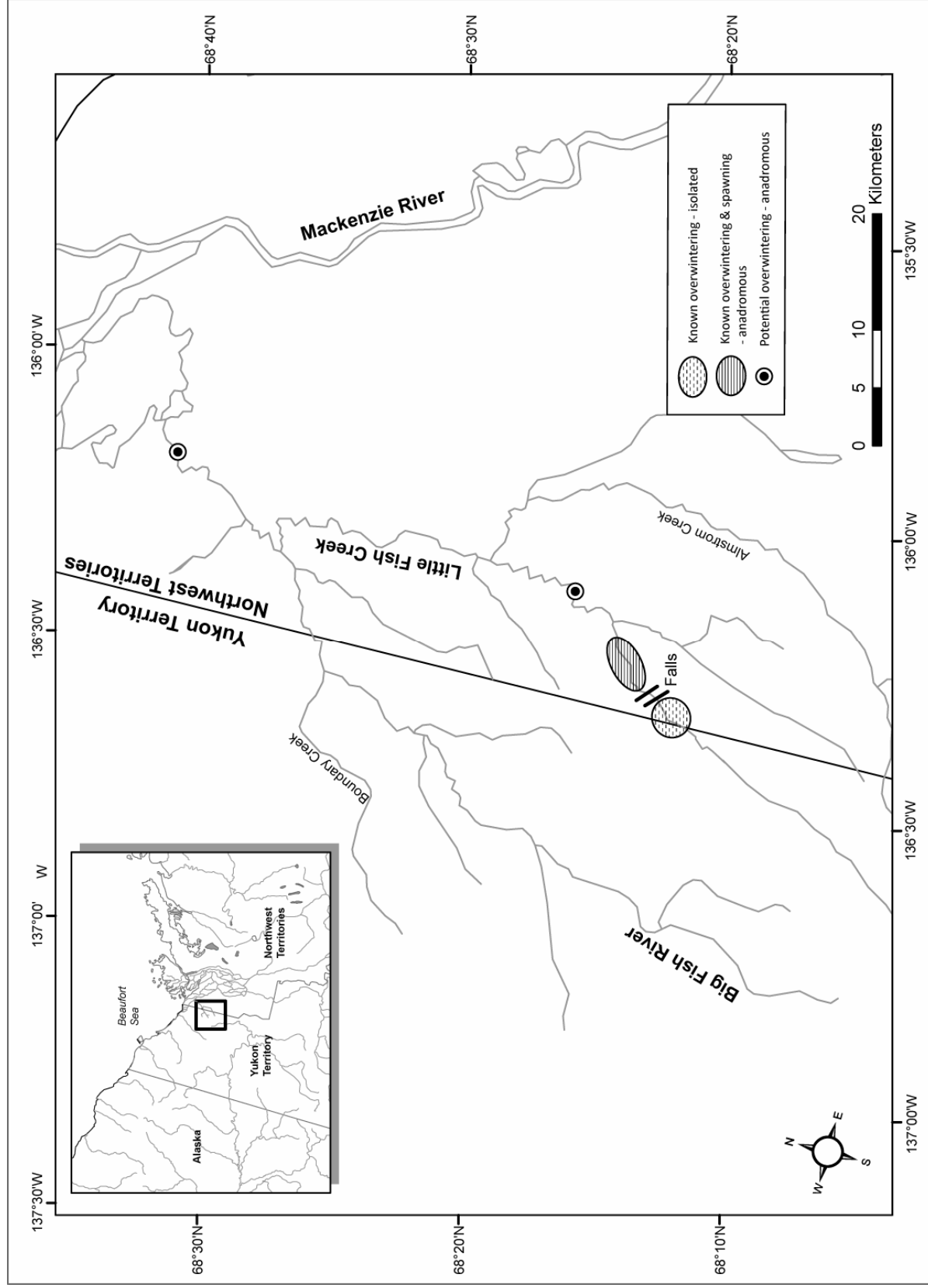


Figure 5. Upper Big Fish River system with the spawning and over-wintering site indicated. Note: spawning and over-wintering site is shown for reference purposes only, it is not to scale. Seasonal use of side tributaries may also occur but is not well documented. Little Fish Creek is often incorrectly identified in the literature as Cache Creek. (after Mochnacz et al. 2010)

Rat River

The Rat River (Fig. 6) originates in the Richardson Mountains of the Yukon Territory and flows 130 km north-east to the Husky Channel of the Mackenzie River (DFO 2001). Field sampling up to about 2000, documented only anadromous Dolly Varden in the Rat River basin (J. Reist, S. Sandstrom pers. comm. cited in DFO 2001). However, subsequent sampling further upstream in the upper Rat River captured residuals that were co-occurring with anadromous fish (S. Stephenson, Fisheries and Oceans Canada, pers. comm.). Only one residual fish has been captured at the spawning and over-wintering site on Fish Creek. The reason for the lack of residual fish is unknown (Sandstrom et al. 2009).

Prior to 2006, the Rat River population was only harvested on the return migration from sea in late summer and early fall (Harwood 2001) and, to a limited extent, in the mixed-stock fishery at Shingle Point (L. Harwood unpubl. data cited in DFO 2001). In 1995, the stock size was estimated at 4,433 fish (95% CI: 3,379 – 5,487) (Petersen estimate, incorporates natural mortality and tag loss) (Sandstrom et al. 2009). In 1997, this estimate increased to 5,106 (95% CI: 3,178 – 7,034) (Petersen estimate, incorporates natural mortality and tag loss). The stock size dropped sharply in 2004 to an estimated 1,430 (95% CI: 939 – 1,921) (Petersen estimate, incorporates natural mortality and tag loss) anadromous fish from an estimated 3,901 (95% CI: 2,196 – 5,606) (Petersen estimate, incorporates natural mortality and tag loss) in 2001. The fishery was voluntarily closed in March 2006 (DFO 2007) and in 2007, the estimated stock size increased to 7,301 (95% CI: 2,956 – 11,686) (Petersen estimate, incorporates natural mortality and tag loss), the highest in the time series (Sandstrom et al. 2009). In the most recent year of an ongoing survey (2007) many juvenile silvers were observed, more than have been observed in any other year of this survey. As well, an increase in size at age, and the maintenance of stable sex and maturity ratios, may be viewed as positive indications for the population (Sandstrom et al. 2009).

Dolly Varden in this system are genetically and meristically distinct from surrounding populations (Reist 1989). Fish spawn and over-winter in Fish Creek, a tributary of the Rat River. Observations by local fishermen of two or more pulses in the fishery (DFO 2001; B. Mitchell; J. Carmichael pers. comm. cited in Harwood 2001) and field observations of spawning activity (DFO 2001; L. Harwood; S. Sandstrom unpubl. data cited in Harwood 2001) support the possibility that the Dolly Varden population in this basin may be made up of more than one temporal stock. However, this suggestion requires explicit testing.

