

Fish life history and habitat use in the Northwest Territories: Dolly Varden (*Salvelinus malma*)

D.B. Stewart, N.J. Mochnacz, J.D. Reist,
T.J. Carmichael, and C.D. Sawatzky

Central and Arctic Region
Fisheries and Oceans Canada
Winnipeg, MB R3T 2N6

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FISH LIFE HISTORY AND HABITAT USE IN THE NORTHWEST
TERRITORIES: DOLLY VARDEN (*Salvelinus malma*)

by

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ABSTRACT

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*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2915: vi + 63 p.

Northern-form Dolly Varden occur west of the Mackenzie River Valley from the Gayna River north to the coast and then west along the North Slope. These fish require cold, clean water and follow a stream-resident, riverine, or anadromous life history. Most stream-resident fish are isolated from the sea. Riverine fish are mostly residual males that mature early and remain in fresh water despite having access to the sea. Most fish with access to the sea undergo smoltification and undertake marine feeding sojourns during the summer. Differences in habitat use by these life-history types and in the seasonal requirements of eggs, fry, juveniles, and adults are summarized. All life histories and life stages are closely associated with discharging groundwater in small streams. These groundwater springs maintain suitable incubation and rearing conditions through the winter, and prevent small areas of streams from freezing, thereby providing overwintering habitat. To support the assessment, avoidance and mitigation of environmental impacts in the Mackenzie Valley, the potential impacts of development activities and climate change on survival of the species are reviewed. Northern populations have narrow habitat requirements for spawning, rearing, and overwintering life stages which make them vulnerable to extirpation by habitat fragmentation and disruption. Their extensive marine migrations and predictable seasonal concentration during freshwater migrations and at wintering areas makes the anadromous fish particularly vulnerable to overharvesting.

Key words: distribution; habitat requirements; seasonal movements; reproduction; life cycle; Mackenzie watershed; hydrological integrity; Salmonidae; Yukon; Alaska; Beaufort Sea.

RÉSUMÉ

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*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2915: vi + 63 p.

On retrouve la forme nordique du Dolly Varden à l'ouest de la vallée du Mackenzie, depuis la rivière Gayna au nord jusqu'à la côte, puis à l'ouest le long du versant nord. Ces poissons requièrent des eaux froides et propres, et suivent un cycle biologique caractéristique des populations résidentes en ruisseaux, fluviales ou anadromes. La plupart des poissons résidents en ruisseaux sont isolés de la mer. Les poissons fluviaux sont surtout des mâles résiduels qui parviennent rapidement à maturité et restent en eau douce malgré leur accès à la mer. La plupart des poissons qui ont accès à la mer subissent une smoltification et entreprennent des séjours d'alimentation marine durant l'été. Nous résumons ici les différences dans l'utilisation des habitats selon ces types de cycles biologiques et les différences dans les besoins saisonniers des oeufs, des alevins, des juvéniles et des adultes. Tous les cycles biologiques et les étapes du cycle de vie sont étroitement associés à l'émergence de l'eau souterraine dans les petits cours d'eau. Ces sources d'eau souterraine maintiennent de bonnes conditions d'incubation et d'alevinage durant l'hiver et empêchent les petites zones des cours d'eau de geler, ce qui fournit une aire de concentration hivernale. Pour appuyer l'évaluation, l'évitement et l'atténuation des impacts environnementaux dans la vallée du Mackenzie, nous examinons les impacts potentiels des activités de développement et du changement climatique sur la survie des espèces. Les populations du Nord ont des exigences strictes en matière des étapes du cycle de vie que représentent la fraie, l'alevinage et l'hivernage, ce qui les rend vulnérables à la disparition en raison de la fragmentation et de la perturbation des habitats. Leur grande migration marine et leur concentration saisonnière prévisible lors de la migration en eau douce et aux aires d'hivernage font en sorte que les poissons anadromes sont particulièrement vulnérables à la surpêche.

Mots clés : répartition; exigences en matière d'habitat; déplacements saisonniers; reproduction; cycle biologique; bassin versant du Mackenzie; intégrité hydrologique; salmonidés; Yukon; Alaska; mer de Beaufort.

1.0 INTRODUCTION

Renewed interest in natural gas pipeline development along the Mackenzie Valley has raised the prospect that fish species in the watershed may be impacted by changes to their habitat. The proposed pipeline would extend from near the Beaufort Sea coast to markets in the south (<http://www.mackenziegasproject.com/>). Fishes in the Mackenzie River depend upon the integrity of their aquatic habitats, so it is important to identify knowledge that can be used to assess potential impacts of this development proposal and others, and to facilitate efforts to avoid and mitigate these impacts.

This report reviews knowledge of the northern form of Dolly Varden, *Salvelinus malma* (Walbaum in Artedi, 1792). These fish occur in the northwest corner of the Northwest Territories (NT), where they have historically supported important subsistence fisheries. They also inhabit the Yukon's Peel River watershed and rivers along the Yukon North Slope and in Alaska north of the Alaska Range (Lee et al. 1980) (Figure 1). The nomenclature of fish in these areas is somewhat confused, as they were often referred to in earlier literature as the "western form of Arctic Char, *Salvelinus alpinus* (Linnaeus, 1758)" (e.g., McPhail 1961; Jessop et al. 1973; McCart 1980).

Since 1980, taxonomic revisions have clarified the specific identity of fish belonging to the Genus *Salvelinus* in western North America (Morrow 1980; Reist et al. 1997, 2002; Sawatzky et al. 2007; Reist and Sawatzky 2010). Within the Northwest Territories and Yukon, the Mackenzie and Gayna rivers form approximate distributional limits for the three species that have been confused with one another. Most fish east of the Mackenzie River are now considered to be Arctic Char (*S. alpinus*), while west of the Mackenzie River those south of the Gayna River are mostly Bull Trout (*S. confluentus*) and north of the Gayna River mostly Dolly Varden (*S. malma*). The only confirmed occurrence of sympatric populations of Dolly Varden and Bull Trout is in the Gayna River (Mochnacz et al. 2009). Because of these revisions, species nomenclature used in the original reports often does not correspond to that used in this report. Consequently, many of the cited reports discuss "Arctic char" or "*Salvelinus alpinus*" that are now considered Dolly Varden. As well, some reports that discuss "Dolly Varden" south of the Great Bear River have not been cited as these fish are likely Bull Trout (Reist et al. 2002).

Information is provided on the distribution, habitat use during the various stages of life history, and threats posed to northern-form Dolly Varden and its habitat by development activities. This information was compiled to assist developers, habitat managers, and researchers. Where gaps in knowledge of Dolly Varden in the Northwest Territories were identified, supplementary information is included, where possible, from other regions; information on southern-form Dolly Varden has been identified as such

since taxonomic differences suggest that its applicability to the northern form may be limited. Similar reports have been prepared for other fishes that inhabit the Mackenzie River watershed.

1.1 TAXONOMIC UNITS

Two subspecies of Dolly Varden have been recognized in coastal North America (Behnke 1980; Reist 2001). The northern form, *S. malma malma*, occurs in the Northwest Territories, in the Yukon's Peel River watershed, along the Yukon North Slope, and in Alaska north of the Alaska Range (Figure 1). Northern-form Dolly Varden populations in Beaufort Sea drainages are separated from those in western Alaska by a 500 km gap in distribution (Rhydderch 2001). This isolation of the Beaufort Sea populations suggests that they should be treated as a distinct evolutionary unit. The southern form, *S. m. lordi*, occurs south of the Alaska Range in Alaska, in the extreme southwest of the Yukon, and along the Pacific coast south to Washington (Behnke 1980; Reist 2001). Additional forms may be present in the interior of the Yukon and Alaska, and a number of subspecies have been recognized on the western side of the Pacific Ocean, south to the Sea of Japan. The phylogenetic relationships among these *S. malma* subspecies, and with *S. alpinus* and *S. confluentus*, are still being resolved (Grewe et al. 1990; Crane et al. 1994, 2004; Phillips et al. 1995, 1999, 2002; DeCicco and Reist 1999; Brunner et al. 2001; Osinov 2001, 2002; Taylor et al. 2001; Redenbach and Taylor 2002; Westrich et al. 2002; Kowalchuk et al. 2010).

Numerous genetically distinct stocks of Dolly Varden occur along the Arctic coast of Canada and Alaska, often organized by river (Reist 1989; Rhydderch 2001; Everett et al. 1997). Dolly Varden stocks in the Rat and Big Fish rivers of the Northwest Territories and the Babbage and Firth rivers of the Yukon are genetically distinct from one another. Within the Firth River system, there is some genetic variation between the anadromous populations that spawn in the upper Firth River and those in Joe Creek, but not enough to consider them distinct stocks. Isolated stream-resident fish do not always belong to the same genetic stock as the anadromous fish that live downstream in the same basin (Reist 1989; Everett et al. 1997, 1998).

There is little genetic evidence of between-river straying, but tagging evidence and other life-history observations show that it does occur between some systems along the North Slope (Glova and McCart 1974; Craig and McCart 1976; McCart 1980). In the Sagavanirktok River drainage of Alaska, the mature overwintering fish originated from the river, whereas 10% of the immature fish were from the Canning River and 4% from the Anaktuvuk River (Crane et al. 2005). Straying between the Big Fish and Babbage river systems appears to be rare (Sandstrom 1995; DFO 2001; Sandstrom and Harwood 2002). Dolly Varden tagged at the Big Fish River between 1984 and 1994 (N = 2,050)

have only been recaptured in the Big Fish River and by mixed-stock coastal fisheries along the Yukon North Slope (Sandstrom and Harwood 2002).

This genetic structuring has important implications for the management and rehabilitation of these stocks. An impacted stock must rely primarily on the genetic and reproductive potential of the survivors, rather than on immigration from other systems.

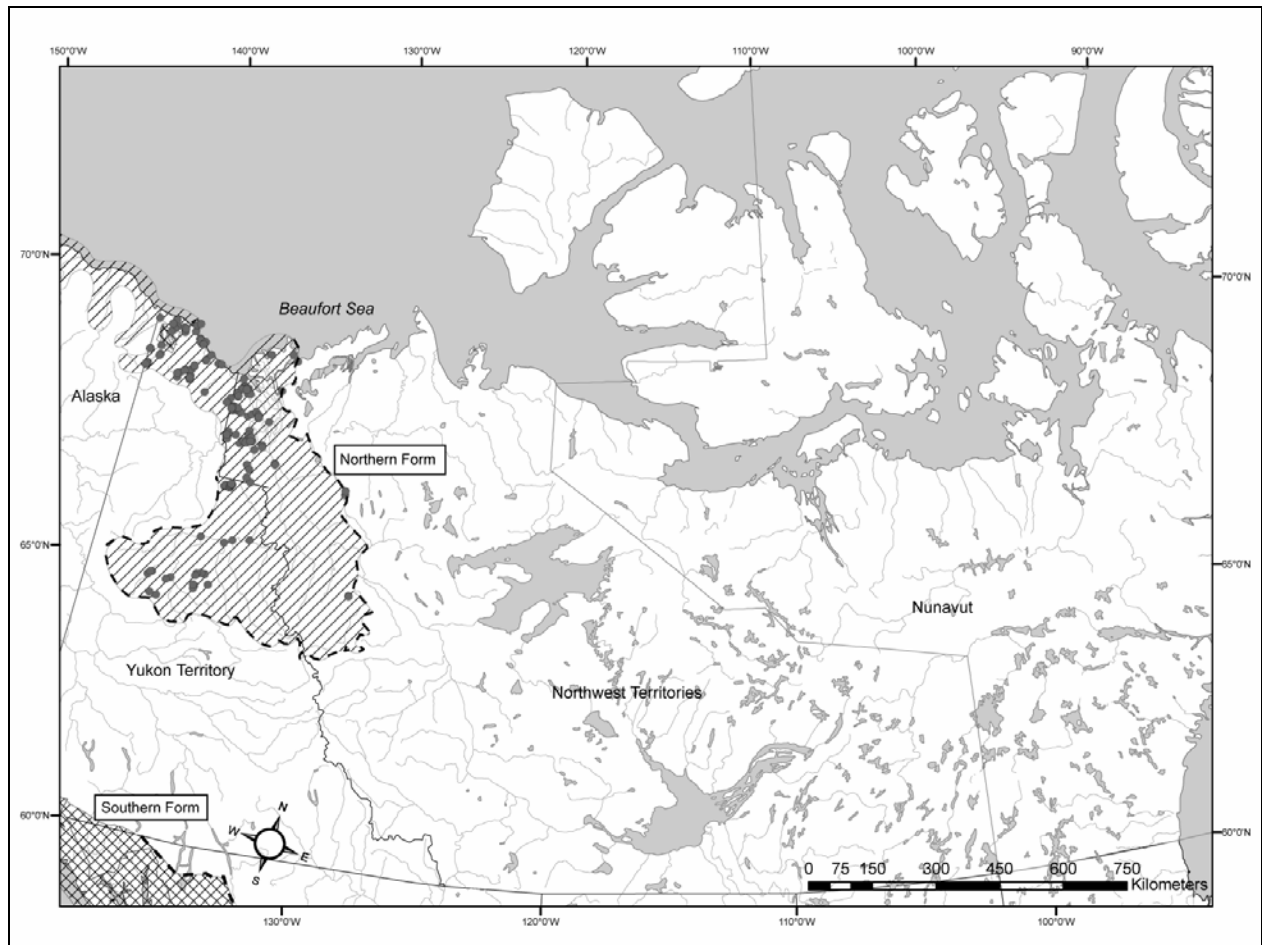


Figure 1. Generalized distribution of northern Dolly Varden (single line hachures) in northwestern Arctic Canada (after Sawatzky et al. 2007). Points indicate confirmed locations for Dolly Varden, however, interior points in the Peel River basin (YT) may represent an interior form rather than the northern form. Dashed boundaries indicate presumed (but unconfirmed) extent of distribution. Distribution of southern Dolly Varden (cross-hachuring) is shown for northern British Columbia. Note that southern Dolly Varden do not occur in drainages east of the continental divide, nor is this taxon present in the southern YT (Haas and McPhail 1991).

1.2 DISTRIBUTION

Within the Northwest Territories, northern-form Dolly Varden inhabit the Gayna, Peel, Rat, and Big Fish river systems (Mann and Tsui 1977; Reist et al. 2002; Mochnacz and Reist 2007; Sawatzky et al. 2007). This is the area where the Taiga Plains, Taiga Cordillera, and Southern Arctic ecozones meet (Marshall and Schut 1999). Within Canada they also occur in the Babbage, Firth, and Fish rivers of the Yukon North Slope (Sandstrom 1995; Sandstrom et al. 1997). Little is known of their distribution or habitat use in the Gayna, Peel and Fish rivers, and the upstream extent of their distribution in the Mackenzie River watershed is uncertain (Reist et al. 2002). These fish have not been reported from Nunavut but may be present in some rivers draining into Coronation Gulf (J.D. Reist, DFO Winnipeg, unpubl. data). They have been introduced successfully into Chester Lake, Alberta (Nelson and Paetz 1992).

Northern-form Dolly Varden are also found in North America along the North Slope of Alaska, in the Colville, Sagavanirktok, Shaviovik, Canning, Hulahula, Aichilik, Egaksrak, Kongakut, and Clarence river systems (McCart 1980; Craig 1984); and in coastal river systems of western Alaska south to the Alaskan panhandle (Behnke 1980), although DeCicco and Reist (1999) have suggested that these latter fish may constitute an intermediate "Bering Sea form". The limits of their distribution in Alaska and Asia remain a matter of debate.

Fish in these areas spawn and overwinter in freshwater streams, typically in upland reaches influenced by groundwater inflow. Given the opportunity, older juveniles and adults may enter brackish and marine coastal waters to feed during the summer. The overall distribution of northern-form Dolly Varden likely reflects their ability to colonize marginal, recently deglaciated streams. Anadromous southern-form Dolly Varden were typically the first salmonids to colonize recently deglaciated streams in southeastern Alaska (Milner and Bailey 1989; Milner et al. 2000). Juvenile Dolly Varden were dominant in the younger streams, while juvenile Coho Salmon (*Oncorhynchus kisutch*) were more abundant in older streams that offered more pool habitat.