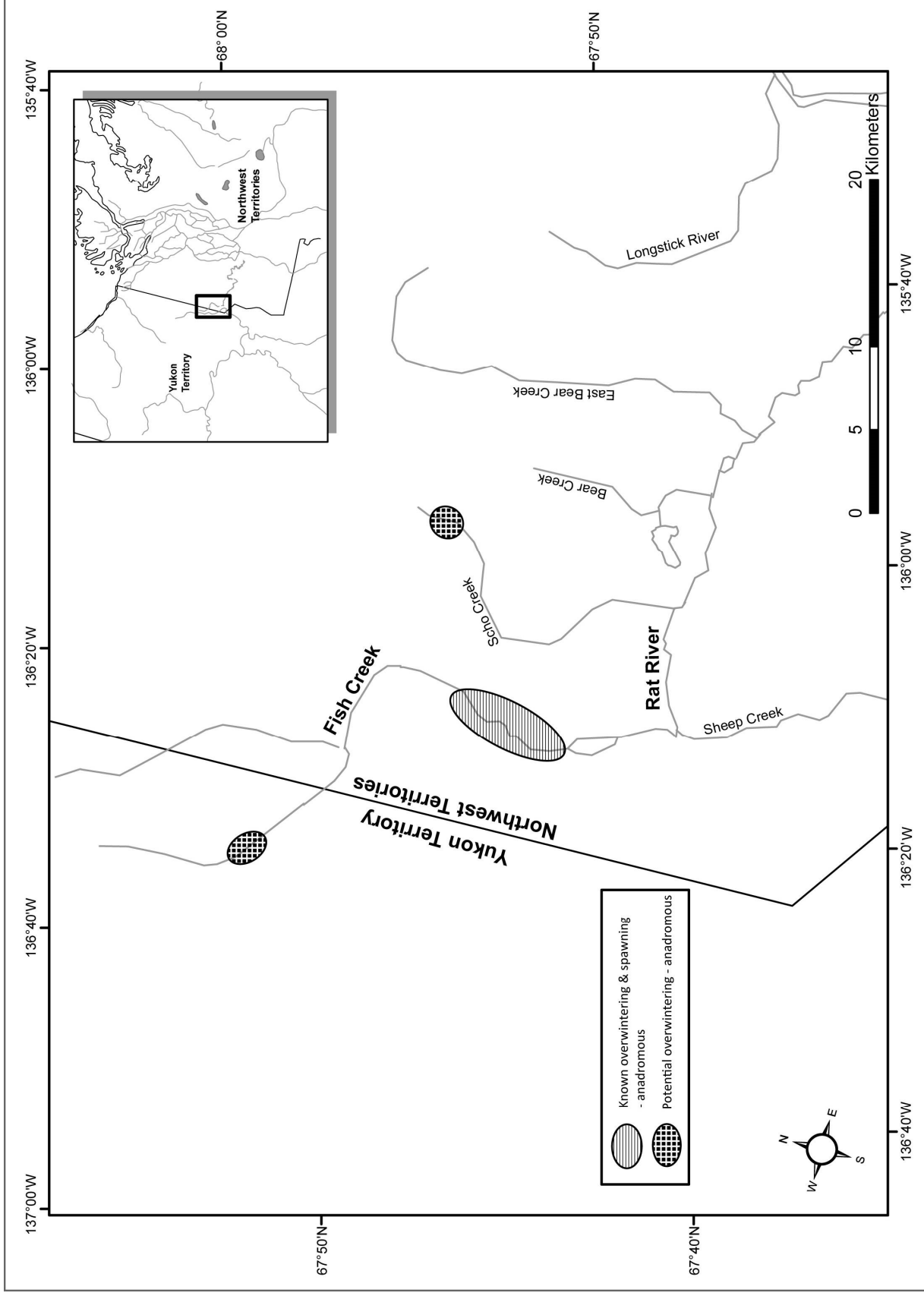


Figure 6. Upper Rat River system with the spawning and over-wintering site indicated. Note: the spawning and over-wintering site is shown for reference purposes only, it is not to scale. Seasonal use of side tributaries may also occur but is not well documented. (after Mochnacz et al. 2010)

SPAWNING BEHAVIOUR

Dolly Varden are iteroparous, meaning they spawn more than once in their life cycle. Spawning occurs between September and October over gravel substrates in upstream reaches of rivers fed by perennial springs (Reist et al. 2001 unpubl.; Stewart et al. 2010). Territories are established and defended by anadromous pairs and the pairs are usually followed closely by several residual males. When the female releases eggs, the males (both anadromous and residual) are stimulated to release milt. The residuals dart through the redd and release milt while the pair is spawning (Reist et al. 2001 unpubl.). This darting tactic is known as "sneaking" and in other salmonids has been found to result in the fertilization of up to 50% of the eggs (e.g., sockeye salmon, *Oncorhynchus nerka* – 48.5% +/- 15.8% of eggs fertilized (Foote et al. 1997)).

The spawning behaviour of northern form Dolly Varden is not well documented but is likely similar to that of the southern form (Armstrong and Morrow 1980) in which both anadromous and residual life history types appear to have similar reproductive success over their life span (Maekawa and Hino 1986, 1987; Hino et al. 1990). Spawning in a land-locked population of southern Dolly Varden in the Tiekkel River, Alaska, has been documented by Maekawa et al. (1991). Three to four males aggregated around a spawning female; the largest and most dominant male (primary male) stayed closest to the female. There was a positive relationship between the number of remaining males, termed satellite males, and the body size of the primary male. The investigators found primary males were generally larger than the spawning female. If a larger male entered the group, the female would then form a pair and sometimes attacked the previous primary male and other satellites. The female never attacked the primary male regardless of body size. Aggressive behaviour was dependent on satellite male body size. The smaller the body sizes of the satellite males, the more aggressive behaviour exhibited by the female. The females spawned from 1-3 times in each redd depending on the number of times a satellite male attempted to release sperm. When a satellite male was successful at releasing sperm, the female would stop spawning and move on to a new redd. Within 15 minutes of spawning, the primary male would begin looking for the next female. Over the course of one day, a primary male was observed spawning with three females (Hino et al. 1990).

Paired males were successful spawners in 97% of attempts. Spawning failure was observed when the paired male chased away a satellite male allowing another satellite male to enter the area and participate in spawning. Satellite male spawning success ranged from 14-68% and decreased with distance from the redd. Dominant satellite males had less success than lower ranking satellite males due to attacks on the larger satellite males by the paired male and better abilities to hide by smaller males thus keeping closer positions to the redd. Satellite males were rarely successful at spawning when only one satellite male was present. However, spawning success rate increased significantly when 2 or more satellites were present as this made it harder for the paired male to

defend the territory. Kitano (1996) documented a similar spawning behaviour in a fluvial population of southern Dolly Varden from a coastal stream on the Shiretoka Peninsula, Hokkaido, Japan. However, in this study three satellite-males that had been unsuccessful at sperm-release were observed eating eggs deposited by the females at two of seven redds.

In a mixed population of anadromous and residual southern form Dolly Varden in Steep Creek, Alaska, the spawning behaviour observed involved one female and one primary male, as many as 4 anadromous males, and up to 2 residual males (Maekawa et al. 1991). There was a positive correlation between the body size of the primary male and the number of satellites. In most pairs, the male was larger than the female. Females never attacked their pair male or other anadromous males, but did attack the residual fish. The females were observed spawning 1-3 times in one redd. If a residual male attempted to release sperm, the female would not spawn again (Maekawa et al. 1991). This behaviour may increase anadromy among the offspring, provided anadromy is heritable (Maekawa et al. 1993). In an earlier study, residual males were observed to be successful at sneaking in 8 of 13 (61.5%) paired spawnings (Maekawa and Hino 1986).

LIFE HISTORY TYPE – FACULTATIVE OR GENETIC AND ASSOCIATED CONSEQUENCES

Life history variation among populations of northern form Dolly Varden may be an adaptation to the local environments that is maintained by homing to natal streams (Sandstrom 1995). Upon return migration from the sea in fall, spawners likely return to their natal streams (homing), while non-spawners may select the most convenient habitat, which leads to intermixing of stocks in freshwater overwintering habitats (Glova and McCart 1974; Craig and McCart 1975, 1976; Furniss 1975; Griffiths et al. 1975; Craig 1977a; Armstrong and Morrow 1980; Reist 1989; Everett et al. 1997, 1998). However, the extent of wandering between drainages appears to be low for North Slope populations based on genetic divergence between drainages (Rhydderch 2001). Furthermore, genetic differences between anadromous spawners, non-spawners, and large juveniles from both the Rat River and Little Fish Creek (Big Fish River system) are not significant (Reist 1989). This suggests that both spawners and non-spawners return to their natal streams. Therefore, immigration from adjacent populations would be unable to preserve the genetic diversity in these populations if they were to collapse. The survivors of the collapse would likely represent only a small portion of the original genetic diversity resulting in a population less able to adapt to environmental change or continued exploitation (Reist 1989).

Whether life history type in northern Dolly Varden is facultative, inherited, or a combination of both is not known, but may have significant impacts on fishery management (Reist et al. 2001 unpubl.). If the trigger to become residual depends only on the environment (e.g., feeding success and subsequent growth of young in freshwater) then the consequences to fishery management are not as

significant since most fisheries target the anadromous segment of the population (Reist et al. 2001 unpubl.). This is the case as long as feeding success remains the same. As climate warms, freshwater productivity may increase, improving feeding success and decreasing the need to go to sea, thereby reducing the size of the anadromous population, although this may be offset by increased marine productivity (Wrona et al. 2005). Alternately, climate warming may cause earlier break-up of Beaufort Sea land-fast ice, resulting in earlier and possibly greater (if marine productivity increases) availability of food resources, and thereby higher growth rates of anadromous Dolly Varden, which potentially could already be occurring in the Rat River (Harwood et al. 2009). If the trigger is genetic the consequences to fishery management are more significant. Undisturbed populations could be exhibiting a balanced genetic polymorphism. Since larger anadromous fish are more often targeted in fisheries, the polymorphism will be/is being disturbed and may lead to selection for the smaller residual fish over time (Reist et al. 2001 unpubl.). It is likely a combination of environmental and genetic factors that determine life history type (Reist et al. 2001 unpubl.) as observed for Arctic char from the Salangen River system, Norway (Nordeng 1983).

Residuals are generally male suggesting variation in life history type is related to the different energetic demands of the sexes. Less energy is needed to produce sperm in comparison to the production of eggs facilitating a sex bias towards males in following alternative life history strategies, particularly in the harsher environment of the North (Reist et al. 2001). Furthermore, it is advantageous for females to attain a larger body size since egg number/egg size is limited to body cavity volume; larger female body size means an increased ability to produce eggs and/or to produce larger eggs, potentially increasing spawning success. The selection pressure for anadromous migration is also lower in males because they are able to successfully reproduce using the sneaking tactic (Sandstrom 1995). Although nuclear DNA markers to distinguish life history types have not been found to date, anticipated and ongoing genetic studies are attempting to address this issue (Rob Bajno, pers. comm.).

If life history is in fact determined by a combination of genetic and environmental factors, then it might be possible for residual fish to eventually smolt and adopt an anadromous life style as observed in some Arctic char (Nordeng 1983). A sequential life history strategy may be possible, however, no supporting evidence for Dolly Varden is available to date.

GENERAL LIFE CYCLE OF NORTHERN DOLLY VARDEN

Dolly Varden have a complex life history as a result of periodicity of spawning and spatial and temporal habitat variability (i.e., seasonal migrations to/from feeding/over-wintering and spawning areas (Reist et al. 2001 unpubl.) As noted previously, Dolly Varden spawn several times over their lifespan, although not always on an annual basis. In northern Canada and Alaska residual, isolated,

and anadromous Dolly Varden spawn in late summer (August) and fall (September – November) (Bain 1974; Glova and McCart 1974; Armstrong and Morrow 1980). Spawning occurs in areas associated with perennial springs (Glova and McCart 1974; Armstrong and Morrow 1980). Young emerge from the gravel substrate in May or June as free swimming fry (Glova and McCart 1974; Armstrong and Morrow 1980; McCart 1980; Reist et al. 2001 unpubl.) to begin exogenous feeding along the stream margin (McCart 1980; Reist et al. 2001 unpubl.) and likely stay near natal streams for the first summer (Armstrong and Morrow 1980; Reist et al. 2001 unpubl.). The general timing of key events in the life cycle of northern Dolly Varden is summarized by river system in Table 2.

The freshwater residence period for seaward juveniles is variable and dependent upon river system. For example, juvenile anadromous Dolly Varden in the Babbage River system spend 1-5 years in freshwater whereas juveniles in the Firth River system spend on average 4 years in freshwater before smolting (Bain 1974; Glova and McCart 1974). Juvenile pre-smolting Dolly Varden utilise freshwater habitats within the river system throughout the summer and return to over-wintering areas in the fall (Yoshihara 1973; Craig and Poulin 1975; Craig 1977a; Armstrong and Morrow 1980; McCart 1980; Reist et al. 2001 unpubl.). The use of freshwater habitats further away from the natal spring is likely related to size and age of the pre-smolt juvenile. Larger and older juveniles move greater distances away from natal springs (Reist et al. 2001 unpubl.). In general, over all North Slope Dolly Varden populations, the age of smoltification is between age 3-4, but may occur as early as age 2 or as late as age 5 and varies between river systems (McCart 1980; Armstrong and Morrow 1980). Females generally smolt one year earlier than males, resulting in a sex ratio biased toward males among the 3 and 4 year classes in the river systems (Armstrong and Morrow 1980).

Anadromous and residual Dolly Varden are indistinguishable from each other before smolting (Glova and McCart 1974). During spring smoltification, anadromous juvenile Dolly Varden undergo complex physiological changes that include changes in colouration from dark brown to silver and the loss of parr markings (Armstrong and Morrow 1980). Migration can begin as early as May with the majority of the migration run occurring in late June to July (Craig 1977a; Armstrong and Morrow 1980). The onset of migration usually occurs immediately following the spring break-up of the river ice and the spring freshet (Yoshihara 1973; DeCicco 1989; Sandstrom 1995). Once at sea young migrants remain in nearshore areas and feed heavily throughout the summer (Glova and McCart 1974; Armstrong and Morrow 1980; Reist et al. 2001 unpubl.). Older and larger fish may move further away from the coast (Armstrong and Morrow 1980). Two Dolly Varden tagged in the upper Firth River and Joe Creek during their migration to sea were recaptured in the Canning River and Kongakut River, Alaska, respectively, 250 km west of the Firth River (Glova and McCart 1974). Both of these fish were non-spawners.

It is not known whether anadromous Dolly Varden make a complete transition to full-strength sea water on their first migration or transition from estuarine waters into increasingly saline waters on

each subsequent annual migration (Reist et al. 2001 unpubl.). Evidence from otolith microchemistry (Babaluk, unpubl. data) indicates the latter may be the most likely case. As a result, estuarine habitats are likely used by young juveniles not only as transitional habitats but also as feeding areas and thus have a greater importance than previously thought (Reist et al. 2001 unpubl.). Several seaward migrations are undertaken before maturity is achieved. Generally, over all North Slope river systems, maturity in anadromous males is reached at approximately age 5 (as early as age 2 and all by age 8-9). Similarly, maturity in anadromous females is reached between ages 4 and 9 (McCart 1980; Reist et al. 2001 unpubl.).

The return migration from the sea to freshwater for spawning and/or over-wintering occurs in late summer and early fall (Glova and McCart 1974; Armstrong and Morrow 1980). Spawning individuals commence a return migration to their natal stream before immature and resting individuals (Glova and McCart 1974; Furniss 1975; Griffiths et al. 1975; Reist 1989). Resting (non-spawning) adults over-winter in other reaches of the natal system or in other streams (Furniss 1975; Craig 1977a; Armstrong and Morrow 1980; Reist 1989). Young making their first return migration from sea to freshwater likely suffer high mortality rates. This is particularly true if finding suitable over-wintering habitat is learned rather than genetic (Craig 1989; Reist et al. 2001 unpubl.). Furthermore, young and those weak from spawning or diseased may be excluded from optimal habitat on the over-wintering grounds by larger, older, and healthier fish (Reist et al. 2001 unpubl.).

Northern anadromous Dolly Varden generally spawn in alternate years with the exception of the Big Fish River population in which females appear to spawn annually upon maturation (Armstrong and Morrow 1980; Sandstrom 1995; DFO 2001; Sandstrom and Harwood 2002). However, few fish in this population live long enough to spawn more than twice as post-spawning mortality is likely high (Savvaitova 1973; Yoshihara 1973; Furniss 1975; Craig 1977a; Armstrong and Morrow 1980), and survival past age 10 is rare (Armstrong and Morrow 1980; McCart 1980). After spawning the fish move downstream to over-wintering habitats.

All stages of anadromous and residual Dolly Varden over-winter in areas fed by perennial springs (Glova and McCart 1974). In the Firth River, Dolly Varden were observed to segregate by size during over-wintering. All pre-smolt Dolly Varden occupied shallow areas with minimal flow, generally under the ice near the bank or in open water areas that were too shallow for larger fish. Immature and mature migrants occupied deeper water, often beneath the ice at the edge of open water areas (Glova and McCart 1974).

Residual Dolly Varden grow at a slower rate than anadromous fish and rarely exceed 220 mm in length (Armstrong and Morrow 1980). They also mature at a younger age, on average between age 2-6 (Armstrong and Morrow 1980). Spawning occurs annually with anadromous females (Savvaitova 1960; Craig 1977a; Armstrong and Morrow 1980). During the summer months, residual fish disperse throughout the river system to feed and return to spawning areas in fall (Reist et al. 2001 unpubl.).

Isolated Dolly Varden are similar to residual Dolly Varden in that they exhibit slow growth, are small in size, and mature early relative to their anadromous counterparts. Initially isolates grow fast, similar to anadromous fish, depending on water temperature, but after the first summer, growth rates decrease (Armstrong and Morrow 1980). Spawning likely occurs later in the year in comparison to residual and anadromous fish. In the Babbage system the isolated population spawns by mid-October (Bain 1974; McCart 1980) but in other isolated populations in Alaska and Canada spawning does not occur until November or later (McCart and Craig 1973; McCart and Bain 1974; Craig 1977b; Armstrong and Morrow 1980). Isolated Dolly Varden produce fewer and smaller eggs than their anadromous counterparts (Armstrong and Morrow 1980). Due to the warmer waters of the springs, egg and embryo development to hatching likely takes less time than for anadromous fish. Males mature by age 2-3, and females by age 3-4 (McCart and Craig 1973; Bain 1974; McCart and Bain 1974; Craig 1977b; Armstrong and Morrow 1980). Isolates live to a maximum of age 10, but few survive past the age 5 (Armstrong and Morrow 1980). The sex ratio in isolated populations is generally slightly biased toward females, and females are dominant in the older age groups (McCart and Craig 1973; McCart and Bain 1974; Craig 1977b; Armstrong and Morrow 1980).

Table 2. General timing of key events in the life cycle of northern Dolly Varden, *S. malma malma*, summarized by river system. Numbers in parentheses refer to data sources listed below.