The Peel, Rat, Big Fish, and Firth river systems span jurisdictional boundaries, complicating stock management. The Peel, Rat, and Big Fish rivers drain from the Yukon via the Northwest Territories into the Mackenzie River. Within the Peel River system, Dolly Varden have been reported from the mainstem, Stony Creek, and the Vittrekwa River in the Northwest Territories and from the mainstem and the Ogilvie, Blackstone, Hart, Bonnet Plume, Snake, Wind, and Vittrekwa rivers in the Yukon, where they may also occur in a small unnamed lake (64°50'N, 138°23'W) (Elson 1974; Mann and Tsui 1977; Reist et al. 2002; Anderton 2006; Millar 2006). In the Rat River system, Dolly Varden occur in the mainstem and in its Fish Creek tributary (67°42'34"N, 136°16'8"W), which extends to the Northwest Territories/Yukon Territory border. In the

Big Fish River these fish occur in the mainstem and in its Little Fish Creek tributary (68°32'59"N, 136°15'9"W). This creek has been incorrectly referred to in much of the scientific literature as "Cache Creek", which is actually a smaller stream closer to the river mouth. The main overwintering area on Little Fish Creek is situated near the territorial border at an elevation of 380 m above sea level (Sandstrom 1995). The Firth River drains from Alaska via the Yukon into the Beaufort Sea. The Babbage and Gayna river systems are situated within the Northwest Territories, and are tributaries of the Mackenzie River. Management of Dolly Varden stocks is further complicated by mixing of anadromous fish from these and other stocks in coastal waters, where they may be vulnerable to harvest by various multi-stock fisheries (Craig and McCart 1976; McCart 1980; Craig 1989; DFO 2001, 2003a-c).

Flow in the streams occupied by northern-form Dolly Varden in northern Canada and Alaska is derived from two main sources: surface runoff and perennial springs (Craig and McCart 1974; Glova and McCart 1974). The surface runoff is seasonal. It peaks with snowmelt runoff in the spring, typically mid-May through late June, and then periodically through the summer in response to heavy rains. During the spring flood, some scouring of the streambeds, shifting of substrates, and undercutting of banks occurs. Willows and other vegetation may be uprooted and carried downstream. The silt load varies in response to discharge and is heaviest during the spring flood when visibilities are reduced to less than 2.5 cm. Turbidity and suspended sediment levels decline as surface runoff declines in late summer, and the bottom can be seen at depths of 2 m or more. Mountain streams in the area flow throughout their length for only 4 or 5 months of the year.

When surface runoff ceases in about mid-October, the only flow is provided by isolated groundwater sources (Craig and McCart 1974). These inflows create small winter "oases" in an otherwise frozen landscape, wherein Dolly Varden and their eggs are able to survive the winter in the company of other species. Stream banks in these areas are often overgrown with vegetation and the stream bed may be covered with a heavy growth of moss or algae. Most of these areas are fed by **karst**-type groundwater that is 0 to 5°C, with moderate ion concentrations (conductivity 120 to 350 µmhos/cm at 25°C) (van Everdingen 1973; Craig and McCart 1974; Mutch and McCart 1974). Oxygen levels in the various inflows range from 2.6 to 14.5 mg/L, suggesting that some aeration occurs, possibly in subsurface channels that are not completely filled with water. Water entering the Firth River has more mineralization (conductivity 446 to 540 µmhos/cm at 25°C) (Craig and McCart 1974), as does that entering the Fish Creek area of the Rat River (411 µmhos/cm), and the Woods Creek Falls main spring on the Babbage River (1,372 µmhos/cm) (Sandstrom and Chetkiewicz 1996). Much warmer water is released by the thermal springs on the Sadlerochit (13°C) and Big Fish (8-16°C) river systems (Clark et al. 2001; N.J. Mochnacz, unpublished data). Water entering the Big Fish River system at the Fish Hole on Little Fish Creek is also heavily mineralized

(conductivity up to 4,800 $\mu\text{mhos/cm}$ at 25°C), and oxygen poor (0.2 mg/L) (van Everdingen 1973; Craig and McCart 1974; McCart and Bain 1974; Mutch and McCart 1974; Sandstrom and Chetkiewicz 1996). The higher temperature and dissolved solids content indicate that the water is being discharged from a deeper (warmer) and longer (slower) flow system. This water is diluted and oxygenated as it flows downstream. The pH of these groundwater inflows is mildly basic (7.6 to 8.8) (Craig and McCart 1974; Sandstrom and Chetkiewicz 1996).

In winter, areas of *aufeis* typically form below the springs (Yoshihara 1973; Craig and McCart 1974; Sandstrom 1995; Sandstrom et al. 2001). These areas of thick layered ice form where the warm spring water is no longer able to follow the river bed and must flow out over the ice surface, where it freezes causing large areas of thick ice to buildup.

The area of habitat available to Dolly Varden at each of the spring-fed overwintering sites will vary from year to year in response to the severity of the winter. During severe winters, overwintering mortality rate may increase based on habitat availability (Sandstrom and Chetkiewicz 1996). The reach of open water below a particular spring will depend upon the volume and temperature of the discharging groundwater, the flow gradient, and the surface exposure of the water to the elements. Measured inflow rates may be stable over the summer (Craig and McCart 1974) but their seasonal and inter-annual stability is unknown.

Anadromous northern-form Dolly Varden are widely distributed in coastal waters of the Beaufort Sea coast during the summer (Craig and McCart 1976). During spring breakup, melting and freshwater runoff create a band of low salinity (10 to 25 ppt), relatively warm (5 to 11°C) water along the coast (Craig 1984; Carmack and Macdonald 2002). This brackish band resists mixing with high salinity (27 to 32 ppt), cold (-1 to 3°C) marine waters of the Beaufort Sea, and persists throughout most of the open water season. It varies in width and depth in response to freshwater inputs to coastal waters, nearshore currents, prevailing winds, and topographical features. In areas influenced by the discharge of coastal rivers, a brackish plume of surface water may extend 20 to 25 km offshore. The brackish water serves as a 750 km corridor along the shore for coastal movements by anadromous Dolly Varden that disperse parallel to the coastline. Continuous brackish corridors, such as these, are unusual outside Arctic coastal waters that receive very large inputs of fresh water from both ice melt and runoff; elsewhere runoff simply forms a series of disjunct estuaries. In the fall, the nearshore waters of the Beaufort Sea freeze solid to a depth of 2 m and the estuarine band is absent.

2.0 LIFE HISTORY TYPES

Dolly Varden exhibit both **non-anadromous** and **anadromous** life history types in response to the local environmental conditions and possibly genetics. It is not uncommon for a river system to support more than one life history type (Armstrong and Morrow 1980; McCart 1980; Babaluk and Reist 1996; Sawatzky and Reist, in prep.). Most non-anadromous Dolly Varden are prevented from undertaking seasonal migrations into coastal waters by impassable barriers that confine them to lakes (**lacustrine—isolated**) or streams (**stream-resident—isolated**). Alternatively, distance from marine environments may also result in local Dolly Varden populations being isolated. Some non-anadromous fish (**riverine—residual**) have access to the sea but remain in fresh water. These latter fish are typically males that follow an alternative reproductive strategy, whereby they mature earlier and at a smaller size than their anadromous counterparts. They participate in spawning with anadromous pairs following a ‘sneaker’ reproductive strategy.

Table 1. Habitat use by northern Dolly Varden populations with different life history types.

HABITAT	POPULATION		
	NON-ANADROMOUS		ANADROMOUS
	Stream-resident (isolated)	Riverine (residual)	
Spring-fed reaches of tributary streams	• Year-round use by all life history stages for all activities. • Impassable barriers (e.g., waterfalls) prevent access to and from the sea. • Geographic distance from marine environments may result in isolation from downstream anadromous populations.	• Spawning and rearing habitat. • Feeding habitat primarily for fry, but some by juveniles and adults. • Migratory corridor for juveniles and adults. • Overwintering habitat for all life history stages. • Residuals are typically small, early-maturing males.	• Spawning and rearing habitat. • Feeding habitat primarily for fry, but some by juveniles and adults. • Migratory corridors for juveniles and adults. • Overwintering habitat for all life history stages.
Rivers	• Migration corridors and feeding habitat for juveniles and adults.	• Migration corridors and feeding habitat for juveniles and adults.	• Migration corridors and feeding habitat for juveniles and adults.
Brackish or marine coastal waters			• Migration corridors and feeding habitat for juveniles and adults. • Rearing habitat for fish as young as age 1, but typically age 3 or older.

Most adults and older juveniles with access to the sea migrate into productive coastal brackish and marine habitats during the summer to feed (anadromous). To do this, they must make two physiological transitions each year, one from fresh water to marine conditions during out-migration in early summer, and another from marine to fresh water conditions during in-migration in autumn. Anadromous fish are larger than non-anadromous fish of the same age and tend to mature later in life. **Fry** of all life history types are reared in fresh water, where spawning occurs and all life stages overwinter.

Life history and habitat parameters used in the discussions that follow are defined in Appendix 1. Stream habitat requirements are summarized in Appendix 2.

2.1 NON-ANADROMOUS

2.1.1 *Lacustrine*

Lake-resident populations of Dolly Varden have not been reported from the Northwest Territories and appear to be rare for the northern form of the species. Lake-resident populations of the genus *Salvelinus* have been found in the Yukon's Firth River and Alaska's Sagavanirktok River watersheds, but these fish are relict Arctic Char (McCart et al. 1972; Reist et al. 1997). The specific identity of fish in a small, deep upland lake (64°50'N, 138°23'W) near the Blackstone River, Yukon, that were originally identified as Arctic Char (Mann and Tsui 1977) has not been confirmed.

2.1.2 *Stream-resident (isolated)*

Isolated stream-resident populations remain in freshwater streams year-round and sometimes spawn and overwinter within a 1.5 km long reach in spring-fed creeks (McCart 1980). In the Northwest Territories, fish caught above the waterfalls on Little Fish Creek belong to an isolated stream-resident population (McCart and Bain 1974), as do those in the Gayna River which are situated upstream of a 15 m waterfall (Mochnacz and Reist 2007; N. Mochnacz, pers. obs.).

Isolated stream-resident populations also occur above a waterfall in the mainstem of the Babbage River, Yukon (68°38'N, 139°21'W) (Bain 1974; Gillman et al. 1985; Babaluk and Reist 1996), and in the Blackstone River (64°57'N, 138°18'N; Mann and Tsui 1977), and Hart River tributaries of the Peel River, upstream of Aberdeen Canyon which is impassable to upstream fish migration (Anderton 2006). The Babbage and Blackstone populations are associated with groundwater inflow. The stream-resident Babbage River population appears to be genetically distinct from the anadromous and riverine (residual) Dolly Varden found downstream (Reist 1989). Isolated stream-

resident populations also occur along the Alaskan North Slope in the Canning (McCart and Craig 1973) and Sadlerochit (Craig 1977b) rivers.

2.1.3 Riverine (residual)

Non-anadromous riverine Dolly Varden occur in the Northwest Territories in the Rat (S. Stephenson, DFO Winnipeg, pers. comm. 2008) and Big Fish River systems (MacDonell 1987; Reist 1989). They are also present in the Yukon Territory in the Babbage (Bain 1974; Babaluk and Reist 1996), Firth (Glova and McCart 1974; Reist 1989; Babaluk and Reist 1996) and Vittrekwa rivers (Millar 2006); and in rivers in Alaska (McCart et al. 1972; Craig 1977a,c, 1984; McCart 1980). Despite having access to the sea, these fish remain in fresh water where they spawn and overwinter with the anadromous fish in areas moderated by groundwater inflow. Most of the residual, riverine fish are males that mature early and at a smaller size than their anadromous counterparts. These males are sneak spawners that participate in reproduction with anadromous pairs. In 1987, residual males comprised about 1.5% of all Dolly Varden examined from the Big Fish River system (MacDonell 1987). The actual proportion of residual fish in the population may be much greater, since these fish shelter under bank overhangs and are under-represented in seine hauls such as were used for part of this study (J. D. Reist, unpubl. data).

The proportion of small residual males in a population may be a direct response to food availability and/or foraging efficiency of young juveniles. In Arctic Char, increasing the available food shortens the juvenile stage and increases the proportion of resident (= residual) individuals (Nordeng 1983). Distance from the sea (N. Millar, Yukon Department of the Environment, pers. comm. 2009) and genetics may also play a role in this determination (Sawatzky and Reist, in prep.).

Non-anadromous female Dolly Varden have been captured in the lower Babbage River, Yukon (Bain 1974) and in the Canning (Craig 1977a) and Kavik (Craig 1977c) rivers of Alaska. These fish may have originated from isolated populations upstream and been swept downstream over the falls. Whatever their origins, the occurrence of riverine-residual female Dolly Varden appears to be quite rare.

2.2 ANADROMOUS

Anadromous stocks of Dolly Varden inhabit the Big Fish, Rat, and lower Peel-Vittrekwa river systems of the Northwest Territories (DFO 2001, 2003a; Millar 2006; Sawatzky et al. 2007). The degree of anadromy among Dolly Varden farther up the Peel River system in the Road and Trail rivers is unknown (Elson et al. 1974; S. Stephenson, unpubl. data cited in DFO 2001; Anderton 2006), however, as distance from the sea increases, anadromy becomes less likely. Anadromous stocks of Dolly Varden also

inhabit the Babbage, Firth (including Joe Creek), and Fish rivers of the Yukon (Sandstrom 1995; DFO 2003b,c), and many river systems along the Alaskan North Slope (Armstrong and Morrow 1980).

Adults and smolts begin migrating downstream to feed at sea as soon as the river ice melts in the spring, typically in June or early July (Roguski and Komarek 1971; Yoshihara 1973; Glova and McCart 1974; McCart 1980; DeCicco 1991; Sandstrom 1995; DFO 2001). Timing of these movements can vary by several weeks depending upon weather and sea-ice conditions. Large fish tend to precede the smaller juveniles on out-migrations. During the summer prior to spawning, females in the Firth River may only spend a short time at sea (Glova and McCart 1974), or remain in fresh water (Griffiths et al. 1975; see also Craig and Haldorson 1981). While fish less than 300 mm in FL can be abundant in the deltas of larger rivers during the summer (Yoshihara 1973), they are not common in marine waters (Winslow and Roguski 1970 cited in Griffiths et al. 1975; Kendel et al. 1975; Griffiths et al. 1975, 1977; Craig and McCart 1976).

The time these fish spend feeding at sea depends largely on when river break-up occurs, since the timing of upstream migrations is quite consistent from year to year (Sandstrom 1995). Sometimes, however, winds that move broken ice inshore can impede spring seaward movements by Dolly Varden (DeCicco 1989). The earlier the migration, the more food energy they can accumulate before returning to fresh water to spawn and overwinter. Current-year spawners typically return upstream earlier in the fall than non-spawners (Glova and McCart 1974; Griffiths et al. 1975, 1977; McCart 1980; Reist et al. 2001). These upstream migrations typically peak from mid-August through early September, and most Dolly Varden leave the coast by the end of September (Yoshihara 1972, 1973; Dryden et al. 1973; Stein et al. 1973a,b; Glova and McCart 1974; Jessop et al. 1974; Griffiths et al. 1975, 1977; Jessop and Lilley 1975; McCart 1980; Gillman and Sparling 1985; MacDonell 1987; Bond and Erickson 1989; Sandstrom et al. 1997; DFO 2001). During the main upstream migration into the Firth River, from late August until 21 September, there was little mixing of immature and mature migrants, and few immature migrants were collected on known spawning grounds in the upper Firth (Glova and McCart 1974). Schools of immature migrants were common in large backwaters or in nearshore areas adjacent to spawning sites in the main channel. Sampling was not conducted to determine whether this segregation continued through the winter.

Northern-form Dolly Varden from western Alaska are well adapted to temporary residence in the marine environment (DeCicco 1997). They are capable of, and may routinely undertake, long-distance ocean movements that are not necessarily oriented along coasts. Fish tagged in the Wulik River of northwestern Alaska, for example, travelled through the Bering Strait and were recaptured near Egavik in Norton Sound, at St. Lawrence Island, and in the Anadyr River of Chukotka (DeCicco 1992). The two fish

recaptured in the Anadyr River had likely originated from that stock, visited the Wulik River as juveniles, and then returned to the Anadyr to spawn. One of the fish was captured 670 km upstream from the sea and had travelled 1,690 km in 14 mo; another fish travelled 1,560 km in about 60 d, averaging 26 km/d (DeCicco 1997). These observations demonstrate that northern-form Dolly Varden are capable of using offshore marine environments and of migrating long distances. While spawning fish show strong fidelity to their natal rivers, non-spawning fish do not always overwinter in their natal river (Glova and McCart 1974; Craig and McCart 1976; DeCicco 1989, 1991, 1997).

The extent of offshore movements by anadromous Dolly Varden entering the Beaufort Sea from rivers along the North Slope is unknown. However, tagging studies to date suggest that these fish disperse primarily to the east and west along the coast (Craig 1984). They can undertake coastal migrations of up to 300 km, with net longshore movements of 3 to 6 km per day (Glova and McCart 1974). Fish move between Canadian and Alaskan waters, with some fish from the Babbage and Firth rivers moving as far west as Prudhoe Bay, Alaska. Contributions by non-local stocks to coastal fisheries can be significant (Krueger et al. 1999). Coastal migrations by smolts are probably less extensive than those undertaken by adults (Armstrong and Morrow 1980). During their first marine sojourns, smolts may remain in the river estuary, feeding and making the physiological adjustments necessary for migrations into more saline waters in subsequent summers. The youngest fish caught in the Firth River delta were age 1, in nearby Nunluk Lagoon age 2, and on the seaward side of Nunluk Spit age 4 (Griffiths et al. 1975).

Both large and small fish may be more abundant in nearshore waters earlier in the summer (Underwood et al. 1996). They tend to remain close to shore, usually within 500 m, in freshened warmer waters (McCart 1980; Sandstrom 1995; Jarvella and Thorsteinson 1997). Individuals probably spend less than 10% of their life feeding at sea (Craig 1989).

Nutritional state, combined with physiological triggers (e.g., responses to shortening day length), likely promote return migrations from marine into fresh water. There is no evidence for northern-form Dolly Varden overwintering in brackish or marine environments but this is not surprising, since winter sampling effort in these environments has been very limited (e.g., Craig et al. 1985). The capture of southern-form Dolly Varden in the ocean north of Auke Bay, Alaska in February 1992, suggests that the species is capable of remaining in salt water for longer than one summer (Bernard et al. 1995; also N. Davis and J. Reist, unpublished info.), provided the winter marine conditions are conducive. Sub-zero winter water temperatures and extensive sea-ice formation that increases salinity (Carmack and Macdonald 2002) make overwintering of Dolly Varden unlikely in the Beaufort Sea.

Anadromous Dolly Varden spawn and overwinter with pre-smolt juveniles and residual adults in areas of freshwater streams, where groundwater inflow maintains areas that do not completely freeze to the bottom, throughout the winter (Bain 1974; Glova et al. 1974; McCart 1980; Craig 1989; Sandstrom et al. 2001). As with those used by isolated stream-resident populations, these habitats are shallow and extremely important because the rest of the river freezes to the bottom. The entire population of Dolly Varden (eggs, juveniles, adults and residuals) as well as any other species living in the river, such as Arctic Grayling (*Thymallus arcticus*), spend 6 to 8 mo of the year in this small pool habitat which is either open water or located under the ice (Sandstrom 1995).

3.0 LIFE HISTORY STAGES AND HABITAT USE

While northern-form Dolly Varden populations in Canada and Alaska may comprise genetically distinct populations, their relationships to habitat are likely similar. In contrast, biological differences between the northern and southern forms suggest that information on habitat use should not be applied from one to the other without careful consideration (Reist 1989, 2001).

Five life history stages for Dolly Varden will be discussed: 1) eggs, 2) **alevins** and fry, 3) small juveniles (pre-smolts), 4) large juveniles (smolts), and 5) adults. The first three stages remain in freshwater environments throughout the year for all life history types. The last two remain in fresh water unless they follow an anadromous life history, in which case they may migrate to sea to feed during the summer. Key transitions in the Dolly Varden life history are illustrated schematically (Figure 2), and habitat use data are summarized (Table 2; Appendix 2). Note that the term 'smolt' applies only to fish which undertake anadromy (i.e., smoltification is the process of first-time transitioning from freshwater to anadromous life history).

3.1 EGGS (SPAWNING AND INCUBATION HABITAT)

Northern-form Dolly Varden spawn in reaches of clear upland streams that are fed by groundwater and do not freeze to the bottom in winter (Yoshihara 1973; Glova and McCart 1974; Reist 1989; Sandstrom 1995; Harwood 2001; Mochnacz and Reist 2007). Individuals spawn more than once, but not necessarily every year following maturity (**iteroparous**) (Table 3) (e.g., McCart 1980; Stephenson and Lemieux 1990; Sandstrom 1995). In most stocks they spawn every second or third year, probably because it takes that long to accumulate the necessary energy. In the Sagavanirktok River watershed of Alaska few, perhaps 10%, of the females spawn during consecutive years (Yoshihara 1973). Anadromous fish in the Big Fish River are unusual in that most

mature fish spawn annually following maturity, whereas fish in the Rat River system typically spawn only every second or third year (Sandstrom and Harwood 2002). The energetic advantages of a shorter migration route to and from the sea and earlier access to coastal feeding resources may facilitate annual spawning in the Big Fish River. Annual spawning may also be more common among large, old fish (Harwood 2001). Populations with a higher proportion of resting females may be slower to recover from adverse impacts.

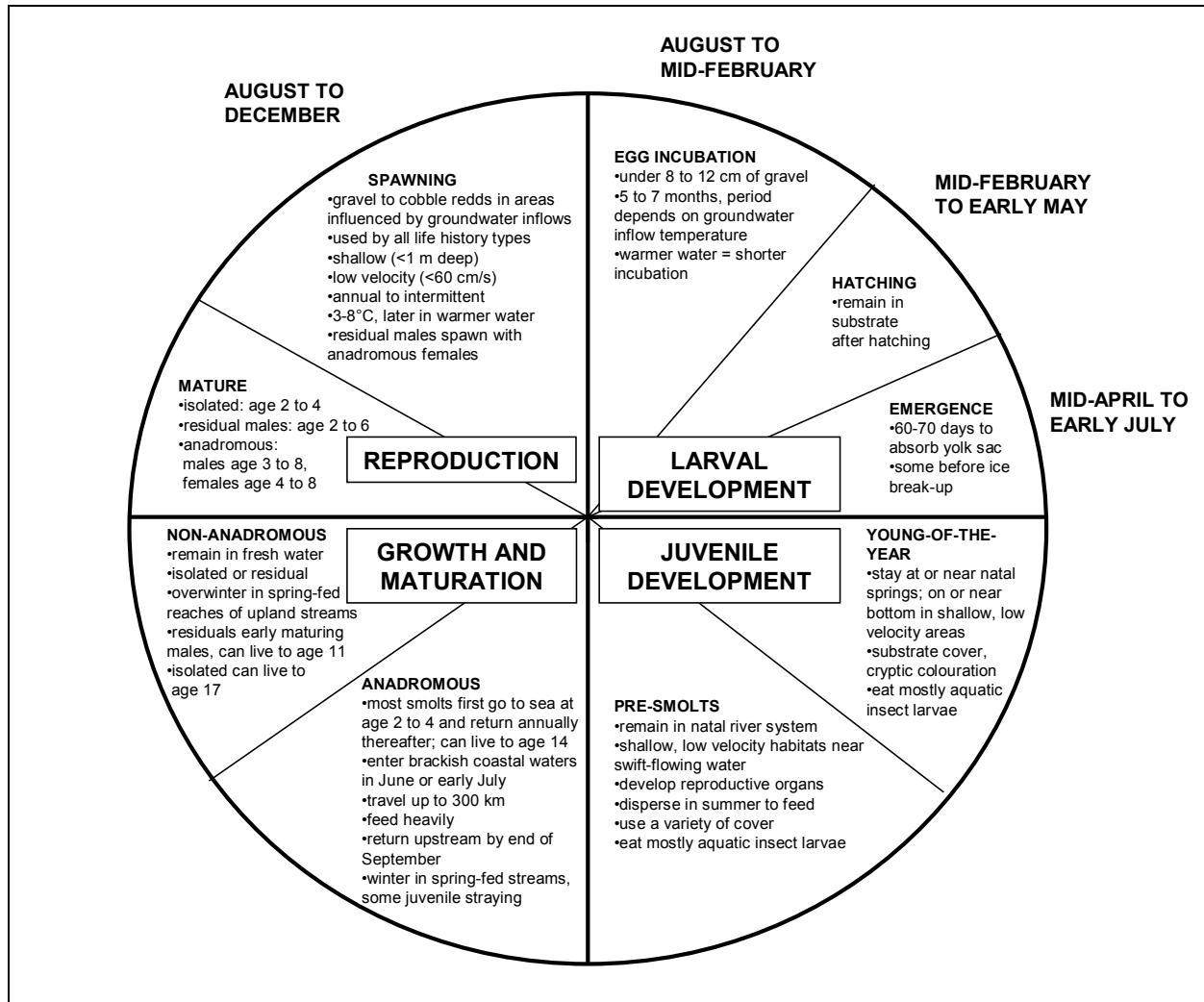


Figure 2. Generic life cycle of Dolly Varden.

Spawning typically takes place from August through to early October (Hatfield et al. 1972; McCart et al. 1972; Stein et al. 1973b; Yoshihara 1972, 1973; Bain 1974; McCart 1980; DFO 2001; Reist et al. 2002; Mochnacz and Reist 2007) but in some systems, can extend into November or early December (McCart and Craig 1973; McCart and Bain 1974; Craig 1977a,b). Most spawning occurs at temperatures between 3 and 8°C (Stein et al. 1973a,b; Glova and McCart 1974; Jessop et al. 1974;). It occurs earlier

Table 2. Observed stream habitat use by Dolly Varden (data from Northwest Territories populations are in bold type; numbers in brackets refer to sources cited below).

HABITAT FEATURES		LIFE STAGE			
		Spawn/egg	Young of the year	Juvenile	Adult
Habitat type		Upland streams in pools and runs associated with discharging groundwater (1, 3, 35)	Upland streams in the vicinity of their natal spring in shallow, quiet water (5, 17, 11, 12, 16, 21)	Overwinter in upland streams in the vicinity of their natal spring (24), disperse throughout streams in summer, smolts summer at sea (16, 21)	Overwinter in upland streams in the vicinity of their natal spring (10), disperse throughout streams in summer, anadromous fish summer at sea (16, 21)
Stream gradient			Mean gradients of up to 15% , but generally captured in step pools (29)	Mean gradients of up to 15% but generally captured in step pools if gradient is high (29)	Upper gradient limits of 15 to 20% (34)
Depth range (m)		1-2 m (3); 0.2-1 (4, 19); mean 0.6 m (35)	0.1-0.4 (11)	0.06-1.2 m (9), <2 m at overwintering areas (10)	<2 m at overwintering areas (10, 31)
Substrate		Fine to coarse gravel (1, 2, 3a, 3b, 35)	Fine to coarse gravel (1, 2, 3a, 3b)	Silt to boulder (9)	Silt to boulder (9)
Cover		8-12 cm of gravel (4)	Cryptic colouration against stream substrate (17)	Ice (24), undercut banks (28)	Ice (12, 24)
Velocity range (cm/s)		30-60 (4, 19); mean 40 (35)		<30 (28)	<60 (17, 32)
Turbidity (NTU)	Range				1-146 during summer in the Beaufort Sea (7a)
	Limits				
Oxygen (mg/L)	Range	5-13 (17, 22, 31)	5-13 (17, 22, 31)	5-13 (17, 22, 31)	5-13 (17, 22, 31)
	Limits				
Temperature (°C)	Range	Spawning: 3-8°C (1, 2, 4, 12, 20, 26, 35); Incubation: 1.5-10°C (10)	Emergence: 1.5°C (12) Summer: 4-6°C (11)	0.5-11°C (7b, 17, 10, 22, 31)	0.5-11°C (7b, 17, 10, 22, 31)
	Limits				Appetite decrease: ≥16°C (33) Thermal mortality: ≥20°C (33) 100% mortality: ≥26°C (33)

Prey items	Primary		Aquatic insect larvae (12, 14, 16, 27)	Pre-smolts: Aquatic insect larvae (1, 5, 12, 14, 17, 27) Smolts: Fish (5, 30)	Anadromous: Fish (5, 12, 27, 30) Non-anadromous: Aquatic and terrestrial insects (5, 12, 27, 30)
	secondary		Amphipods (12)	Pre-smolts: Terrestrial insects (5, 12) Smolts: Aquatic insect larvae (5, 27)	Anadromous: Aquatic and terrestrial insects , amphipods (5, 12, 27, 30) Non-Anadromous: Fish eggs, amphipods, nematodes (5, 12)
Period		Spawning: August through early October (1, 2, 5, 17, 20, 21), November and December in areas fed by warmer springs (22, 23-25) Incubation: 7-9 months (5, 17)	Hatch: mid-February-early May (16) Emerge: mid-April-early July but mostly in May and June (4, 7, 11, 12, 16, 17)	Anadromous Female: 3 to 7 y (21) Male: 2 to 7 y (21) Riverine (residual): Male: 1 to 5 y (21) Stream-resident (isolated): Both sexes: 1 to 3 y (21)	Anadromous Female: 6 to 10 y (21) Male: 5 to 9 y (21) Riverine (residual): Male: 1 to 5 y (21) Stream-resident (isolated): Both sexes: 7 to 9 y (21)
Size/age range (Note: fish are considered to be age 0 until December 31 of the year they are hatched; only otolith ages are reported)		Egg diameter (mm): ripe ova anadromous: mean 4.4, range 4.2-4.9 (5), mean 4.2, range 3.5-4.7 (4), maximum 5.2 (15) ; water hardened eggs: mean 4.8, range 4.4-5.2 (4) Ripe ova riverine residual: Mean 3.6 (14, 18) Ripe ova stream-resident: mean 3.5, range 3.0-3.9 (5) Redds: 1.2 m wide, 3.5 m long (4)	At hatch (mm FL): 15-20 (16) Pre-emergent: 17-32 (4, 5, 12) Emergent: 20-27 (4, 17) Late summer: 34-65 (5, 12, 17)	Anadromous Female: 4 to 8 y (21) Male: 3 to 8 y (21) Riverine (residual): Male: 2 to 6 y (21) Stream-resident (isolated): Both sexes: 2 to 4 y (21)	Anadromous Female: Maximum: 649 mm FL, 1,996 g, age 14 (8); Male: Maximum: 676 mm FL, 2,395 g, age 12 (otolith) (8); Sex unknown: 694 (13); 734 mm (6) Riverine (residual): Male Maximum: 395 mm FL (5), age 11 (12, 14, 18) Stream-resident (isolated): Female: Maximum: 404 mm FL, age 17 (5); Male: Maximum: 547 mm FL, age 16 (otolith) (5).