Event	Firth River System	Babbage River System	Big Fish River System	Rat River System
Spawning	Joe Creek (anadromous): September – October (1, 2) Upper Mainstem (anadromous): mid-August - early October (1, 2, 3, 4)	Upper Babbage (isolated): September - mid-October (2, 3, 5) Fish Hole Creek (anadromous): September - early October (2, 4, 5, 6)	Little Fish Creek (isolated): Late fall/early winter (2, 7) Little Fish Creek (anadromous): September - October (2, 4, 8, 9, 10, 11) late October – November (18)	Fish Creek (anadromous): mid-August - early October (2, 4, 8, 9, 10, 11, 12, 13)
Emergence of Fry	Prior to spring break-up; Joe Creek (anadromous): first observed on May 11 (1)	Fish Hole Creek (anadromous): likely late May (4, 5)	Little Fish Creek (isolated): Late April - early May (7) Little Fish Creek (anadromous): Spring; varies by several months depending on water temperature (14)	May – June (for North Slope Dolly Varden in general) (2)
Spring Migration to Sea	May - June (1, 4)	June (15)	Early July (shortly after break-up) (4)	Early to mid-June (non-spawners) (4)
Fall Return Migration	Late summer to fall (1, 4)	July - September (5, 15)	Mid-August - early September (4, 18)	Late July - mid-September (4, 12, 16, 17)

1. Glova and McCart 1974; 2. McCart 1980; 3. Craig and McCart 1974; 4. Baker 1987; 5. Bain 1974; 6. Bryan et al. 1973; 7. McCart and Bain 1974; 8. Dryden et al. 1973; 9. Jessop et al. 1974; 10. Jessop and Lilley 1975; 11. Stein et al. 1973a; 12. Jessop et al. 1973; 13. Stein et al. 1973b; 14. S. Sandstrom, unpubl. data cited in DFO 2003c; 15. W. Bond, pers. comm. cited in Baker 1987; 16. DFO 2001; 17. Harwood et al. 2009; 18. Byers 1993

LIFE HISTORY STAGES

The life cycle of Dolly Varden can be divided into a series of stages: egg, fry, immature juvenile, maturing juvenile, and adult. Some of these categories can be further subdivided depending on the activities being undertaken. For example, adults can be sexually mature but not yet spawned (virgin), spawning (or near to it), exhibiting activity preparatory to spawning (e.g., summer feeding), and resting (i.e., adults that spawned in the past and will again at some time in the future but not in the current year). For populations of only one life history type, the life history is a straightforward unfolding of the above sequence of events. However, for populations consisting of two or more life history types, the life history patterns of each are linked. This linkage is illustrated in Figure 7 using the residual and anadromous forms as the model.

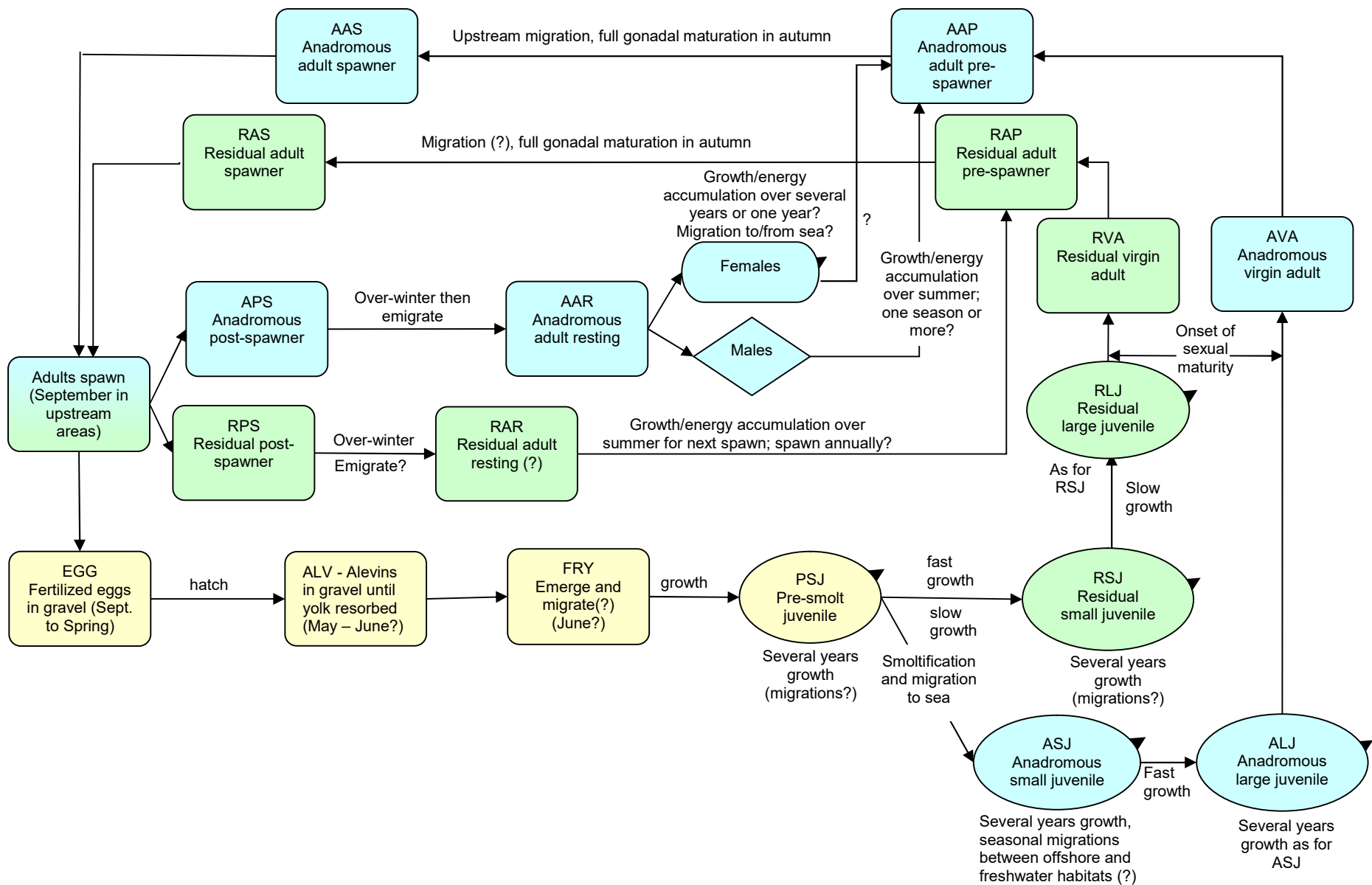


Figure 7. Diagrammatic representation of the linkage between anadromous and residual life history types of northern form Dolly Varden, *S. malma malma* (modified from Reist, 1988 unpubl.).

Mixed Types and Stages and Criteria Used for Identification

Any attempt to classify an individual specimen in either the field or the lab has to consider the criteria that define different life history types as well as life history stages. Table 3 provides a complete listing of types and stages and their corresponding acronyms.

The first step in classifying individuals is to examine geographic locality and period of collection time to determine the life history type. For example, if the sample originated from above impassable falls, it represents the isolated type. Samples from a marine, estuarine or other similar environment would be the anadromous type. During certain life history stages residual and anadromous types overlap significantly, especially during spawning. Depending on the degree of local movement of the residual type, overlap may also occur during spawning migrations in areas distant from the actual spawning sites. Consequently, caution must be exercised in these situations. The following types of individuals may be present on or near the spawning grounds or in the upstream migratory run: anadromous and residual spawners both likely originating from that river system, anadromous non-spawners consisting of both juveniles and resting adults from either the specified river system or elsewhere, residual non-spawners from that river system, and small juveniles. These possibilities exist for the Firth, Babbage and Big Fish rivers and possibly for the Rat River (S. Stephenson, pers. comm.).

In addition to locality, date/season of collection, and the possibilities noted above, several criteria intrinsic to the individual fish are useful to identify life history type and stage. These include size, age, colouration, and maturity stage when available. Generally, stream-resident fish (isolated and residual) are small, slow-growing, and retain parr marks throughout life. Once spawning colouration is achieved by resident fish, it is retained throughout the fishes' lifespan, although it may fade slightly when in a non-reproductive state. Anadromous fish are larger, and after smoltification no longer exhibit parr marks (see Fig. 8).

The stage of the seasonal life cycle for anadromous fish is indicated by colour. Pre-spawning and spawning adults, particularly males, exhibit the typical black, white, and red colouration as well as kype formation. Females exhibit the same colouration as males, although the intensity may be muted, and no kype is developed. Immature or resting anadromous fish exhibit the silvery colouration of sea-run char. The spawning colouration of resident fish is superimposed on parr marks, whereas for anadromous fish it is superimposed on the silver ground colour. The presence of parr marks and small size may therefore indicate either a pre-smolt anadromous, or a juvenile resident, fish. These criteria have been combined into a dichotomous key for the classification of anadromous and residual individuals. If information on gonadal maturity is available a more resolved classification of individuals to life history stage is possible. The criteria used for scoring maturity are those of McGowan (1987; reproduced here as Table 4).

Table 3. Description of life history acronyms used for northern form Dolly Varden, *S. malma malma* (after Reist 1988 unpubl.). Life history type photos are shown in Figure 8 and maturity codes are defined in Table 4.

Life History Stage	Acronym	Notes
1. All Life History Types		
Egg	EGG	Common to all types.
Alevin	ALV	Common to all types, yolk-sac present.
Fry	FRY	Common to all types, no yolk-sac.
Young-of-the-year	YOY	Common to all types.
Parr	PSJ	Pre-smolt juvenile, parr marks present but immature and may be age 1-3; can be of any life history type although the identification to type is tenuous at best (includes ASJ, RSJ, etc.).
2. Anadromous Life History Type		
Smolt	ASJ	Anadromous small juvenile, fish age 2-3 moving downstream to the sea and undergoing relevant physiological changes for marine environment, parr marks disappear. Near the natal area and prior to sea-run, may be indistinguishable from RSJ therefore included in PSJ group.
Juvenile	ALJ	Anadromous large juvenile, silver in colour, fish between smolt and pre-spawning stages of life which may be age 3-8. Larger individuals have spent several summers/winters in seasonal migrations between feeding (marine) and over-wintering (freshwater) habitats.
Maturing fish	AVA	Anadromous virgin adult maturing for the first time, cannot be distinguished without gonadal examination, live fish will be either AAP or AAS.
Pre-spawner	AAP	Anadromous adult pre-spawner, adult (virgin or not) coming into condition to spawn in that year, i.e., colour or secondary sexual characters developing but fish are not yet ready to spawn.
Spawner	AAS	Anadromous adult spawner, full colour developed, gonads mature and products can be expelled.
Post-spawner	APS	Anadromous adult post-spawner, adult finished spawning for that year.
Resting	AAR	Anadromous adult resting, adult that is accumulating energy in order to spawn again but which will not spawn in the forthcoming season. On the spawning grounds these are obvious when examining both colour and gonads. These are silver in colour, thus without a gonadal examination or during non-spawning times (e.g., summer feeding) they may be indistinguishable from AVA, AAP, or ALJ.
3. Residual (riverine) Life History Type		
Juvenile	RSJ	Residual small juvenile, fish from PSJ stage to large juvenile stage (a subset of PSJ that may not be distinguishable as such), parr marks retained.
Juvenile	RLJ	Residual large juvenile, fish that are older and larger than RSJ (i.e., clearly too large/old to be PSJ or ASJ), parr marks retained.
Maturing Fish	RVA	Residual virgin adult maturing for the first time, indistinguishable from RAP and RAS without gonadal examination.
Pre-spawner	RAP	Residual adult pre-spawner, adult (virgin or not) coming into condition to spawn in that year.
Spawner	RAS	Residual adult spawner.
Post-spawner	RPS	Residual adult post-spawner, adult finished spawning for that year.
Resting	RAR	Residual adult resting, adult but will not spawn that year based on gonadal examination. Note: unknown if this stage exists.
4. Isolated (stream-resident) Life History Type		
As above	As Above	Isolated life history type with stages parallel to the residual form noted above; all stages designated by the appropriate letters prefaced by "I" (e.g., ISJ, ILJ, IAS, etc.).

Table 4. Codes for the determination of maturity stages of northern fishes (after McGowan 1987).

Maturity State	Maturity Code	Female Characteristics	Maturity Code	Male Characteristics
Immature (virgin)	1	<ul style="list-style-type: none"> - ovaries granular in texture - hard and triangular in shape - up to full length of body cavity - membrane full - eggs distinguishable 	6	<ul style="list-style-type: none"> - testes long and thin - tubular and scalloped shape - up to full body length - putty-like firmness
Mature	2	<ul style="list-style-type: none"> - current year spawner - ovary fills body cavity - eggs near full size but not loose - not expelled by pressure 	7	<ul style="list-style-type: none"> - current year spawner - testes large and lobate - white to purplish colour - centers may be fluid - milt not expelled by pressure
Ripe	3	<ul style="list-style-type: none"> - ovaries greatly extended and fill body cavity - eggs full size and transparent - expelled by slight pressure 	8	<ul style="list-style-type: none"> - testes full size - white and lobate - milt expelled by slight pressure
Spent	4	<ul style="list-style-type: none"> - spawning complete - ovaries ruptured and flaccid - developing oocytes visible - some retained eggs in body cavity 	9	<ul style="list-style-type: none"> - spawning complete - testes flaccid with some milt - blood vessels obvious - testes violet-pink in colour
Resting	5	<ul style="list-style-type: none"> - ovary 40-50% of body cavity - membrane thin, loose and semi-transparent - healed from spawning - developing oocytes apparent with few atretic eggs - some eggs may be retained in body cavity 	10	<ul style="list-style-type: none"> - testes tubular, less lobate - healed from spawning - no fluid in center - usually full length - mottled and purplish in colour
Maturity State	Maturity Code	Characteristics		
Unknown (virgin)	0	<ul style="list-style-type: none"> - cannot be sexed - gonads long or short and thin - transparent or translucent 		
Unknown (non-virgin)	11	<ul style="list-style-type: none"> - resting fish - has spawned but gonads regenerated - sexing not possible 		

Data Required in the Field to Work the Key

The following data in tabular form are minimally required to key specimens to life history type: locality of collection (waterbody name and coordinates); date(s) of collection; fork length (at least approximately to a category e.g., < 150 mm, 150-200 mm, etc.); status of parr marks (present/absent) and colour (silver, pre-spawn, or spawning). To further categorize individuals to life history stage, the following data are also needed: maturity index derived from either internal (Table 4) or external criteria (e.g., rigid sides, gametes expelled with pressure, etc.). Secondary sexual characters (see below) can sometimes be used to externally sex anadromous fish. This tabular data should include: kype presence/absence, dorsal ridge presence/absence, and/or enlarged teeth.

Notes on Colouration and Secondary Sexual Characteristics of Dolly Varden

As outlined above, the colour of non-spawning anadromous Dolly Varden is silver. Pale pink to orange spots are scattered along the sides. Anadromous fish develop brilliant colours during spawning. For males this includes: brown-black dorsal surface and orange-red ventral surface, tip of upper and sides of lower jaw are orange, white streaks present under the maxilla and along the inner edge of the lower jaw, spots on the sides are bright orange-red and are surrounded by a blue halo to make the entire spot the same size as the eye diameter, dorsal and adipose fins are darkly pigmented, and the leading edge of the caudal and ventral fins is white (Bain 1974). Generally, the spawning colouration of males is more vivid than that of females, although the latter has similar distribution of colour. Non-anadromous (isolated and residual) fish have a dark dorsal surface, dark fins with white leading edges on pelvic and anal fins, parr marks are present at all times, the belly and spots on the sides are yellow-orange with the largest spots smaller than their pupil. Females, where present, are similar in colouration. Once achieved, non-anadromous fish retain this colour throughout life although it may be muted during non-spawning periods.

Male anadromous char develop significant secondary sexual characters which often precede the development of spawning colouration. Thus, these can be used as clues to sex and/or spawning condition of apparently “silver” fish. The secondary sexual characteristics include: 1) prominent dorsal ridge developed anterior to the dorsal fin; 2) a prominent kype is developed on the lower jaw with an associated notch on the upper jaw; and 3) teeth on the lower jaw (kype included) are enlarged. In addition to preceding the development of spawning colours, these morphological changes also persist for a considerable time after spawning is finished and colour has faded, possibly into the following summer. Male non-anadromous char either do not develop such secondary sexual characters or do so poorly.

Key for the Determination of Life History Type and Stage of Northern Dolly Varden – anadromous and residual forms (Northern Northwest Territories & Yukon North Slope)

1. a) Parr marks present	2
b) Parr marks absent	5
2. a) Small size (<175 mm FL), not mature (i.e., maturity code 0) pre-smolt juvenile ¹ (RSJ or ASJ ²) (Fig. 8a)	
b) Large size (>175 mm FL)	3
3. a) Fork or total length greater than about 175 mm (approx. age 3), colour is typical of spawning fish, gonads are mature (i.e., maturity code 1-4 or 6-9) residual adult spawner (RAS) ³ (Fig. 8b)	
b) As for 3a) but colour is not that of a spawning fish and not mature (or no evidence)	4
4. a) Larger fish (up to 395 mm FL), evidence of previous spawning activity, gonadal maturation evident (i.e., maturity code 5, 10)	residual adult ⁴ non-spawner (i.e., resting, RAR)
b) Smaller fish (175-250 mm), no evidence of previous spawning (i.e., maturity code 0)	residual sub-adult non-spawner (RLJ) or possibly pre-smolt juvenile (i.e., 2a) (Fig. 8a)
5. a) Small size (age 2, 3 and ~ 100-175 mm)	smoltifying juvenile (ASJ, downstream run only)
b) Larger size (>300 mm)	6
6. a) Silver in colour	7 ⁵
b) Spawning colours evident or developing, maturity code 1-4 or 6-9.....	8
7. a) Maturity indicated as 0.....	anadromous large juvenile ⁶ (ALJ, over-wintering) (Fig. 8c)
b) Maturity indicated as 5 or 10	anadromous adult resting ⁷ (AAR, over-wintering)
8. a) Maturity as 1 or 6.....	anadromous adult virgin ⁶ (AVA)
b) Maturity as 2, 3, 4, or 7, 8, 9.....	anadromous adult spawner (AAS) (Fig. 8d, e, f)

Notes on Use of the Key

1. Small fish not in spawning colour are difficult to assign to a life history type. That is, these can be either juveniles of the anadromous form (ASJ), residual form (RJu), or less likely resting residual adults (RAR) should such exist and lose their colour. This also applies to key lines 4 and 5.

2. See Table 3 for maturity codes.

3. The detailed categorization of resident adults as virgins, spawners or resting fish was not done but could be done as a parallel to key lines 6-8.

4. The existence of resting residual males is unknown at present; this possibility may not exist.

5. The time course of development of spawning colours, especially for females, is unknown. Fish classed as silvers when tagged downstream have been found later in the same season to be spawning when recaptured upstream. Male secondary sexual characters (kype, dorsal ridge, elongated teeth) can be used to aid in classifying them without reference to colouration.

6. These individuals cannot be distinguished without gonadal examination (i.e., all fish in key line 7 are "silvers", and all in key line 8 are "spawners").