1 = Stein et al. 1973a,b—Fish Creek on the Rat River system and Little Fish Creek (Fish Hole) on the Big Fish River system, Northwest Territories

2 = Hatfield et al. 1972—Fish Creek on the Rat River system, Northwest Territories

3 = Gillman et al. 1985— 3a = Little Fish Creek (Fish Hole) on the Big Fish River system, Northwest Territories, 3b = Firth River, Yukon

4 = Yoshihara 1973—Lupine River, Alaska

5 = Bain 1974—Babbage River, Yukon

6 = Underwood et al. 1996—nearshore Beaufort Sea, Alaska

- 7 = Craig 1984—a) nearshore Beaufort Sea, Alaska, b) freshwater, Alaska
- 8 = Sandstrom et al. 1997—Babbage River, Yukon
- 9 = Netsch 1975—Yukon River headwaters, Alaska
- 10 = Sandstrom and Chetkiewicz 1996— Fish Creek on the Rat River system, Northwest Territories
- 11 = Craig 1978—Canning River, Alaska
- 12 = Glova and McCart 1974—Firth River, Yukon
- 13 = Harwood 2001—Rat River, Northwest Territories
- 14 = Craig 1977a—Canning River system, Alaska
- 15 = MacDonell 1987—Little Fish Creek (Fish Hole) on the Big Fish River system, Northwest Territories
- 16 = Armstrong and Morrow 1980—northern-form review
- 17 = McCart et al. 1972—Sagavanirktok River, Alaska
- 18 = Craig 1977c—Kavik River, Alaska
- 19 = DeCiccio 1991—Noatak, Wulik, and Kivalina rivers of northwestern Alaska
- 20 = Mochnacz and Reist 2007—Gayna River, NT
- 21 = McCart 1980—northern-form review
- 22 = McCart and Bain 1974—Little Fish Creek (Fish Hole) on the Big Fish River system, Northwest Territories
- 23 = McCart and Craig 1973—Canning River, Alaska
- 24 = Sandstrom et al. 2001— Rat River, Northwest Territories
- 25 = Craig 1977b—Sadlerochit River, Alaska
- 26 = Jessop et al. 1974— Fish Creek on the Rat River system and Little Fish Creek (Fish Hole) on the Big Fish River system, Northwest Territories
- 27 = Jessop et al. 1973— Fish Creek on the Rat River system, Northwest Territories
- 28 = DenBeste and McCart 1984—Sagavanirktok River system, Alaska
- 29 = Bryant et al. 2004—southeast Alaska, southern form
- 30 = Bryan et al. 1973—Babbage and Firth rivers, Yukon
- 31 = West and Wiswar 1984—Huahula River, Alaska
- 32 = Stephenson and Lemieux 1990—Rat River, Northwest Territories
- 33 = Takami et al. 1997—southern-form laboratory study, Japan
- 34 = M. O'Donoghue, Government of the Yukon, pers. comm. 2008—Peel River system, Yukon
- 35 = N. Mochnacz, DFO Winnipeg, unpubl. data.—Rat River, Northwest Territories and Babbage River, Yukon

Table 3. Habitat and life history parameters related to Dolly Varden reproduction, with data from the Northwest Territories in bold font. Numbers in brackets refer to data sources listed below.

PARAMETER	STREAM (data source)
Form of reproduction:	Iteroparous (5, 6)
Age at maturity (y):	Anadromous Female: 5-7 (4, 8-10) ; 4-8 (12-16) Male: 3-7 (4, 8-11) ; 3-8 (12-15) Riverine (residual): Male: 4 (10) , 2-3 (12, 14, 15) Stream-resident (isolated): Female: 6 (17) Male: 8 (17)
Fecundity (eggs/female):	See Table 4
Spawning:	May not occur annually following maturity (4)
Habitat type	Upland streams in pools and runs with groundwater inflow (1, 3, 19)
Builds nest	Gravel redds, 0.3-0.4 m across channel by 0.4-0.5 m down channel (19); 1.5 m across channel by 3.5 m down channel (6)
Temperature (°C)	3-8°C (1-3, 6, 14)
Depth (m)	0.2–1 (6, 7); 1-2 (8); mean 0.6 m (19)
Substrate	Fine gravel (1, 2); gravel (18, 19); gravel and cobble (8)
Current velocity (cm/s)	30-60 (6, 7); mean 40 (19)
Maximum age: (Note: fish are considered to be age 0 until December 31 of the year they are hatched)	Anadromous: Female: 14 (9, 13) , 18 (6) Male: 12 (13) , 14 (6) Riverine (residual): Male: 9 (10) , 10 (12) Stream-resident (isolated): Female: 17 (12) Male: 16 (12)
Age at senescence:	No evidence of senescence

1 = Stein et al. 1973a,b—Fish Creek on the Rat River and Little Fish Creek (Fish Hole) on the Big Fish River, Northwest Territories

2 = Hatfield et al. 1972—Fish Creek tributary of the Rat River, Northwest Territories

3 = Jessop et al. 1974—Fish Creek tributary of the Rat River, Northwest Territories

4 = Stephenson and Lemieux 1990—Rat River, Northwest Territories

5 = Sandstrom 1995—Yukon and Northwest Territories north slopes

6 = Yoshihara 1973—Lupine River, Alaska

7 = DeCiccio 1991—Noatak, Wulik, and Kivalina rivers, northwest Alaska

8 = Gillman and Sparling 1985—Rat River, Northwest Territories

9 = Sparling and Stewart 1986—Big Fish River, Northwest Territories

10 = MacDonell 1987—Big Fish River, Northwest Territories

11 = Sandstrom and Harwood 2002—Big Fish River, Northwest Territories

12 = Bain 1974—Babbage River, Yukon

13 = Sandstrom et al. 1997—Babbage River, Yukon

14 = Glova and McCart 1974—Firth River, Yukon

15 = McCart et al. 1972—Sagavanirktok River, Alaska

16 = DeCiccio 1991—Noatak, Wulik, and Kivalina rivers of northwestern Alaska

17 = Mochnacz and Reist 2007—Gayna River, Northwest Territories

18 = Gillman et al. 1985—Firth River, Yukon

19 = N. Mochnacz, DFO Winnipeg, unpubl. data—Rat River, Northwest territories and Babbage River, Yukon

in the season in areas that receive cold groundwater inflow than in those that receive warm inflow (Glova and McCart 1974; Jessop et al. 1974; Sandstrom and Chetkiewicz 1996). Populations in Fish Creek on the Rat River and in Little Fish Creek on the Big Fish River, for example, both spawned at 4 to 6°C but spawning began a month earlier in Fish Creek, which was fed by a “cold” spring (i.e., late August cf. late September) (Jessop et al. 1974). Early spawning reduces the time these fish spend feeding at sea and their exposure to coastal and delta fisheries (Sandstrom and Chetkiewicz 1996). It may also affect spawning success by exposing the fish and eggs to water level fluctuations caused by August rainfalls.

Some northern-form Dolly Varden in the Wulik River of Alaska spawn in the summer, while others spawn in the fall (DeCicco 1989). Summer and fall spawners may also occur in the Rat River system, although this has not yet been confirmed. Spent anadromous fish have been captured in its Fish Creek tributary in mid-August, and a second group of fish was observed spawning in a separate area of the creek in mid-September (DFO 2001). Fishermen have also observed two or more pulses in the fishery suggesting that there may be more than one group of Dolly Varden using the basin. After spawning, some Dolly Varden from the Rat River population move downstream through the Mackenzie Delta, possibly to overwintering areas (Jessop et al. 1973).

3.1.1 Spawning behaviour

Mature anadromous females are usually the first to arrive on the spawning ground, where they select a suitable site to dig a shallow depression (**redd**) in which to deposit their eggs (Yoshihara 1973; Sandstrom 1995). In some systems they arrive as early as late July (McCart et al. 1972; Bain 1974). The female excavates redds in gravel habitats in areas with slow currents, but may spawn in areas with cobble substrates (McCart 1980; see also southern form descriptions in Needham 1952, Leggett 1980, Kitano and Shimazaki 1995). Pairing with an anadromous male occurs when the location for the redd is selected, or shortly after. The redd and female are defended by the anadromous male until spawning takes place. Fish in Little Fish Creek on the Big Fish River have been observed selecting and defending territories in late August and early September (Gillman et al. 1985). Most of them exhibited bright spawning colouration and secondary sexual characteristics (e.g., kype, humped back).

The mating pair may be shadowed by several residual males that dart in to release milt as the anadromous female releases her eggs (Yoshihara 1973; McCart 1980). Eggs in the redd are then covered with gravel and left to incubate until early spring. The female remains on the redd for several more days to defend it from other females searching for spawning sites; the anadromous male may also remain in the vicinity to spawn with other females. Segregation of spawners and non-spawners has

been observed during the spawning period (Yoshihara 1972, 1973; Glova and McCart 1974).

Spawning habits of isolated northern form populations have not been described. Female southern-form Dolly Varden in a landlocked population in the Tiekell River of Alaska formed a pair bond with the largest courting male, which was generally larger than she (Maekawa et al. 1993). There was a positive relationship between the body size of the courting male and the number of satellite males (0 to 4). The smaller the size of the satellites, the more often they were attacked by the female, which never attacked her pair male. A female spawned in her redd from 1 to 3 times, depending upon whether subordinate males attempted to release sperm. If they did, spawning was suspended and resumed later. This behaviour may be to avoid egg eating by the residual males, rather than to avoid fertilization. Large, dominant males in another landlocked population in south-central Alaska were observed spawning with up to 3 females in one day (Hino et al. 1990). Spawning success by the paired males was 97%, and among satellites varied depending upon their size and number from 14 to 68%.

3.1.2 Spawning habitat

The “Fish Hole” area of Little Fish Creek, where anadromous and residual Dolly Varden spawn in the Big Fish River system, is situated immediately below an impassable 3 m waterfall (Jessop et al. 1974; Gillman and Sparling 1985; Gillman et al. 1985; DFO 2003a; N. Mochnacz, unpubl. data). The spawning area of the creek consists of an alternating series of riffles, pools, and runs that are 1 to 2 m deep and 1 to 5 m across. Bottom substrates and shorelines are fine to coarse gravel (<60 mm diameter), and the banks are steep and 10 to 15 m high. Spring water that flows into this area originates deep in the earth’s crust and can be as warm as 16°C at the orifice above the falls (McCart and Bain 1974; Sandstrom 1995; Clark et al. 2001). The spawning site is located about 2 km downstream from the groundwater discharge area. This is unusual since spawning in other systems, such as the Babbage River, occurs on or very near to the discharge area. This distance separation between the inflow and spawning site is made possible by the warmer water inflow, which may also make the separation necessary for successful spawning. The warm inflow keeps the area from the waterfalls to about 4 km downstream ice-free during the winter.

Spawning in the Rat River occurs in its Fish Creek tributary where the fish spawn in pools and in the runs immediately downstream, over fine gravel (Jessop et al. 1974; DFO 2001; N. Mochnacz, unpubl. data). The creek has many deep pools and is fed by one or more perennial groundwater springs. The springs discharge 4 to 5°C water that maintains sections of open water year-round. As it flows downstream in winter, this water eventually cools and freezes, forming a large field of *aufeis*. During the summer

most, or all, of this ice melts, exposing a gravel plain with shallow, braided flow channels that are used by fish ascending in the fall to overwinter (Sandstrom et al. 2001).

In both the Babbage and Rat rivers, most redds are located at the downstream end of the pool and in the run following the pool (N. Mochnacz, unpubl. data). At least 100 redds have been examined in each river. They are constructed of gravel 16 to 64 mm in diameter, and situated at an average water depth of 0.6 m with an average current of 0.4 m/s. Redds in the Rat River were typically 0.3 m across channel by 0.4 m down channel while those in the Babbage River were a bit larger, 0.4 m by 0.5 m. What appeared to be larger redds, 1.0 m by 2.0 m, were actually clusters of small redds.

Redds in the Lupine River of Alaska were situated in a spring-fed area, immediately upstream of *aufeis* areas and at canyon mouths of the Brooks Range (Yoshihara 1973). The river in this area averaged 3.4 m across and 0.2 m deep, with a flow velocity of 0.3 m/s and water temperature of 4°C. Alkalinity of the water ranged from 140 to 170 ppm and pH from 8.0 to 8.5. The water depth over one redd was 20 cm, and the velocity 0.6 m/s (Yoshihara 1973). The substrate consisted of small gravel with some pea-sized chips and silt. The eggs were located near the centre of the redd, about 10 cm below the surface of the substrate.

In the Yukon, northern-form Dolly Varden spawn in the Ne'edilee Creek tributary of the Vittrekwa River in September (Millar 2006). Spawning has not been confirmed in the springs between the Malcolm and Firth river deltas although eggs and embryos have been found in the stomachs of fish captured in the springs (Glova and McCart 1974).

Spawning is successful below spring inflow with widely different oxygen and ion content. Water upwelling at the main spring orifice into Little Fish Creek (Big Fish River system), contains little dissolved oxygen (<0.2 mg/L) (McCart and Bain 1974; Mutch and McCart 1974; Sandstrom 1995). The conductivity at this site is very high (>3,963 $\mu\text{hos/cm}$ @ 25°C) relative to other overwintering sites on the North Slope such as the Babbage River (>4.6 mg/L O_2 , <306 $\mu\text{hos/cm}$ @ 25°C) that are fed by groundwater upwellings. As it flows downstream, inflow from the Little Fish Creek spring is oxygenated and cools. On 10 May 1973, at 650 m downstream, which is 250 m downstream of the falls, the water was 11°C and contained 8.8 mg/L of dissolved oxygen (82% saturation) (McCart and Bain 1974).

Over 80% of the discharge in the "Fish Hole" area of Little Fish Creek is contributed by groundwater, except during spring runoff (Clark et al. 2001; DFO 2001). While inflow of warm, saline water from deep in the earth's crust is relatively constant, inflow from shallow groundwater sources and surface drainage slows or stops during the winter. These changes expose fish using the area to higher salinity water during the winter.

Little is known about the spawning habitats used by isolated northern form populations. However, their requirements are likely similar to those of the anadromous and residual fish.

3.1.3 Fecundity

Anadromous females are more fecund than their smaller, non-anadromous counterparts (Table 4). Fecundity has been positively correlated with length and weight for mature anadromous females from Fish Hole Creek and isolated females from the upper Babbage River (Bain 1974). The relatively low fecundity of fish in Little Fish Creek tributary of the Big Fish River was due primarily to the small size of spawners within the stock (MacDonell 1987). Southern-form Dolly Varden sampled by Blackett (1973) were smaller and less fecund than the northern form for both anadromous and non-anadromous life history types.

3.1.4 Egg size

The diameter of ripe ova from anadromous females ranges from 3.4 to 5.2 mm (McCart et al. 1972; Yoshihara 1973; Bain 1974; MacDonell 1987); few data are available for isolated (3.0 to 3.9, $n = 2$ Bain 1974; 3.7 to 4.0, $n = 4$, McCart and Craig 1974) or residual females (3.6, $n = 3$) (Craig 1977a,c). Indeed, the latter may be displaced fish from isolated populations upstream (Craig 1977a). Water hardening increases the egg diameter about 14% (i.e., from an average of 4.2 mm Yoshihara 1973).

In the Big Fish and Sagavanirktok River systems, egg size was positively correlated with the fork length of the anadromous female, whereas in the Babbage River it was not (McCart 1980; Sandstrom 1995; Sandstrom and Harwood 2002). Consequently, a 475 mm FL female in the Big Fish River may have 500 fewer eggs than a female the same length from the Babbage River. The higher overwintering temperature in the Big Fish River may require females to produce larger eggs to ensure that fry emerge at an optimal size (Sandstrom 1995). While larger fish are less fecund on a per unit weight basis than smaller fish, the survival rate of smaller eggs produced by smaller fish may be lower. The larger eggs have longer developmental periods and this may represent an adaptation to warmer spring waters of the Little Fish River to ensure emergence at the appropriate time in the spring. Selective removal of the large fish may then have a greater than expected effect on the reproductive potential of the population and on its ability to recover from overharvesting. The effects of selective removal of large females may not be as significant in systems such as the Babbage River, where egg size may be less important to survival.

Table 4. Dolly Varden fecundity.

Location	Sample size	Fork Length (mm)	Fecundity (eggs/female)		Reference
			Mean	Range and/or $\pm$ SD	
ANADROMOUS					
Rat River, Northwest Territories	21		4,221	1,787 – 8,395	Gillman and Sparling 1985
Little Fish Creek, Big Fish River, Northwest Territories	19	Mean = 435	2,186	1,500 – 2,963	MacDonell 1987
Fish Hole Creek, Babbage River, Yukon	27	Range = 355–525	3,468	1,700– 5,100 $\pm$ 936	Bain 1974; ranges taken from Figure 15 in Bain 1974 by McCart 1980
Firth River, Yukon	20	Mean = 530	4,955	$\pm$ 463	Glova and McCart 1974
Sagavanirktok River system, Alaska	49	Mean = 499 Range = 424–630	4,154	2,698–6,326	Yoshihara 1973
	66	Mean = 499 $\pm$ 55	3,670	$\pm$ 114	McCart et al. 1972
Noatak, Wulik, and Kivalina rivers, northwest Alaska	nd	Mean = 557 Range = 478–760	6,218	3,556–10,558	DeCiccio 1991
Kavik River, Alaska	28	Mean = 477 Range = 366–516	3,737	2,140–5,840	Craig 1977c
STREAM-RESIDENT (ISOLATED)					
Upper Babbage River, Yukon	78	Range = 132–251	294	132–605; $\pm$ 119	Bain 1974; ranges taken from Figure 15 in Bain 1974 by McCart 1980
Shublik Spring, Canning River, Alaska	18	Mean = 154.2 $\pm$ 14.6 Range = 117–183	143	84–199; $\pm$ 31.6	McCart and Craig 1973
unnamed spring, Canning River, Alaska	17	Mean = 137.5 $\pm$ 13.0 Range = 121–158	113	42–187; $\pm$ 36.6	McCart and Craig 1973

3.1.5 Incubation

The temperature differential created by cold or warm spring inflow extends through the winter season, affecting egg incubation. In early April, the temperature of water at the main spawning/overwintering area in Fish Creek (1.5°C) was lower than in Little Fish Creek (10°C) or the Babbage River (4°C) (Sandstrom and Chetkiewicz 1996). Differences in spawning timing between isolated stream-resident populations and

anadromous populations are likely a function of average water temperature, rather than other factors.

The period from spawning to emergence varies from 7 to 9 months depending upon water temperature, with eggs of equivalent size in warmer water having a shorter incubation. In the Sagavanirktok River drainage of Alaska, fish in warmer springs spawned later in the season and the young emerged after about 7 months, while those in colder water spawned earlier and young emerged after about 9 months (McCart et al. 1972). Young spawned by anadromous females in Fish Hole Creek did not emerge from the gravel for at least 8 months, and those from non-anadromous females in the upper Babbage River remained in the gravel for at least 7.5 months (Bain 1974).

3.2 ALEVINS AND FRY (REARING HABITAT)

Newly hatched Dolly Varden are 15 to 20 mm long, with a large yolk sac (Armstrong and Morrow 1980). They remain in the gravel of the redd, 8 to 12 cm below the surface, until the yolk sac has been absorbed (Yoshihara 1973). Armstrong and Morrow (1980) estimated that this process took 60 or 70 days in the Sagavanirktok River of Alaska, but Radtke et al. (1996) estimated the time between hatching and first feeding in western Alaska at 41.6 d, and in Russia's Cha'atam River at 52.1 d. Free-swimming alevins emerge from the gravel in mid-April to early July — mostly in May and June (McCart et al. 1972; Yoshihara 1973; Glova and McCart 1974; Craig 1977a, 1978; Armstrong and Morrow 1980; McCart 1980). In Joe Creek, Yukon, they began emerging before spring break-up, at a water temperature of 1.5°C (Glova and McCart 1974). The severity of the winter can alter the time of emergence by at least a month from one year to the next (McCart et al. 1972).

The growth rate of fry increases significantly with the switch to exogenous feeding, increasing in the spring, peaking in summer (July and August) and slowing again in the fall (September) (Radtke et al. 1996). At emergence, fry in the Sagavanirktok River system of Alaska averaged 23.7 mm FL (N = 69, range 20 to 27 mm) (McCart et al. 1972). By September 1st, near the end of their first summer, fry in Section and Accomplishment creeks had grown to a mean length of 53.9 mm (n = 43, range 34 to 65 mm). Growth continues to be slow as long as the fish remain in fresh water.

Fry undertake local movements but typically remain in the vicinity of their natal springs for the first summer (Glova and McCart 1974; Craig 1978; Armstrong and Morrow 1980; McCart 1980). They are found in the highest densities in these habitats, in both summer and winter (McCart et al. 1972; Glova and McCart 1974). Individuals that are swept downstream from the spawning grounds may have to undertake extensive

migrations prior to freeze-up to return to suitable overwintering habitat. The Little Fish Creek tributary of the Big Fish River and the Fish Creek tributary of the Rat River are important rearing areas for young stages of anadromous Dolly Varden in the Northwest Territories (Stein et al. 1973b).

Young-of-the-year stay on the bottom, in the shallow water of stream edges, gravel bars, backwaters, braided-stream channels, river deltas, and small side-channels (McCart et al. 1972; Bain 1974; Glova and McCart 1974; Craig 1978; Armstrong and Morrow 1980; McCart 1980). Their silver grey colour and **parr marks** provide cryptic colouration that disguises them against the stream bottom. In Alaska's Canning River, they were abundant during the growing season throughout the spring channel which ranged in width from 5 to 15 m, depth from 10 to 40 cm, and in water temperature from 4 to 6°C (Craig 1978). Fry of southern-form Dolly Varden in southeast Alaska have been captured in streams with mean gradients of at least 15%, generally in step pools (Bryant et al. 2004). Fry are relatively inactive except when feeding (Armstrong and Morrow 1980). Their diet consists largely of insect larvae and small crustaceans that are captured on or near the bottom (Jessop et al. 1973; Glova and McCart 1974; Craig 1977a; Armstrong and Morrow 1980; Stewart et al. 2008).

One of the reasons that fry and small juveniles often remain in the vicinity of their natal springs may be the richer food supply offered by these habitats. The CS-10 spring channel on Alaska's Canning River system, for example, supported 1,279 to 6,642 organisms/m², whereas the braided channels of the Marsh Fork or Canning rivers only supported 3 to 1,077 organisms/m², predominately chironomid larvae and ephemeroptera nymphs (Ward and Craig 1974; Craig 1978).

3.3 SMALL JUVENILES (PRE-SMOLTS) (REARING HABITAT)

Small pre-smolt juvenile Dolly Varden, typically less than 220 mm FL, overwinter in their natal spawning areas (McCart 1980). Indeed, the highest densities of these fish in the Firth River and Joe Creek, Yukon, were found in the vicinity of groundwater sources during the overwintering period (2.0 to 3.1 fish/m²; Glova and McCart 1974). During April, juveniles in the Hulahula River of Alaska were distributed throughout the spring area, with a congregation of over 50 fish in a shallow, quiescent pool of the spring (West and Wiswar 1984). Following spring break-up, they disperse throughout their natal river systems to feed (Craig and Poulin 1975; Glova and McCart 1974; McCart 1980), although they tend to be more abundant near the spring areas (West and Wiswar 1984). Their summer dispersal and winter concentration suggests that many small juveniles undertake extensive migrations prior to freeze-up to return to suitable overwintering habitat.

During August and September, small juvenile Dolly Varden have been caught in clear water over gravel in the Fish Creek tributary of the Rat River and the Little Fish Creek tributary of the Big Fish River (Dryden et al. 1973). Their silver colour and parr marks provide cryptic colouration that disguises them against the stream bottom. In the Yukon and Alaska, small juveniles were most abundant during the open-water period in shallow pools with low current velocities (<0.3 m/s), along undercut banks and in quiet water on the downstream side of large boulders, usually adjacent to swift-flowing water (>0.5 m/s) (McCart et al. 1972; Glova and McCart 1974; DenBeste and McCart 1984). Substrates in these areas ranged from silt to boulders, but medium to coarse rock may be preferred (Netsch 1975; DenBeste and McCart 1984). Channel widths ranged from 1 to 15 m and depths from 0.06 to 1.2 m. Instream vegetation, bank vegetation, shade, instream tundra slumps and rocks were used for cover, but the fish were also common in braided flood plains that lacked vegetation (DenBeste and McCart 1984). Juveniles in Alaska (75 to 220 mm FL, southern and northern forms combined) selected habitats with banks that were 20 cm or less in height. They used an average habitat area of 23 m² but sometimes used less than 1 m² in boulder-controlled pools of high-gradient streams. Southern-form Dolly Varden parr in southeast Alaska have been captured in streams with mean gradients of at least 15%, generally in step pools (Bryant et al. 2004).

Unlike Arctic Grayling, juvenile Dolly Varden tend to select habitats with higher than average standing stocks of **benthic** invertebrates (DenBeste and McCart 1984). They eat primarily aquatic insect larvae, particularly midges (Chironomidae), caddisflies (Trichoptera), and stoneflies (Plecoptera) (McCart et al. 1972; Bain 1974; Glova and McCart 1974; Craig 1977a,b; Stewart et al. 2008). They also eat the adults of these and other insects that fall into the streams.

Prior to **smoltification** juvenile anadromous fish cannot be distinguished from those that will remain in freshwater to mature as residual males (McCart et al. 1972; Glova and McCart 1974). This changes when the residual males mature, since they retain their parr marks and exhibit spawning colouration year-round (i.e., bright orange to yellow on the belly, ventral fins, and lateral spots although colour intensities may fade outside the spawning season). They are readily distinguished from the immature anadromous fish which are larger, lack parr marks, and silver in colour.

3.4 LARGE JUVENILES (SMOLTS) (REARING HABITAT)

The age and size at smoltification varies. Some juvenile Dolly Varden migrate to sea for the first time at age 1, most at age 2 to 4, and some at age 5 (McCart et al. 1972; Yoshihara 1973; Bain 1974; Griffiths et al. 1975, 1977; Craig 1977a; McCart 1980; Craig and Haldorson 1981; Gillman and Sparling 1985; Bond and Erickson 1987, 1989; DeCiccio 1991; Underwood et al. 1996; Sandstrom and Harwood 2002). Few anadromous migrants smaller than 100 mm FL have been reported (AEL data cited in

McCart 1980; Griffiths et al. 1975), and those less than 300 mm FL tend to remain in delta and lagoon areas (Griffiths et al. 1975). Juveniles that have migrated to sea are typically about twice the length of stream-residents the same age (McCart et al. 1972; Glova and McCart 1974). Because of their growth spurt following smoltification, the anadromous fish spend a relatively short time in the intermediate size classes (Craig 1977a).

Juveniles from the Sagavanirktok River in Alaska entered the Beaufort Sea in early June (Yoshihara 1973). They were not taken in water flowing over grounded sea-ice but moved between the floes after the ice lifted. Smolts (100 to 350 mm FL) using the Prudhoe Bay region during July through mid-August were strongly associated with low salinities (<8 ppt) and moderate temperatures (4 to 10°C) (Houghton et al. 1990). This may reflect their relative abundance in the Sagavanirktok Delta area early in the open-water season and their general absence from fyke net catches later in the season. They appeared to prefer waters adjacent to river deltas in the outer portions of the mixing zone between the river plumes and marine water (Prewitt et al. 1990). Salinity in this habitat ranged from 1 to 15 ppt and temperature from 6 to 10°C. The area of this habitat is generally more extensive from mid-June to mid-July before ice in the region breaks up. These estuarine habitats provide an important transitional zone between freshwater and marine environments for juveniles during smoltification (Glova and McCart 1974).

When southern-form Dolly Varden smolts were exposed to artificial seawater concentrations of 28 to 32 ppt, their plasma sodium levels indicated that 80% were physiologically prepared to enter the ocean (Johnson and Heifetz 1988). The rest were stressed and might have had to acclimate in brackish water before entering the ocean. The relatively high salinity tolerance of the southern-form smolts and apparently lower salinity preference of the northern-form smolts suggest that the latter may have a lower salinity tolerance.

Most growth by anadromous Dolly Varden occurs during the short summer season (Craig 1984; Underwood et al. 1996; Fechhelm et al. 1997). Growth rates of smolts in the Prudhoe Bay region of Alaska peaked in mid-summer and were lower early and late in the season (Fechhelm et al. 1997). This was in contrast to growth patterns reported for juvenile Broad Whitefish (*Coregonus nasus*) and Arctic Cisco (*C. autumnalis*) in the region, which grew quickly early in the summer (Fechhelm et al. 1992; Griffiths et al. 1992).

The fish feed heavily on mysids and amphipods in the coastal waters, which are very productive relative to the freshwater habitats where they overwinter. In coastal areas with a strong freshwater influence, the small fish (<300 mm FL) eat primarily aquatic insect larvae (Griffiths et al. 1975). The proportion of fish in the diet increases as

they grow larger. Feeding is limited during the overwintering period in fresh water, when chironomid larvae are eaten but many of the fish have empty stomachs (Bain 1974).

Juvenile anadromous Dolly Varden (298 to 443 mm FL) radio-tagged at the mouth of the Rat River in late August, moved upstream into the Fish Creek tributary by mid to late September, where most occupied areas within and below the main *aufeis* field (Sandstrom et al. 2001). Movement upstream into the deeper spawning and overwintering pools above the *aufeis* field occurred under the ice, likely some time in late November. By delaying their arrival at the main overwintering area, the juveniles may avoid agonistic interactions with the spawning adult Dolly Varden upstream. The downstream holding area, with its large boulders and deep riffles, may also offer better cover from predators and/or enable the juveniles to conserve energy prior to freeze-up. These movements are in contrast to those of anadromous juveniles in other North Slope rivers, where the lower river is shallow and freezes to the substrate, forcing non-spawning Dolly Varden to occupy the spring-fed spawning/overwintering areas earlier in the season. During the winter, smolts aggregate in the deeper water of pools or near the centre of main channels, often beneath ice at the periphery of open water areas (Glova and McCart 1974).

Most anadromous juveniles return to their natal stream to overwinter, but some overwinter in other systems (DeCicco 1997; Crane et al. 2005). These fish should provide seed stock for the recovery of the natal population if it winterkills.

3.5 ADULTS

3.5.1 Age at maturity

The age (otolith) at which Dolly Varden attain sexual maturity varies within and among populations, and between life history types. Fish in isolated populations, and residual males, tend to mature earlier in life than their anadromous counterparts (see also Blackett 1973 — southern form). The smallest, youngest mature male in the isolated stream-resident population in the upper Babbage River was age 2 and 96 mm FL, and the female was age 3 and 131 mm FL (Bain 1974). Dolly Varden from the small Gayna River sample were mature by age 6 ($n = 8$) (Mochnacz and Reist 2007). Residual males in the Little Fish Creek tributary of the Big Fish River were mature by age 4 ($n = 9$) (MacDonell 1987), but in systems in the Yukon and Alaska can mature by age 2 or 3 (McCart et al. 1972; Bain 1974; Glova and McCart 1974; McCart 1980; DeCicco 1991). Some anadromous male Dolly Varden mature by age 3, and females by age 4, but most do not mature until age 5 to 7 (McCart et al. 1972; Jessop et al. 1973; Yoshihara 1973; Bain 1974; Glova and McCart 1974; Griffiths et al. 1975; Gillman and Sparling 1985; Sparling and Stewart 1986; MacDonell 1987; Bond and Erickson 1989;

Stephenson and Lemieux 1990; DeCicco 1991; Sandstrom et al. 1997; Sandstrom and Harwood 2002).

Studies of southern-form Dolly Varden support the hypothesis that these fish reach sexual maturity at an age that maximizes their overall reproductive potential (Jonsson et al. 1984). Age-at-maturity may also be adjusted non-genetically in response to changes in growth rate, and genetically by natural selection.