7. Recent data have indicated that all anadromous fish classified as resting were females. This may be coincidental (sampling bias) or it may be a real phenomenon. The latter makes biological sense in that females may need more than a single 'growing' season to accumulate energy reserves sufficient for egg production and spawning, whereas males, with lesser energy requirements for sperm production, may not. Thus, there is a distinct possibility that only female char exhibit a resting adult form and that males regularly do not (although both sexes are likely facultative in this such that in climatically extreme years spawning is foregone).



Figure 8. Photos of Northern form Dolly Varden identified by life history type. **a.** ASJ, RSJ, or RLJ (?) from the Firth River; **b.** RAS from the Firth River; **c.** ALJ from the Babbage River; **d.** AAS male from the Firth River; **e.** AAS female from the Firth River; **f.** AAS female from Joe Creek.

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LITERATURE CITED

- Anderton, I. 2006. Peel River watershed fisheries information summary report – preliminary assessment. Prepared for Peel Watershed Planning Commission by EDI Environmental Dynamics Inc., Whitehorse, YT. iv + 42 p. [available from: http://peel.planyukon.ca/old/index.php?option=com_docman&task=doc_download&gid=52; Accessed: 17/05/2010].
- Andrusak, H., and Northcote, T.G. 1971. Segregation between adult cutthroat trout (*Salmo clarki*) and Dolly Varden (*Salvelinus malma*) in small coastal British Columbia lakes. *Journal of the Fisheries Research Board of Canada* 28: 1259-1268.
- Armstrong, R.H., and Morrow, J.E. 1980. The Dolly Varden charr, *Salvelinus malma*. In *Charrs: Salmonid fishes of the genus Salvelinus*. Edited by E.K. Balon. Dr. W. Junk, The Hague, Netherlands, pp. 99-140.
- Babaluk, J.A., Reist, J.D., Sahanatian, V.A., Halden, N.M., Campbell, J.L., and Teesdale, W.J. 1998. Preliminary results of stock discrimination of charrs in Ivvavik National Park, Yukon Territory, Canada, using microchemistry of otolith strontium. In *Linking protected areas with working landscapes conserving biodiversity, Proceedings of the Third International Conference on Science and Management of Protected Areas, 12-16 May 1997*. Edited by N.W.P. Munro and J.H. Martin Willison. Science and Management of Protected Areas Association, Wolfville, Canada, pp. 991-998.
- Bain, L.H. 1974. Life histories and systematics of Arctic char (*Salvelinus alpinus*, L.) in the Babbage River system, Yukon Territory. *Arctic Gas Biological Report Series* 18(1): xvi + 156 p.
- Baker, R.F. 1987. Status report for Arctic charr stocks of the Rat, Big Fish, Babbage and Firth rivers of the Northwest Territories and Yukon North Slope. Unpublished report, Department of Fisheries and Oceans, Western Region, Winnipeg, MB. 62 p.
- Behnke, R.J. 1980. A systematic review of the genus *Salvelinus*. In *Charrs: Salmonid fishes of the genus Salvelinus*. Edited by E.K. Balon. Dr. W. Junk, The Hague, Netherlands, pp. 441-480.
- Bodaly, R.A., and Lindsey, C.C. 1977. Pleistocene watershed exchange and the fish fauna of the Peel River Basin, Yukon Territory. *Journal of the Fisheries Research Board of Canada* 34: 388-395.
- Bryan, J.E. 1973. The influence of pipeline development on freshwater fishery resources of northern Yukon Territory. Aspects of research conducted in 1971 and 1972. Environmental-Social Committee Northern Pipelines, Task Force on Northern Oil Development Report No. 73-6: viii + 63 p.
- Bryan, J.E., Walker, C.W., Kendel, R.E., and Elson, M.S. 1973. Freshwater aquatic ecology in the northern Yukon Territory. Canada Task Force on Northern Oil Development, Environmental-Social Committee Northern Pipelines Report 73-21: 64 p.
- Byers, T. 1993. Aklavik traditional knowledge – Big Fish River: A study of indigenous wisdom in fishery science. Prepared for The Aklavik Hunters and Trappers Committee, Aklavik, Northwest Territories. 21 p. + apps.
- Craig, P.C. 1977a. Ecological studies of anadromous and resident populations of Arctic char in the Canning River drainage and adjacent coastal waters of the Beaufort Sea, Alaska. *Arctic Gas Biological Report Series* 41: 1-116.

- Craig, P.C. 1977b. Arctic char in Sadlerochit Spring, Arctic National Wildlife Refuge. Arctic Gas Biological Report Series 41: 1-29.
- Craig, P.C. 1989. An introduction to anadromous fishes in the Alaskan Arctic. Biological Papers of the University of Alaska 24: 27-54.
- Craig, P., and McCart, P.J. 1974. Fall spawning and over-wintering areas of fish populations along routes of proposed pipeline between Prudhoe Bay and the Mackenzie Delta 1972-73. Arctic Gas Biological Report Series 15(3): 36 p.
- Craig, P.C., and McCart, P.J. 1975. Fish utilization of nearshore coastal waters between the Colville and Mackenzie rivers with an emphasis on anadromous species. Canadian Arctic Gas Biological Report Series 34: 172-219.
- Craig, P.C., and McCart, P.J. 1976. Fish use of nearshore coastal waters in the western Arctic: Emphasis on anadromous species. *In* Assessment of the Arctic marine environment: selected topics. *Edited by* D.W. Hood and D.C. Burrell. Occasional Publication 4 of the University of Alaska Institute of Marine Science, Fairbanks, AK, pp. 361-388.
- Craig, P.C., and Poulin, V.A. 1975. Movements and growth of grayling (*Thymallus arcticus*) and juvenile Arctic char (*Salvelinus alpinus*) in a small Arctic stream, Alaska. Journal of the Fisheries Research Board of Canada 32: 689-697.
- DeCicco, A.L. 1989. Movements and spawning of adult Dolly Varden charr (*S. malma*) in the Chukchi Sea drainages of northwestern Alaska: evidence for summer and fall spawning populations. *In* Biology of Charrs and Masu Salmon. Physiology and Ecology Japan, Special Volume 1. *Edited by* H. Kawanabe, F. Yamazaki, and D.I.G. Noakes, pp. 229-238.
- DeCicco, A.L. 1997. Movements of postsmolt anadromous Dolly Varden in northwestern Alaska. American Fisheries Society Symposium 19: 175-183.
- DeCicco, F., and Reist, J. 1999. Distribution of Dolly Varden in northern Bering and Chukchi Sea drainages, a provisional organization. Proceedings of the Eighth and Ninth International Society of Arctic Char Fanatics (ISACF) Workshops on Arctic Char, 1996 & 1998, ISACF Information Series 7: 13-18.
- DFO [Fisheries and Oceans Canada]. 2001. Rat River Dolly Varden. DFO Science Stock Status Report D5-61: 15 p. [available from: www.fjmc.ca/publications/SSR-D5-61.pdf; Accessed: 17/05/2010].
- DFO [Fisheries and Oceans Canada]. 2003a. Firth River Dolly Varden. DFO Science Stock Status Report D5-63: 12 p. [available from: www.dfo-mpo.gc.ca/csas/Csas/status/2002/SSR2002_D5-63_e.pdf; Accessed: 17/05/2010].
- DFO [Fisheries and Oceans Canada]. 2003b. Babbage River Dolly Varden. DFO Science Stock Status Report D5-62: 12 p. [available from: www.dfo-mpo.gc.ca/csas/Csas/status/2002/SSR2002_D5-62_e.pdf; Accessed: 17/05/2010].
- DFO [Fisheries and Oceans Canada]. 2003c. Big Fish River Dolly Varden. DFO Science Stock Status Report D5-60: 15 p. [available from: www.dfo-mpo.gc.ca/csas/Csas/status/2002/SSR2002_D5-60_e.pdf; Accessed: 17/05/2010].