3.5.2 Growth and longevity

Anadromous Dolly Varden grow faster and to a larger maximum size than those that remain in fresh water (Table 2). In the Yukon's Babbage River system, for example, anadromous male Dolly Varden can grow to 676 mm in fork length (FL), weigh 2,395 g, and live to age 12; females to 649 mm FL, 1,996 g, and age 14 (Sandstrom et al. 1997). Those in the isolated stream-resident population in the upper Babbage River can live to at least age 17 and grow to 547 mm FL, but few (<1%) live past age 9 or grow longer than 250 mm FL (n = 502) (Bain 1974). Residual males in Fish Hole Creek on the Babbage River ranged in age from 3 to 10, and in length from 128 to 395 mm (n = 70) (Bain 1974). Few fish of any life history live past age 10 or 12 (Bain 1974), and in the Rat River, few live past age 8 (DFO 2001).

As with the large juveniles, most growth by mature anadromous Dolly Varden occurs during the short summer season (Craig 1984; Underwood et al. 1996; Fechhelm et al. 1997). The coastal waters are very productive relative to the freshwater habitats where they overwinter. In the coastal waters, the anadromous adults feed heavily on amphipods, mysids, and fish (Yoshihara 1973; Furniss 1975; Griffiths et al. 1975, 1977; Kendel et al. 1975; Bendock 1977; Craig 1977a; McCart 1980; Craig and Haldorson 1981; West and Wiswar 1984; Bond and Erickson 1987; Knutzen and Jewett 1988; Stewart et al. 2009). As they grow, the proportion of crustaceans in their diet declines and the proportion of fish increases (Griffiths et al. 1975). Anadromous Dolly Varden do not feed extensively in fresh water and are often captured with empty stomachs (Jessop et al. 1973; Bain 1974; Bryan et al. 1974; Glova and McCart 1974; McCart 1980). When they do feed, it is primarily on fish and fish eggs and immature stages of aquatic insects, occasionally on terrestrial insects and amphipods. Non-anadromous adults eat the same species but more aquatic insect larvae and fewer fish (Bain 1974; Glova and McCart 1974; McCart 1980).

Lower body condition has been reported among anadromous Dolly Varden along the Beaufort Sea coast during years when the pack ice does not recede appreciably from the mainland (Underwood et al. 1997). Factors that may be responsible, either alone or in combination, include: 1) lower water temperatures that would slow metabolic activity, 2) reduced access to productive marine feeding areas due to late river break up,

3) lower offshore primary production due to shading by pack ice, and 4) pack-ice inhibition of wind-driven upwellings that transport food from offshore marine to nearshore brackish water areas (Craig 1984; Gallaway et al. 1991; Underwood et al. 1997). Differences in body condition occur within seasons, among areas, and among years but not between sexes (Underwood et al. 1997).

3.5.3 *Habitat use*

During the summer (late June to September), anadromous Dolly Varden along the Beaufort Sea coast of Alaska occupy temperatures ranging from 0.5 to 14°C, salinities of 2 to 32 ppt, and turbidities ranging from 1 to 146 **NTU** (Roguski and Komarek 1971; Craig and Haldorson 1981; Craig 1984; West and Wiswar 1984; Nelson et al. 1987; Prewitt et al. 1990; Houghton et al. 1990; Jarvela and Thorsteinson 1997). During July through mid-August, larger Dolly Varden (>350 mm FL) in the Prudhoe Bay region of the Beaufort Sea, used the entire range of temperature (2 to 12°C) and salinity (0 to 28 ppt) (Houghton et al. 1990). They showed little association with temperature but were associated with low salinities (4 to 8 ppt) (Prewitt et al. 1990). This type of habitat occurs in the bays adjacent to the river deltas and is most extensive in early and mid summer (Prewitt et al. 1990). It often has more amphipods and copepods than the warmer, lower salinity water.

The summer sojourn into salt water is a time of intense feeding and growth for anadromous Dolly Varden (Craig 1984). The highest concentrations of these fish are often found within 100 m of the coast, but individuals have been caught up to 18 km offshore from the Sagavanirktok River of Alaska. In coastal lagoons along the Alaskan North Slope, they tend to concentrate along the shorelines of the mainland and barrier islands (West and Wiswar 1984; Craig et al. 1985). However, the number of fish using the lagoon centre may be greater as it offers a much larger area of habitat (Craig et al. 1985). The movements of radio-tagged fish in Camden Bay appeared random but most displayed an affinity for the shoreline (Jarvela and Thorsteinson 1997). Their average gross ground speed was 55.8 cm/s (1.06 lengths/s).

In late winter, Dolly Varden overwintering in fresh water on the North Slope of Canada and Alaska inhabit spring-fed streams and sometimes deep pools (Craig 1989). They aggregate in the deeper water, particularly beneath ice at the periphery of open water areas (Glova and McCart 1974). In the spring-fed stream habitats, the average water depth ranges from 0.1 to 0.8 m — sometimes with pools up to 2 m deep, the depth of ice cover from 0 to 2.0 m, dissolved oxygen from 5 to 13 ppm, and water temperature from 0.5 to 11°C (McCart et al. 1972; McCart and Bain 1974; Ward and Craig 1974; Craig 1984; West and Wiswar 1984; Sandstrom and Chetkiewicz 1996). Water velocity in Lupine Creek, Alaska, was about 0.5 m/s (1.5 ft/sec) (McCart et al. 1972).

Warm spring water inflow from the headwaters of Little Fish Creek, on the Big Fish River, creates channels in the *aufeis* downstream that are about 2 m in diameter and 0.5 m deep (Sandstrom 1995). These tunnels are used by overwintering Dolly Varden and appear to be a unique feature of this creek, caused by the particularly warm inflow of spring water.

Residual male Dolly Varden in Fish Hole Creek of the Babbage River system were generally found in shallow runs and near spring water pools and channels during the summer, but some were captured in deep pools downstream in the vicinity of the *aufeis* (Bain 1974). During the spawning period they move onto the spawning ground and then remain there in association with the anadromous fish throughout the winter. Residual males in the Canning River of Alaska disperse in the summer to feed in tributaries before returning to the spawning areas in the fall (Craig 1978).

During the summer months, the isolated stream-resident Dolly Varden were found throughout the upper Babbage River (Bain 1974). They concentrated in spring-fed areas of open water during the winter. Stream gradients of 15 to 20% appear to limit the upstream extent of their summer distribution in the Peel River system, Yukon (M. O'Donoghue, Government of the Yukon, pers. comm. 2008). In lesser gradients, they occupy a wide variety of habitats ranging from *aufeis* fields to fast-flowing streams (N. Millar, Yukon Department of the Environment, pers. comm. 2009).

3.5.4 Sex Ratio

Females can significantly outnumber males in the catches of anadromous Dolly Varden during migration, at sea, and on the spawning grounds (Yoshihara 1973; Glova and McCart 1974; Griffiths et al. 1975; McCart 1980; Gillman and Sparling 1985; Baker 1987; Bond and Erickson 1987; Harwood 2001; Sandstrom and Harwood 2002; DFO 2003c). The preponderance of large anadromous females means that they are exposed to greater harvesting pressure than males in the same stock (Sandstrom and Harwood 2002). Extreme examples of skewed male:female ratios exist among spawners in the Big Fish River (1:6; Sandstrom and Harwood 2002) and in Fish Creek on the Rat River (1:9.5; Sandstrom et al., in prep.). Heavy fishing pressure in the past may have contributed to this skewing by selectively removing mature males, whose large kype makes them particularly vulnerable to capture in gillnets. Their removal may then have created favorable energetic conditions for the development of more residual males. The sex ratio of the lightly-exploited anadromous population in Fish Hole Creek on the Yukon's Babbage River was much less skewed (1:1.42, $n = 448$) and when residual males were included, it was nearly even (1:1.03, $n = 518$) (Bain 1974). The prevalence of skewed sex ratios and their occurrence in isolated stream-resident populations (McCart and Bain 1973; McCart and Craig 1973; Bain 1974), albeit to a lesser degree

(1:1.21, $n = 1,017$, McCart 1980), suggest that other factors such as the time or method of sampling may also contribute to the sexual imbalance observed. Skewing of the sex ratio may have important implications for the size and fitness of offspring (Maekawa et al. 1993).

4.0 HABITAT IMPACTS ON FISH BIOLOGY

Management of northern Dolly Varden stocks in Canada and Alaska is made difficult by:

- the existence of numerous discrete genetic stocks;
- their dependence on specialized, geographically discrete habitats such as freshwater springs, small streams, and brackish coastal waters;
- their vulnerability to harvest by multiple, often mixed-stock, fisheries;
- their seasonal movements between jurisdictions, including crossing the international boundary between Canada and Alaska and moving between land claim and fisheries management areas within Canada; and
- proposed regional economic development activities in both countries (Krueger et al. 1998, 1999; Ayles et al. 2007; Kowalchuk et al., in prep.).

In Beaufort Sea drainages, where these fish spawn and overwinter in spring-fed areas, virtually all members of a particular stock, from eggs in the gravel to adult fish, may be confined to a small reach of river for 8 or 9 months of each year (Craig 1989). Not only are all the eggs in one basket, so to speak, but so are the young and adults! These stocks are remarkably vulnerable to human activities and/or environmental factors that alter these habitats or their connection to the ocean. They are also very vulnerable to harvest by humans and predation by other species.

The fidelity of Dolly Varden to a specific river system increases the vulnerability of individual stocks to damage, since their rehabilitation must rely on the genetic and reproductive potential of the survivors, not on immigration from other systems (Reist 1989; Everett et al. 1997, 1998). Harvests of these fish from their natal streams and during long-distance marine sojourns, also increase the vulnerability of individual stocks by making it difficult to determine stock-specific exploitation rates. To preserve and foster Dolly Varden in the Northwest Territories, the spawning and overwintering area(s) of each stock must be protected. Their stream and coastal migration corridors must be maintained, and their vulnerability to harvesting by local single-stock fisheries and distant multi-stock fisheries must be determined and regulated. These measures require effective coordination among management agencies in the Northwest Territories, Yukon, and Alaska, and the cooperation of harvesters and developers.

Many of the activities, such as logging, farming, and mining that have affected southern-form Dolly Varden are unlikely to affect northern-form Dolly Varden in the Northwest Territories in the foreseeable future. Activities with the most immediate potential for impacts are those associated with oil and gas development and transport. Harvesting and climate change are also important considerations when assessing cumulative effects on populations.

Activities with the potential to affect key aspects of Dolly Varden habitat and thereby, the biology of the species, are discussed below and summarized in Table 5. Habitat degradation, habitat fragmentation, species introductions, and improved access are all aspects of development that could affect the species, and their effects might also be modified by climate change. Impacts to one stock could affect others through loss of access by non-spawning fish to overwintering areas in non-natal streams (Craig 1977a, 1989) and shifts in harvesting pressure.

4.1 HABITAT DEGRADATION

Areas of river fed by perennial springs provide vital spawning, rearing, and overwintering habitat for all life-history types of Dolly Varden. During the winter these fish are often confined to small areas of freshwater streams because the rest of the river channel freezes to the bottom (Krueger et al. 1998, 1999). Due to their limited availability and intensive use, these habitats must be a limiting factor for populations (Yoshihara 1972; Glova and McCart 1974; DFO 2001). Any activity that alters the flow, depth, water temperature, water quality (e.g., dissolved oxygen, turbidity, pH) and/or bottom substrate in these areas could severely damage local stocks (DFO 2003c).

Consequently, these critical habitats and the groundwater sources that supply them should be carefully avoided by development activities. Where this is not possible, affected areas and fish populations must be carefully monitored (Jones 1974). Further detailed investigations are needed to identify and protect these habitats (Richardson et al. 2001).

Overwintering areas for both fish and eggs should be avoided whenever possible (Craig and McCart 1974). Neither gravel nor water should be withdrawn from these locations and siltation must be controlled to avoid egg mortalities during the period when eggs are in the gravel (September-May). Activities that disturb the gravel between spawning and fry emergence should be avoided, as these activities have the potential to destroy redds and damage eggs or alevins. Redds dug by smaller females may be

Table 5. Some activities with the potential to affect key aspects of Dolly Varden habitat and their potential effects on the species.

Activity	Potential impact		
	Habitat	Species	Directly affected life stage(s)
• water removal • drainage alterations • seismic testing	• reduced groundwater flow • altered baseflow and ice and temperature regimes	• degradation, reduction or loss of spawning, rearing, and winter habitat • increased winter mortality of eggs, larvae, fry, juveniles, and adults of all life history types	• all
• construction of roadways, pads, and structures • stream crossings	• streambed alteration by removal or disturbance of sand, gravel, and cobble substrates • sediment mobilization • streambed destabilization	• egg, larval, fry and juvenile mortality from physical damage, exposure, loss of cover, sediment mobilization • degradation, reduction or loss of spawning habitat	• all
• logging, • clearing for right-of-ways, camps, etc. • stream crossings	• inland clearing • loss of riparian and instream cover (i.e. shoreline, large woody debris) • altered hydrological regime with more abrupt runoff • warming, increased sediment inputs	• degradation of spawning and rearing habitat • higher mortality rates for all life stages	• all
• culvert installation for stream crossings • dam construction • in-stream construction	• flow impoundment • changes in seasonal flow regimes, water depth, water velocity • habitat fragmentation	• interruption of spawning migrations • restricted access to coldwater summer refugia in headwater tributaries • inundation or dewatering of spawning areas • population extirpation • creation of new wintering areas	• adults, mainly spawners
• road and right-of way construction • population growth	• improved access to Dolly Varden habitat	• increasing harvest pressure on adults and possibly large immature fish • visual and physical disturbance of fish and fish eggs • increased potential for introductions of species and diseases • population reduction or extirpation	• adults and large juveniles by harvesting • all life stages by introductions
• contaminants releases	• chemical pollution	• reduction in fish quality • increased mortality	• all
• climate change	• changes in the temperature and precipitation regimes • warming	• altered access to spawning and overwintering habitats • changes to the carrying capacity of freshwater habitats • increasing competition and predation by warmer water species	• all

shallower than those of larger fish, making them more vulnerable to damage by gravel disturbance and water level fluctuations (Kitano and Simazaki 1995).

Coastal movements of anadromous Dolly Varden make them vulnerable to the effects of activities that degrade their habitat in other geographical areas (Krueger et al. 1998, 1999). Oil and gas development activities along the Alaskan coast of the Beaufort Sea that affect local Dolly Varden populations may also have a similar effect on fish from Canadian stocks that travel along this coast. In Alaska, large volumes of seawater are pumped into oil fields to maintain well pressures (Craig 1984). Where the pump intakes are located at the seaward end of a causeway, juvenile fish that move along the causeway shoreline may be directed to the intake and subject to entrainment. The impact of a series of such intakes could be significant.

Small earthquakes that occurred in the vicinity of the Big Fish River in the 1980s may have reduced the flow of groundwater into Little Fish Creek, although this has not been confirmed (DFO 2003a; Sandstrom and Harwood 2002; Stephenson 2003). Compared to the 1960s and 1970s, harvesters have indicated that the pools are fewer and shallower and that the water tastes less salty (see also Byers 1993). A reduction in flow could alter the temperature of water over the spawning beds and the size of the spawning area, thereby limiting reproductive success of the fish stock. High levels of sedimentation have also been observed at the spawning beds, but it is not known whether the sedimentation rate has changed or whether it has affected egg survival. The extent to which these habitat changes may continue into the future is unknown. Potential exists for similar natural occurrences to alter spring-fed spawning and overwintering habitats in other areas.

Blasting or other, perhaps distant, activities that alter groundwater inflow to Dolly Varden habitat might cause impacts similar to those observed in Little Fish Creek. However, recent *in situ* studies of Lake Trout (*Salvelinus namaycush*) suggest that existing guidelines provide adequate protection for fish eggs from the direct effect of explosives used for industrial development (Faulkner et al. 2006).

Winterkill occurs periodically at wintering grounds on the Big Fish River and at other rivers on the North Slope (Norton 1997; Stephenson 2003). Dolly Varden, sometimes hundreds, are stranded on the ice following a rapid increase and then decrease in water level. The exact cause of these events is unknown, although the formation and subsequent failure of ice dams, snow slides that create snow plugs that later fail, and sudden warm spells that cause flash floods, have been suggested as possible explanations. The impact of these events at the population level is unknown. Human activities that create similar changes in flow, even drilling holes in the ice in areas with positive hydraulic pressure (Sandstrom et al. 1996), could cause significant winterkill by flushing fish onto the ice to freeze.