- DFO [Fisheries and Oceans Canada]. 2007. News Releases: Voluntary closure of the Rat River char fishery, NWT. Fisheries and Oceans Canada. 1 p. [available from: <http://www.grrb.nt.ca/pdf/news/2007.08.03%20-%20DFO%20News%20Release%20-%20voluntary%20closure.pdf>; Accessed: 17/05/2010].
- Dryden, R.L., Sutherland, B.G., and Stein, J.N. 1973. An evaluation of the fish resources of the Mackenzie River Valley as related to pipeline development, Volume II. Canada Task Force on Northern Oil Development, Environmental-Social Committee Northern Pipelines Report 73-2: 175 p.
- Everett, R.J., Wilmot, R.L., and Krueger, C.C. 1997. Population genetic structure of Dolly Varden from Beaufort Sea drainages of northern Alaska and Canada. *In* Fish ecology in Arctic North America. American Fisheries Society Symposium 19, Proceedings of the Fish Ecology in Arctic North America Symposium, Fairbanks, Alaska, 19-21 May 1992. *Edited by* J.B. Reynolds. American Fisheries Society, Bethesda, MD, pp. 240-249.
- Everett, R.J., Wilmot, R.L., and Krueger, C.C. 1998. Population genetic structure of Dolly Varden char from Beaufort Sea drainages of northern Alaska and Canada. *In* Genetics investigations of Dolly Varden char (*Salvelinus malma*) of the North Slope of Alaska, Part I. Alaska Fisheries Technical Report 43, pp. 1-16.
[available from: http://alaska.fws.gov/fisheries/genetics/pdf/1001_rf_1998_EverettWilmotKrueger_t_1998_43.pdf; Accessed: 17/05/2010].
- Foote, C.J., Brown, G.S., and Wood, C.C. 1997. Spawning success of males using alternative mating tactics in sockeye salmon, *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 54: 1785-1795.
- Furniss, R.A. 1975. Inventory and cataloging of Arctic area waters. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Project F-9-7, Job G-I-I, Annual Performance Report 16: 47 p.
- Gillman, D.V., Sparling, P., and Gillis, B. 1985. NOGAP Project 2-109: Arctic char population studies 1. Big Fish River 2. River system survey. Department of Fisheries and Oceans, Winnipeg, MB. 57 p.
- Glova, G., and McCart, P. 1974. Life history of Arctic char (*Salvelinus alpinus*) in the Firth River, Yukon Territory. Arctic Gas Biological Report Series 20(3): viii + 50 p.
- Griffiths, W.B., Craig, P.C., Walder, G., and Mann, G.J. 1975. Fisheries investigations in a coastal region of the Beaufort Sea (Nunavut Lagoon, Yukon Territory). Arctic Gas Biological Report Series 24: 1-219.
- Harden, D., Barnes, P., and Reimnitz, E. 1977. Distribution and character of naleds in northeastern Alaska. Arctic 30: 28-40.
- Harwood, L.A. 2001. Status of anadromous Dolly Varden (*Salvelinus malma*) of the Rat River, Northwest Territories, as assessed through community-based sampling of the subsistence fishery, August – September 1989-2000. Canadian Science Advisory Secretariat (CSAS) Research Document 2001/090: 30 p.
[available from: www.grrb.nt.ca/pdf/fisheries/StatusDollyVardenRatRiver2001.pdf; Accessed: 17/05/2010].

- Harwood, L.A., Sandstrom, S., and Linn, E. 2009. Status of anadromous Dolly Varden (*Salvelinus malma*) of the Rat River, Northwest Territories, as assessed through sampling of the subsistence fishery (1995-2007). Canadian Technical Report of Fisheries and Aquatic Sciences 2891: vii + 52 p.
- Hino, T., Maekawa, K., and Reynolds, J.B. 1990. Alternative male mating behaviors in landlocked Dolly Varden (*Salvelinus malma*) in south-central Alaska. Journal of Ethology 8: 13-20.
- Jessop, C.S., and Lilley, J.W. 1975. An evaluation of the fish resources of the Mackenzie River Valley, based on 1974 data. Canada Fisheries and Marine Service Technical Report Series CEN/T-75-6: 97 p.
- Jessop, C.S., Porter, T.R., Blouw, M., and Sopuck, R. 1973. Fish resources of the Mackenzie River Valley. Special report: An intensive study of the fish resources of two mainstem tributaries. Canada Task Force on Northern Oil Development, Environmental-Social Program Northern Pipelines. 148 p.
- Jessop, C.S., Chang-Kue, K.T.J., Lilley, J.W., and Percy, R.J. 1974. A further evaluation of the Mackenzie River Valley as related to pipeline development. Canada Task Force on Northern Oil Development, Environmental-Social Program Northern Pipelines Report 74-7: 95 p.
- Kitano, S. 1996. Size-related factors causing individual variation in seasonal reproductive success of fluvial male Dolly Varden (*Salvelinus malma*). Ecology of Freshwater Fish 5(2): 59-67.
- Kowalchuk, M.W., Sawatzky, C.D., and Reist, J.D. 2010a. A review of the taxonomic structure within Dolly Varden *Salvelinus malma* (Walbaum 1792) of North America. Canadian Science Advisory Secretariat (CSAS) Research Document 2010/013: vi + 16 p. [available from: http://www.dfo-mpo.gc.ca/CSAS/Csas/Publications/ResDocs-DocRech/2010/2010_013_e.pdf; accessed 17/05/2010].
- Kowalchuk, M.W., Reist, J.D., Bajno, R., Mochnacz, N.J., and Sawatzky, C.D. 2010b. Population structuring and inter-river movements of northern form Dolly Varden *Salvelinus malma malma* (Walbaum 1792) along the north slope of Canada and Alaska. Canadian Science Advisory Secretariat (CSAS) Research Document 2010/038: vi + 17 p.
- Kristofferson, A.H., and Baker, R.F. 1988. Stock status of Arctic charr in the Big Fish River, Northwest Territories. Unpublished report presented to the Arctic Fisheries Scientific Advisory Committee, Department of Fisheries and Oceans, 87/88-8: 12 p.
- Krueger, C.C., Wilmot, R.L., and Everett, R.J. 1998. Stock origins of Dolly Varden collected from Beaufort Sea coastal sites of Arctic Alaska and Canada. In Genetic Investigations of Dolly Varden char (*Salvelinus malma*) of the North Slope of Alaska, Part II. Alaska Fisheries Technical Report 43, pp. 17-33. [available from: http://alaska.fws.gov/fisheries/genetics/pdf/1001_rf_1998_EverettWilmotKrueger_t_1998_43.pdf; Accessed: 17/05/2010].
- Krueger, C.C., Wilmot, R.L., and Everett, R.J. 1999. Stock origins of Dolly Varden collected from Beaufort Sea coastal sites of Arctic Alaska and Canada. Transactions of the American Fisheries Society 128: 49-57.
- Maekawa, K., and Hino, T. 1986. Spawning behaviour of Dolly Varden in southeastern Alaska, with special reference to the mature male parr. Japanese Journal of Ichthyology 32(4): 454-458.

- Maekawa, K., and Hino, T. 1987. Effect of cannibalism on alternative life histories in charr. *Evolution* 41: 1120-1123.
- Maekawa, K., Hino, T., and Nakano, S. 1991. A preliminary study on direct mate preference of female anadromous and land-locked Dolly Varden in Alaska. *In* Reproductive biology and population genetics of Dolly Varden (Salmonidae). *Edited by* F. Yamazaki. Report of Overseas Work supported by Grant-In-Aid for Overseas, Scientific Survey of the Ministry of Education, Science & Culture of Japan, pp. 5-12.
- Maekawa, K., Hino, T., Nakano, S., and Smoker, W.W. 1993. Mate preference in anadromous and landlocked Dolly Varden (*Salvelinus malma*) females in two Alaskan streams. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2375-2379.
- Mann, G.J., and Tsui, P.T.P. 1977. Fall and early winter aquatic resource inventory: Dempster lateral pipeline route. Volume II, stream and lake catalogue. Prepared for Foothills Pipe Lines (Yukon) Ltd. v + 188 p.
- McCart, P. 1974. Late winter surveys of lakes and streams in Canada and Alaska along the gas pipeline routes under consideration by Canadian Arctic Gas Study Limited, 1972-1973. *Arctic Gas Biological Report Series* 15(1): 183 p.
- McCart, P.J. 1980. A review of the systematics and ecology of Arctic char, *Salvelinus alpinus*, in the western Arctic. *Canadian Technical Report of Fisheries and Aquatic Sciences* 935: vii + 89 p.
- McCart, P., and Bain, H. 1974. An isolated population of arctic charr (*Salvelinus alpinus*) inhabiting a warm mineral spring above a waterfall at Cache Creek, N.W.T. *Journal of the Fisheries Research Board of Canada* 31: 1408-1414.
- McCart, P., and Craig, P. 1973. Life history of two isolated populations of Arctic char (*Salvelinus alpinus*) in spring-fed tributaries of the Canning River, Alaska. *Journal of the Fisheries Research Board of Canada* 30: 1215-1220.
- McGowan, D.K. 1987. Data on Arctic charr, *Salvelinus alpinus* (L.), from the Diana River, Northwest Territories, 1986. *Canadian Data Report of Fisheries and Aquatic Sciences* 666: iv + 19 p.
- McPhail, J.D. 1961. A systematic study of the *Salvelinus alpinus* complex in North America. *Journal of the Fisheries Research Board of Canada* 18: 793-816.
- McPhail, J.D. 2007. The freshwater fishes of British Columbia. The University of Alberta Press, Edmonton, AB. lxxiv + 620 p.
- Mecklenburg, C.W., Mecklenburg, T.A., and Thorsteinson, L.K. 2002. Fishes of Alaska. American Fisheries Society, Bethesda, MD. xxxvii + 1037 p.
- Millar, N. 2006. Investigation of Dolly Varden (*Salvelinus malma*) in the Vittrekwa River, NWT/Yukon. Gwich'in Renewable Resource Board, Inuvik, NT. 7 p.
- Mochnac, N.J., and Reist, J.D. 2007. Biological and habitat data for fish collected during stream surveys in the Sahtu Settlement Region, Northwest Territories, 2006. *Canadian Data Report of Fisheries and Aquatic Sciences* 1189: vii + 40 p.
- Mochnac, N.J., Schroeder, B.S., Sawatzky, C.D., and Reist, J.D. 2010. Assessment of critical habitat for northern Dolly Varden, *Salvelinus malma malma* (Walbaum, 1792) in Canada. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* xxxx: vi + 52 p. [draft].