Attempts to rehabilitate degraded habitat should only be undertaken after proper consideration. In southeastern Alaska removing woody debris from past logging operations reduced the population densities, production, and carrying capacity of southern-form Dolly Varden streams (Dolloff 1986; Elliott 1986). Vegetation buffer strips were found to protect winter habitat of juvenile Dolly Varden by maintaining pool areas and cover within pools (Heifetz et al. 1986), and stream reaches with more debris and greater channel stability had a higher density of parr (Murphy et al. 1986). In-channel debris, shoreline vegetation, and undercut banks may serve similar functions in streams supporting northern-form Dolly Varden and should not be altered without considering the consequences to the fish populations.

4.1.1 Pollution

Dolly Varden (southern form) were studied following the *Exxon Valdez* oil spill to assess the effects of petroleum exposure on fish inhabiting the nearshore subtidal zone (Collier et al. 1996). Measurement of fluorescent aromatic compounds in their bile showed them to be strongly exposed in the months immediately after the spill. A year later, after a winter storm cycle, their exposure was significantly lower. There was no evidence of increased formation of petroleum-derived DNA adducts, which are an indicator of exposure to contaminants that may damage the fish's genetic material.

In populations associated with spilled oil, growth over the year following the spill was 24% slower for subadult and 22% slower for adult Dolly Varden (Hepler et al. 1996). The following year growth was slower for populations not associated with oil. The average survival rates for populations associated with spilled oil were 32% and 22% less for subadult and adult Dolly Varden, respectively, during the year following the spill (i.e., spring 1989 to spring 1990) although the differences were not statistically significant. Chronic starvation and direct exposure to petrogenic hydrocarbons were hypothesized as the pathways by which crude oil could have slowed the growth of Dolly Varden. While the spill occurred along the coast, by affecting the anadromous Dolly Varden it also affected the freshwater aquatic systems where they spawn and overwinter (Peterson 2001).

Spilled oil may also cause declines in female reproductive parameters (Sol et al. 2000). Significant negative correlations were observed between oil exposure and Dolly Varden plasma estradiol-17 β in the year following the oil spill, and were likely greater in the year of the spill. Declines in reproductive hormones can interfere with gonadal development and spawning. Their biological significance will depend upon the number of fish affected. While the reproductive parameters measured tended to return to the normal range in the years following the spill, the long term impacts of oil exposure on endocrine processes and on fish populations are not fully understood.

In the laboratory, the ability of southern-form Dolly Varden to metabolize naphthalene and toluene, two toxic aromatic hydrocarbons found in crude oil and petroleum products, was significantly lower in sea water than in fresh water (Thomas and Rice 1981, 1986b). Metabolism of toluene was significantly greater at 12°C than 4°C, while that of naphthalene was similar at both temperatures (Thomas and Rice 1986a).

4.2 HABITAT FRAGMENTATION

Habitat fragmentation could affect Dolly Varden in both freshwater and marine environments. Fragmentation that prevents seasonal access between spawning, rearing and overwintering areas would severely damage or extirpate both anadromous and isolated stocks. Fragmentation that prevented access to and from marine feeding areas would eliminate anadromy, reducing the size of individuals and likely their numbers. The development of causeways that extend offshore to connect land-based operations with offshore docks and drilling platforms can alter local salinity regimes by deflecting along-shore flow (Craig 1984). A series of such causeways might adversely impact movements by anadromous fishes, particularly small juveniles.

The ability of northern-form Dolly Varden to surmount flow barriers is poorly known, as is their ability to respond to measures designed to mitigate flow impacts. Dolly Varden (southern form) less than 120 mm FL were able to move upstream through a 90 cm diameter offset baffle culvert, that was set at a 10% gradient, in flows ranging from 5.23 and 17 L/s (Bryant 1981). When a fish ladder was installed to improve access to upstream habitats in Margaret Creek, southeast Alaska, anadromous Dolly Varden (southern form) were quick to colonize the system (Bryant et al. 1999). Whether they were immigrants or whether resident individuals became anadromous is unclear.

4.3 SPECIES INTRODUCTIONS

The overall distribution of northern-form Dolly Varden likely reflects their ability to colonize marginal, recently deglaciated streams (Milner and Bailey 1989; Milner et al. 2000). Few fish species are capable of successfully colonizing the stream environments that support northern-form Dolly Varden in Canada, or of relying on groundwater inflow for spawning and overwintering. The remoteness of these streams also makes it very unlikely that fish or other species would be introduced into these waters. However, climatic warming might facilitate the natural expansion of some species into these areas (see Section 4.5).

Infectious pancreatic necrosis virus is endemic among Dolly Varden in the Rat, Big Fish, Babbage, and Firth rivers (Souter et al. 1984, 1986; Yamamoto 1989). This virus causes mortality of young fish and survivors can become lifelong carriers. Care should be taken to avoid introducing fish from these stocks into other areas.

4.4 IMPROVED ACCESS

Changes in where people live and in the ease of access to fisheries, through the use of motorized transport, have had a major impact on fishing activities for Dolly Varden (Cosens and Martin 2003; Papik et al. 2003). The size and location of populations and access to harvesting sites will continue to change. These shifts will be an important consideration for resource managers as they strive to eliminate or mitigate changes in harvesting pressure on stocks of Dolly Varden.

Dolly Varden are valued as food fish and have been harvested in quantity from the Rat and Big Fish river systems and the Mackenzie Delta (Jessop et al. 1974; Sparling and Stewart 1986; Sandstrom 1995; Stewart 1996; Papik 2003). These fisheries concentrate on the migratory segment of the population because the fish are large, predictably available, and offer a better return on effort than the non-anadromous fish. The preponderance of females among the mature migratory population has important management implications, since fisheries that are unselective for sex will take more females than males (McCart et al. 1972). This reduces the reproductive potential of the population out of proportion to the number of fish taken. A sport fishery concentrated at the spawning grounds could have a similar impact, since mature spawning females may be more susceptible to capture by angling than spawning males (McCart et al. 1972).

Anadromous Dolly Varden from populations that winter in the Rat and Big Fish rivers, and perhaps in the Vittrekwa River, are vulnerable to harvest by mixed-stock coastal fisheries, during their seasonal migrations in fresh water, and at their spawning and overwintering areas (Sandstrom 1995; Harwood 2001). Anadromous fish are harvested at whaling and fishing camps from Nuneluk Spit west of Herschel Island east to Shingle Point during July and August (Stephenson and Lemieux 1990; Sandstrom 1995; Norton 1997; Papik et al. 2003; Stephenson 2004). These mixed-stock fisheries also harvest fish that originate from other rivers along the North Slope of the Yukon and Alaska. Unfortunately, the annual contribution by each river to each fishery is unknown, making some stocks potentially vulnerable to overharvesting.

Residents of Aklavik have traditionally harvested Dolly Varden from the Big Fish River for subsistence and in the past, harvested some for commercial sale (Gillman and Sparling 1985; Byers 1993; DFO 2003a; Papik et al. 2003; see also Stephenson 2003,

2004). They travel by boat to the river mouth in late August and to the upper reaches by snowmobile in October and November, and fish mostly with gillnets and seines. Introduction of the snowmobile in the 1960s reduced the journey to the Fish Hole from about two days by dog team to an afternoon (Stephenson 2003). The stock was heavily exploited during the 1970s and early to mid-1980s, and has yet to recover despite a protracted voluntary moratorium on fishing in the system (DFO 2003a).

Residents of Aklavik also harvest Dolly Varden from the Rat River population as the fish migrate past the town site and into the mouth of Husky Channel (Stephenson and Lemieux 1990; Sparling and Stewart 1986; Norton 1997; Harwood 2001). Residents of Fort McPherson harvest fish from this population at Big Eddy, at the mouth of the Rat River, and at “Destruction City” (Stephenson and Lemieux 1990; Sparling and Stewart 1986; Gwich’in Elders 1997; Norton 1997; Harwood 2001). They occasionally catch Dolly Varden, likely from the Vittrekwa River, in nets set in the Peel River (N. Millar, Yukon Department of the Environment, pers. comm. 2008). The red meat is considered a delicacy and is usually dried and smoked (Gwich’in Elders 1997).

In 1990-92, the lightly exploited Babbage River stock, in the Yukon, had an estimated instantaneous mortality rate (Z) of 0.28 (Sandstrom et al. 1997). This value, which includes both natural and fishing mortality, was much higher in the heavily exploited Rat River population, where it rose from 0.57 in 1987 (MacDonell 1987) to 0.94 in 1989 (Harwood 2001), and 1.5 in 2000 (DFO 2001). These high mortality rates mean that mature individuals in the Rat River population may have few opportunities to spawn before being killed.

Fish aggregated at overwintering sites are vulnerable to capture and many can often be harvested in a short time (DFO 2003c; Papik et al. 2003). Large harvests from the fish holes in the 1970s were likely an important factor contributing to the historical decline of the Rat River stock (Stephenson and Lemieux 1990). Improved access to areas where these fish can be harvested could increase the harvest of mature fish and thereby reduce recruitment, damaging the population. Community efforts to protect these stocks are ongoing (DFO 2001, 2003a; Papik et al. 2003).

4.5 CLIMATE CHANGE

Global warming has the potential to cause profound changes in the life history of northern-form Dolly Varden (Crane et al. 2004). Populations of all life-history types are particularly vulnerable to hydrological changes that reduce groundwater inflow during the winter. Changes in the volume, seasonality, and/or temperature of these inflows could profoundly alter spawning success and winter survival. These populations are likewise vulnerable to changes in the timing and volume of the stream discharges that

enable populations to reproduce and summer successfully, and to use the streams as reliable, seasonal migration corridors.

Melting permafrost could affect water quality and stream habitat negatively by releasing sediments and causing bank slumping, and positively by releasing nutrients. The former might increase egg mortality, infill overwintering sites, and temporarily block migration; the latter could increase biological productivity.

Temperature changes that alter biological productivity and metabolic activity could alter the ecology of streams inhabited by Dolly Varden. In laboratory studies of Japanese Dolly Varden, their feeding rates on caddisfly larvae (*Glossosoma* sp.) were low at 3°C which coincided with the mean winter stream temperature, and low above 18°C which was near the maximum summer temperature (Kishi et al. 2005). Feeding rates were high at 12°C. Top-down effects on the abundance of caddisfly larvae were only evident at this intermediate temperature. They suggest that thermal habitat alteration could change the food web structure of stream communities inhabited by Dolly Varden via combinations of direct and indirect trophic effects.

In laboratory studies of temperature tolerance, southern-form Dolly Varden collected in Japan showed a decrease in appetite at temperatures $\geq 16^{\circ}\text{C}$ (Takami et al. 1997). Thermal death of Dolly Varden occurred at 20°C and above, with no fish surviving beyond 26°C. The applicability of these data to northern-form Dolly Varden in the Northwest Territories is uncertain, however, it is unlikely that northern-form fish have higher thermal tolerances.

In Japan, the lower limits of the altitudinal distribution of southern-form Dolly Varden were delineated by the 8°C groundwater isotherm (Nakano et al. 1996). This apparent limit may reflect the interaction of numerous environmental factors, including warming by groundwater, solar warming and competition by species adapted to warmer water. Modelling results suggest that increases of 1 to 4°C in mean annual air temperature might reduce the geographical distribution of the species by 28 to 90%, respectively, and cause habitat fragmentation and local extinctions with little possibility of the populations compensating by expanding their distributions upstream.

If climate continues to warm as projected, Arctic specialists such as northern-form Dolly Varden may be displaced by species adapted to warmer conditions (Rhydderch 2001). Warming might, for example, facilitate northward colonization by Bull Trout (Reist 1994; Mochnacz 2002). The two species do occur in the Gayna River system of the Northwest Territories (Mochnacz and Reist 2007). Concern has been expressed that hybridization of Bull Trout with northern-form Dolly Varden might affect the genetic integrity of both species (Reist et al. 2002). However, **sympatric** wild populations of Dolly Varden and Bull Trout maintain their genetic integrity in spite of gene flow (Baxter

et al. 1997; Hagen and Taylor 2001). Whether this would be the case in northern river systems, given that both species make extensive use of groundwater inflows for spawning and overwintering, is unknown.

Other species that might expand their ranges affecting northern-form Dolly Varden in Canada include various Pacific salmon species which utilize riverine habitats (e.g., Coho Salmon). In southeastern Alaska, southern-form Dolly Varden were the dominant fish species in moderate- (mean gradient = 5.5%) and high-gradient (mean gradient = 12.9%) zones of streams; Coho Salmon were dominant in the low-gradient zones (mean gradient = 3.1%) but were present in higher-gradient zones (Bryant et al. 2004). Coho Salmon have been reported from the North Slope (Craig and Haldorson 1986; Babaluk et al. 2000). If their numbers increase, they may compete successfully with Dolly Varden for low-gradient stream habitat.

Whether affected Dolly Varden populations could, or would, respond to climate amelioration by colonizing marginal habitats to the north and east is likewise unknown. To do so, they would likely have to displace Arctic Char and since there is so little distributional overlap between the two species, this seems unlikely (Sawatzky et al. 2007). Arctic Char are well established and the Dolly Varden are strongly associated with upland streams fed by groundwater.

5.0 SUMMARY

Northern-form Dolly Varden inhabit clear, cold rivers and streams west of the Mackenzie River Valley, from the Gayna River north to the coast and west along the North Slope of Yukon and Alaska. Within the Northwest Territories, they occur in the Gayna, Peel, Rat, and Big Fish river systems. There are numerous genetically distinct stocks, often organized by river. These fish were often referred to in the past as the western form of Arctic Char, so the literature referencing these taxa is somewhat confused. Taxonomic and life history differences suggest that habitat use by the southern form of Dolly Varden may not be directly transferable to the northern form.

Northern-form Dolly Varden follow a stream-resident, riverine, or anadromous life history in response to local environmental conditions. Non-anadromous stream-resident fish are prevented from migrating into coastal waters by impassable barriers that isolate them in upland streams, or by distance from the sea. Fish with access to the sea are typically anadromous. After spending 1 to 5 years in fresh water, they smoltify and undertake summer feeding sojourns into productive coastal brackish and marine habitats. Some fish with access to the sea remain in fresh water. These “residuals” are typically fast-growing, early-maturing males that follow a riverine life history. Lacustrine

life histories have not been reported for northern-form Dolly Varden in Canada, however, some lacustrine populations of uncertain taxonomic affinity are known from the upper Peel River basin in the Yukon.

Typically, the anadromous fish are larger than non-anadromous fish the same age, grow to a larger maximum size, and mature later in life. They undertake extensive freshwater and marine migrations, moving downstream at ice breakup in the spring (June-July) and returning to fresh water by the end of September. A late breakup shortens the time they have to feed at sea, and *vice versa*. At sea, the anadromous fish are found over a broad range of salinity (≤ 32 ppt), temperature (0.5 to 14°C) and turbidity (1-146 NTU). The smaller fish (150-350 mm FL) tend to be associated with river deltas and lagoons, and show preference for low salinities < 8 ppt and moderate temperatures (4 to 10°C). Larger fish show preference for salinities of 4 to 8 ppt but little association with temperature, and their coastal movements may be more extensive. In coastal waters, the migrants mix with Dolly Varden from other stocks. They have not been reported from marine waters in winter, when the water is likely too cold and saline for them to survive. The migrants show strong fidelity to their natal streams for spawning but during non-spawning years sometimes overwinter in other streams.

All life histories rely on cold, clear streams with groundwater inflow for spawning and overwintering. These inflows are also important for rearing fry. For most of the year outside the open-water season, the entire population from a river or reach of river is confined to a very small volume of water that is prevented from freezing by the inflow of groundwater. Elsewhere, the rivers are typically frozen solid. Fields of thick ice (*aufeis*) build up downstream of the open water where flow can no longer follow the channel and spreads out on top of the ice.