- Morrow, J.E. 1980. Analysis of the Dolly Varden charr, *Salvelinus malma*, of northwestern North America and northeastern Siberia. In Charrs: Salmonid fishes of the genus *Salvelinus*. Edited by E.K. Balon. Dr. W. Junk, The Hague, Netherlands, pp. 323-338.
- Mutch, R.A., and McCart, P. 1974. Springs within the northern Yukon drainage system (Beaufort Sea drainage). Arctic Gas Biological Report Series 15(9): 30 p.
- Nordeng, H. 1983. Solution to the "char problem" based on Arctic char (*Salvelinus alpinus*) in Norway. Canadian Journal of Fisheries and Aquatic Sciences 40: 1372-1387.
- Osinov, A.G. 2001. Evolutionary relationships between the main taxa of the *Salvelinus alpinus*-*Salvelinus malma* complex: results of a comparative analysis of allozyme data from different authors. Journal of Ichthyology 41(3): 192-208.
- Palmisano, J.F. 1971. Freshwater food habits of *Salvelinus malma* (Walbaum) on Amchitka Island, Alaska. M.Sc. Thesis, Utah State University, Logan, UT. 76 p.
- Phillips, R.B., Gudex, L.I., Westrich, K.M., and DeCicco, A.L. 1999. Combined phylogenetic analysis of ribosomal ITS1 sequences and new chromosome data supports three forms of Dolly Varden char (*Salvelinus malma*). Canadian Journal of Fisheries and Aquatic Sciences 56: 1504-1511.
- Reid, D., and Skinner, S. 2008. Conservation priorities assessment report. Peel Watershed Planning Commission, Whitehorse, YT. vi + 131 p. [available from: www.peel.planyukon.ca; Accessed 22/10/2008].
- Reist, J.D. 1988. Life history types and stages of western form Arctic charr. Unpublished manuscript. Fisheries and Oceans Canada, Winnipeg, MB. 12 p.
- Reist, J.D. 1989. Genetic structuring of allopatric populations and sympatric life history types of charr, *Salvelinus alpinus/malma*, in the western Arctic, Canada. Physiology and Ecology Japan 1: 405-420.
- Reist, J. 2001. Taxonomic issues, life history and stock discrimination – Rat River Dolly Varden. Canadian Science Advisory Secretariat (CSAS) Research Document 2001/091: 5 p. [available from: www.dfo-mpo.gc.ca/csas/Csas/DocREC/2001/RES2001_019e.pdf; Accessed 17/05/2010].
- Reist, J.D., and Sawatzky, C.D. 2010. Diversity and distribution of chars, genus *Salvelinus*, in Northwestern North America in the context of northern Dolly Varden (*Salvelinus malma malma* Walbaum 1792)). Canadian Science Advisory Secretariat (CSAS) Research Document 2010/014: vi + 18 p. [available from: http://www.dfo-mpo.gc.ca/CSAS/Csas/Publications/ResDocs-DocRech/2010/2010_014_e.pdf; accessed 17/05/2010].
- Reist, J.D., Johnson, J.D., and Carmichael, T.J. 1997. Variation and specific identity of char from northwestern Arctic Canada and Alaska. In Fish ecology in Arctic North America. American Fisheries Society Symposium 19, Proceedings of the Fish Ecology in Arctic North America Symposium, Fairbanks, Alaska, 19-21 May 1992. Edited by J.B. Reynolds. American Fisheries Society, Bethesda, MD, pp. 250-261.
- Reist, J.D., Papst, M.A., and Babaluk, J.A. 2001. Biodiversity, life history and management of the anadromous fish of the western Canadian Arctic. Unpublished manuscript. Fisheries and Oceans Canada, Winnipeg, MB. 77 p.

- Rhydderch, J.G. 2001. Population structure and microphylogeographic patterns of Dolly Varden (*Salvelinus malma*) along the Yukon North Slope. M.Sc. Thesis, University of Guelph, Guelph, ON. v + 128 p.
- Sandstrom, S. 1995. The effect of over-wintering site temperature on energy allocation and life history characteristics of anadromous female Dolly Varden char (*Salvelinus malma*) from the Yukon and Northwest Territory North Slope, Canada. M.Sc. Thesis, University of Manitoba, Winnipeg, MB. xii + 161 p.
- Sandstrom, S.J., and Harwood, L.A. 2002. Studies of anadromous Dolly Varden (*Salvelinus malma*) (W.) of the Big Fish River, NT, Canada 1972-1994. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2603: vi + 31 p.
- Sandstrom, S., Reist, J., and Carder, G. 1994. Summarization of biological data for Dolly Varden char (*Salvelinus malma*) (Walbaum) from the northwestern Northwest Territories and Yukon North Slope, 1980 to 1994. Fisheries and Oceans Canada, Winnipeg, MB, 7 volumes. [Available from Eric Marshall Aquatic Research Library, 501 University Crescent, Winnipeg, MB R3T 2N6].
- Sandstrom, S.J., Lemieux, R.J., and Reist, J.D. 1997. Enumeration and biological data from the upstream migration of Dolly Varden charr (*Salvelinus malma*) (W.), from the Babbage River, Yukon North Slope, 1990 to 1992. Canadian Data Report of Fisheries and Aquatic Sciences 1018: iv + 132 p.
- Sandstrom, S., Harwood, L., and Howland, K. 2009. Status of anadromous Dolly Varden char (*Salvelinus malma*) of the Rat River, Northwest Territories, as assessed through mark-recapture and live-sampling at the spawning and over-wintering site (1995-2007). Canadian Technical Report of Fisheries and Aquatic Sciences 2842: vi + 75 p..
- Savvaitova, K.A. 1960. Dwarf males of the genus *Salvelinus* (Salmonidae). Dokl. Akad. Nauk. SSSR 135: 217-220.
- Savvaitova, K.A. 1973. Ecology and systematics of freshwater chars of the genus *Salvelinus* (Nilsson) from some bodies of water in Kamchatka. Journal of Ichthyology 13: 58-68.
- Sawatzky, C.D., Michalak, D., Reist, J.D., Carmichael, T.J., Mandrak, N.E., and Heuring, L.G. 2007. Distributions of freshwater and anadromous fishes from the mainland Northwest Territories, Canada. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2793: xiv + 239 p.
- Schmidt, A., and Robards, S.F. 1976. Interspecific relationships for space and food between Dolly Varden and introduced rearing coho salmon in a landlocked lake. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Performance Report, Project F-9-8, 17: 32-53.
- Schutz, D.C., and Northcote, T.G. 1972. An experimental study of feeding behaviour and interaction of coastal cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*). Journal of the Fisheries Research Board of Canada 29: 555-565.
- Stein, J.N., Jessop, C.S., Porter, T.R., and Chang-Kue, K.T.J. 1973a. Fish resources of the Mackenzie River Valley, Interim Report II. Canada Task Force on Northern Oil Development, Environmental-Social Committee Northern Pipelines Report 73-2: 260 p.

- Stein, J.N., Jessop, C.S., Porter, T.R., and Chang-Kue, K.T.J. 1973b. An evaluation of the fish resources of the Mackenzie River Valley as related to pipeline development. Volume I. Canada Task Force on Northern Oil Development, Environmental-Social Committee Northern Pipelines Report 73-1: 121 p.
- Stephenson, S.A. 1999. Big Fish River, Cache Creek char enumeration project – 1988. Unpublished report, Department of Fisheries and Oceans, Central and Arctic Region, Inuvik, NT. 16 p.
- Stephenson, S.A. 2003. Local and scientific observations of Dolly Varden (*Salvelinus malma*) (W.) in the Big Fish River, Northwest Territories, Canada: 1995-2002. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2644: v + 20 p.
- Stewart, D.B., Mochnacz, N.J., Reist, J.D., Carmichael, T.J., and Sawatzky, C.D. 2010. Fish life history and habitat use in the Northwest Territories: Dolly Varden (*Salvelinus malma*). Canadian Manuscript Report of Fisheries and Aquatic Sciences 2915: vi + 63 p.
- Wrona, F.J., Prowse, T.D., and Reist, J.D. 2005. Freshwater ecosystems and fisheries. *In Arctic Climate Impact Assessment (ACIA). Edited by C. Symon, L. Arris, and B. Heal.* Cambridge University Press, Cambridge, pp. 353-452.
- Wydoski, R.S., and Whitney, R.R. 2003. Inland fishes of Washington, second edition. American Fisheries Society, Bethesda, MD in association with University of Washington Press, Seattle. xiii + 322 p.
- Yoshihara, H.T. 1973. Monitoring and evaluation of Arctic waters with emphasis on the North Slope drainages, A: Some life history aspects of the Arctic char. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Progress Report, Project F-9-5, Study G-III-A, 14: 1-63.
- Yukon Department of Environment. 2000. Unpublished data. Fish sampling (1999 & 2000) of Bonnet Plume River and associated lakes and tributaries. [Not seen; cited in Anderton 2006].
- Yukon Department of Environment. 2004. Fisheries investigations in Tombstone Park, Yukon. Draft interim report on southern portion field work, August 25-28, 2004. Fisheries Section, Department of Environment, Yukon Territorial Government. [Not seen; cited in Anderton 2006].