Dolly Varden can spawn more than once following maturity. Anadromous fish in the Big Fish River appear to spawn annually, but individuals in most populations only spawn every second or third year. Residual males participate in spawning with anadromous females, not as their mate but as “sneaks” that rush in to participate in the spawning act. Few observations of spawning behaviour have been reported for northern-form Dolly Varden.

Spawning typically occurs over fine to coarse gravel at temperatures of 3 to 8°C. Most populations spawn in August to early October but in areas influenced by particularly warm groundwater, spawning can occur in November and December. Gravel redds are constructed at depths < 2 m in areas with moderate current (30 to 60 cm/s). After spawning, the eggs are covered with 8 to 12 cm of gravel. They hatch in mid-February to early May but the fry do not emerge from gravel until mid-April to early July. Young-of-the-year typically remain near their natal stream. During the summer, non-anadromous juveniles and adults disperse in the rivers and/or streams to feed.

Immature stages of aquatic insects are important foods for smaller Dolly Varden (<300 mm FL) in fresh water and in coastal areas with a strong freshwater influence. Marine crustaceans are eaten in quantity by anadromous fish of intermediate size (301 to 500 mm FL). The proportion of fish in the diet increases with size, and Dolly Varden will eat the eggs and members of their own species. Anadromous fish feed mostly at sea, and often have empty stomachs when caught in fresh water.

The species' requirements and preferences for habitat parameters such as water quality, current velocity, substrate, depth, and cover are not well documented except at the spawning and overwintering sites. Physiological tolerances to temperature maxima and minima, to low oxygen, high turbidity, and strong currents must often be inferred from other *Salvelinus* forms or species. Southern-form Dolly Varden, for example, begin showing signs of thermal stress at 16°C. However, the applicability of these data given differences in life history is uncertain. Northern-form Dolly Varden clearly are capable of adjusting to a wide range of ion concentrations and temperatures, since the quality of groundwater they are exposed to in winter varies widely. They are also able to inhabit streams with gradients of at least 15%, so they must also be capable of swimming against strong currents.

Habitat degradation and fragmentation, improved access, and climate change all have the potential to damage or extirpate Dolly Varden populations. In Beaufort Sea drainages, virtually all members of a particular stock, from eggs in the gravel to adult fish, may be confined to a small spring-fed reach of river for 8 or 9 months of each year. Not only are all the eggs in one basket, so to speak, but so are the young and adults! These stocks are remarkably vulnerable to human activities and/or environmental factors that alter these habitats or their connection to the ocean. Seismic activities or water withdrawals that alter groundwater inflow, gravel removal from spawning sites, and improperly constructed stream crossings are examples of some activities with the potential to damage these stocks.

Anadromous Dolly Varden are a valued food fish, and the object of traditional harvests by various Aboriginal groups. Their predictable availability at spawning and overwintering sites, in shallow streams during migration, and in nearshore coastal waters makes these fish easy to harvest. Because they move widely, individuals from a particular stock may be targeted by fisheries at various locations, making it difficult to determine the stock-specific exploitation rate. Improved access to Dolly Varden habitats could increase harvesting opportunities and lead to overharvesting.

The fidelity of Dolly Varden to a specific river system increases the vulnerability of individual stocks to damage, since their rehabilitation must rely on the genetic and reproductive potential of the survivors, not on immigration from other systems. The

ability of these fish to adapt to climatic warming is uncertain given that they could be subject to competition by other salmonid species such as Bull Trout and Coho Salmon. Furthermore, they might have difficulty expanding their range to the north and east where Arctic Char are already well established.

To preserve and foster Dolly Varden in the Northwest Territories, the spawning and overwintering area(s) of each stock must be protected. Their stream and coastal migration corridors must be maintained, and their vulnerability to harvesting by local single-stock fisheries and distant multi-stock fisheries must be determined and regulated. These measures require effective coordination among management agencies in the Northwest Territories, Yukon, and Alaska, and the cooperation of harvesters and developers.

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8.0 ABBREVIATIONS

FL = fork length—distance from the tip of the fish's snout to the notch in its tail.

9.0 GLOSSARY

Alevins are newly hatched, incompletely developed fishes (usually salmonids) still in the nest or inactive on the bottom and living off stored yolk.

Anadromous fish populations move downstream into marine waters to feed, and return upstream into fresh water to spawn and/or overwinter.

Aufeis is ice formed when water from a spring or stream emerges and freezes on top of previously formed ice.

Baseflow is stream flow derived from groundwater.

Benthic organisms are associated with the bottom substrate.

Fry are young fish, newly hatched, after yolk has been used up and active feeding has commenced.

Iteroparous fish spawn more than once in their lives.

Karst describes an area of irregular limestone in which erosion has produced fissures, sinkholes, underground streams, and caverns.

Lacustrine populations remain in lakes throughout their lives.

Larval fishes (plural larvae) are young fish, newly hatched, before the yolk has been used up (see also **Alevins**).

Non-anadromous fish populations remain in fresh water year-round.

Parr marks are vertical bars of dark pigment on the sides of young salmonids.

Pelagic habitats in waterbodies are not near the bottom or shore.

Riverine (residual) Dolly Varden remain in rivers and streams throughout their lives despite having access to the sea, and are typically small, early maturing males.

Smoltification is a complex developmental transformation, involving physiological, biochemical, morphological, and behavioral changes, that allows young Dolly Varden (parr) to transition from living in freshwater to living in saltwater.

Stream-resident (isolated) fish populations remain in streams throughout their lives and are prevented from migrating to sea by impassable barriers.

Appendix 1. Life history and habitat parameters

The emphasis of this work is on observations from within the Mackenzie Valley region. Terms such as “dominant”, “preferred” and “optimum”, which have been used in other summaries (e.g., Ford et al. 1995; Roberge et al. 2002), are avoided unless they are supported by directed research studies. This is because sampling observations may not accurately reflect a species’ preferences unless the spatial and temporal biases related to sampling design and gear are carefully controlled. The following sections define what is meant by the various life history and habitat use parameters used in the text and tables and in the appendices that follow. Some parameters described here may not be used in this report because this description applies to all of the habitat use reports in the series.

TABLE 2

Habitat use and requirements

These tables summarize habitat associations during the life history stages of the species. Separate tables may be included for stream, river, and lake environments. Observations from areas within the Mackenzie River watershed are in bold type. The following parameters are included, with the units of measurement typically used:

- **Habitat type** – habitat type most commonly associated with observations of the life history stage (e.g., streams–pools, runs, riffles; lakes–littoral, **pelagic**, benthic);
- **Stream gradient** – percent (%) slope;
- **Depth range (m)** – range of depths from which the species has been reported;
- **Substrate** – substrate type(s) most commonly associated with observations of the species;
- **Cover** – cover type(s) most commonly associated with observations of the species;
- **Habit** – typical distribution within the habitat type (e.g., surface, midwater, benthic, above or below thermocline, inshore or offshore);
- **Velocity range** – water velocities (cm/s) wherein the species is most commonly observed;
- **Turbidity (NTU):**
 - o **range** – turbidity range wherein the species has been reported, 1 represents clear water with greater than 1 m visibility, 146 represents very turbid water with about 5 cm visibility (Craig 1984);
 - o **limits** – upper and lower lethal limits as tested experimentally;
- **Oxygen (mg/L):**
 - o **range** – dissolved oxygen levels wherein the species has been reported;
 - o **limits** – upper and lower lethal limits as tested experimentally;
- **Temperature (°C):**
 - o **range** – water temperatures wherein the species has been reported;
 - o **limits** – upper and lower lethal limits as tested experimentally;
- **Prey:**
 - o **Primary** – taxa or taxon typically comprising the majority (by weight/volume/food value) of the food found in the stomachs of fishes sampled, or that were seen to be eaten during *in situ* behavioural studies;
 - o **Secondary** – taxa or taxon comprising the minority (by weight/volume/food value) of food found in the stomach of fish sampled, or that were seen to be eaten during *in situ* behavioural studies. [Note: Differences in prey selection (i.e., primary/secondary) may reflect changes in the seasonal availability rather than the relative importance of food items.];
- **Duration** – number of seasons, months, or years in which each specific life stage exists or occurs;
- **Size/Age range** – average and/or maximum size range (mm) of the life history stage; or maximum size range (mm); FL = fork length, SL = standard length, TL = total length. A fish is age 0 until December 31 of the year it was hatched unless otherwise indicated.

Reproduction

This table summarizes habitat and life history parameters related to the species' reproduction. Observations from areas outside the Mackenzie River watershed are italicized. The following parameters are included:

- **Reproductive strategy** – *oviparous* species produce eggs that hatch outside the body of the mother; *iteroparous* species produce their young in annual or seasonal batches (most fishes); *semeloparous* species (e.g., salmon) produce all of their offspring at one time and then usually die; *annual* spawners reproduce each year following maturity until they die or reach reproductive senescence; under marginal conditions a portion of the reproductive population may rest for a year or more between spawning events (*% resting*);
- **Age at maturity** – range of ages at which males (M) and females (F) become sexually mature, with any estimate of the most common age at maturity provided in brackets;
- **Fecundity** – range in the number of eggs produced by females;
- **Spawning habitat** – habitat types wherein spawning has been observed, ripe and running fish have been caught, ripe and spent fish have been caught together, or eggs or sac larvae have been found. The presence of mobile young-of-the-year was used to identify nursery areas, and sometimes “suspected” spawning areas;
- **Spawning habit** – some species *build a nest* by altering the bottom substrates to meet their requirements before spawning; others *use existing nests* constructed by other species; *broadcast spawners* spread their eggs over suitable areas of unaltered bottom substrates; some species *care for the eggs or care for the young*;
- **Spawning temperature** – temperature range at which spawning has been observed;
- **Spawning depth** – depth range at which spawning has been observed;
- **Spawning substrate** – substrate type(s) observed at spawning locations;
- **Spawning current velocity** – current velocity observed at spawning locations;
- **Maximum age** – life expectancy of the species;
- **Reproductive senescence** – age at which the species stops reproducing.

APPENDIX 2

The seasonal habitat requirements for each life history stage are presented below for stream environments. Within these appendices, observations from the Mackenzie River watershed are in bold type.

Life history stage

Observations on habitat use are summarized by life history stage. Four stages are recognized:

- **Spawning/eggs** – includes habitats on the spawning grounds where adults spawn and eggs mature and hatch;
- **Young of the year (YOY)** – larvae and fry less than age 1 (age 0 until December 31 of the year they are hatched);
- **Juveniles** – sexually immature fish older than age 1;
- **Adults** – include fish that have attained sexual maturity.

Seasons

Habitat use was divided into four seasons, which correspond to the environmental conditions rather than to the calendar seasons. Calendar months are also provided if possible, but the correspondence between environmental variables and calendar months varies from south to north and from year to year. In the north of the Mackenzie watershed (Inuvik; S. Stephenson, DFO, pers. comm.), the seasons used are:

- **Spring (Sp)** – the period of ice breakup and spring runoff, typically late April to mid June;

- **Summer (Su)** – the period of open water, typically mid-June to late September;
- **Fall (Fa)** – the period of ice formation, typically late September to late November;
- **Winter (Wi)** – the period of ice cover, typically late November to late April.

In the south (Hay River; G. Low, Hay River, NT, pers. comm.) they are:

- **Spring (Sp)** – the period of ice breakup and spring runoff, mid-April to early June;
- **Summer (Su)** – the period of open water, typically early June to late-September;
- **Fall (Fa)** – the period of ice formation, typically late-September to mid-November;
- **Winter (Wi)** – the period of ice cover, typically mid-November to mid-April.

These date ranges are averages, since the timing of breakup varies from river to river and lake to lake depending upon factors such as stream gradient, exposure to sunlight, and lake size.

Water depth

Five water depth categories are used for stream environments: 0-0.2, >0.2-0.6, >0.6-1, >1-2, and >2 m. Depth represents the distance from the surface of the water downwards. The depth association of a fish found in the upper metre of the water column, for example, would be reported as 0-0.2, >0.2-0.6 and >0.6-1.0. Depth is reported as stated in the reference, but if “shallow” water was the only descriptor, a depth of 0-20 cm was used to represent “shallow” water.

Substrate type

Substrate type was reported as stated in the reference. However, if particle size was provided, substrate type was classified as follows:

- **bedrock** = uniform continuous substrate;
- **boulder** = >25 cm;
- **cobble** = 17-<25 cm;
- **rubble** = 6.4-<17 cm;
- **gravel** = 0.2-<6.4 cm;
- **sand** = <0.2 cm;
- **silt/clay** = finer than sand with fine organic content;
- **muck (detritus)** = mud with coarse organic content;
- **hard-pan clay** = clay; and
- **pelagic** = open water.

Cover type

Cover features that may provide protection, or a refuge, from predators, competitors, and adverse environmental conditions include:

- **None** – no cover;
- **Submergent vegetation** – aquatic plants that grow entirely below the surface and are attached to the bottom by roots or rhizomes;
- **Emergent vegetation** – aquatic plants with foliage that is partly or entirely borne above the water surface (e.g., cattail *Typha* spp.) or float on the surface of the water (e.g., milfoil);
- **Algae** – aquatic algae present on the bottom or within the water column;
- **Wood** – large (LWD) or smaller woody debris (SWD) on the bottom or within the water;
- **In situ** – submerged cavities and/or crevices, undercut banks;
- **Substrate** – interstitial spaces between any size of substrate (boulder–sand);
- **Overhead** – cover originating outside the riparian zone that overhangs the stream and/or banks, which includes overhanging banks or riparian vegetation, woody debris outside the channel, or anything above the surface that provides shade.

Habitat

In flowing water, habitat refers to the type of channel unit, and typical water velocity within the unit that the species inhabits, including:

- **Pool** – velocity range $<0.25 \text{ m}\cdot\text{s}^{-1}$;
- **Run** – velocity range $0.25\text{-}0.50 \text{ m}\cdot\text{s}^{-1}$;
- **Riffle** – velocity range $0.50\text{-}1.00 \text{ m}\cdot\text{s}^{-1}$;
- **Rapid** – velocity range $>1.00 \text{ m}\cdot\text{s}^{-1}$;
- **River margin** – habitat along the banks of the mainstem channel, often low velocity;
- **Off-channel** – any habitat that is outside the mainstem flow including side channels, backwaters, and off channel habitats, often low or no velocity.

Appendix 2. Stream habitat requirements for northern-form Dolly Varden.

Stream habitat features:	LIFE STAGES [Season of use (reference)]				LEGEND/COMMENTS/REFERENCES
	Spawn/egg	YOY	Juvenile	Adult	
Depth (m)					Season of use:
0-0.2		All (5)	All (12, 15)	All (12, 15)	Sp = spring
>0.2-0.6	Fa (4, 17)	All (5)	All (12, 15)	All (12, 15)	Su = summer
>0.6-1	Fa (4, 17)		All (12, 15)	All (12, 15)	Fa = fall
>1-2	Su, Fa (3)		All (12, 15)	All (12, 15)	Wi = winter
>2					All = year-round
Substrate					Late summer and early fall (3)
Bedrock					
Boulder				Su (14)	
Cobble				Su (14)	
Rubble				Su (14)	
Gravel	Fa (1, 2, 3, 4, 17)	All (1, 2, 3)	Sp, Fa, Wi (1,2,3)	Sp, Fa, Wi (1,2,3)	
Sand			Su (14)	Su (14)	
Silt/Clay	Fa (4)*		Su (14)	Su (14)	Some silt.
Muck (Detritus)					
Hard-pan clay					
Pelagic					
Cover					
None					
Submergents					
Emergents					
Algae					
Wood					
In situ		Su (11)			
Substrate					
Undercut bank/overhang			Su (11)		
Overhead		Sp, Fa, Wi (12) *	Sp, Fa, Wi (12, 13)*; Su (11)**	Sp, Fa, Wi (12, 13) *	*Ice, **Vegetation
Other*					
Velocity/Habitat					
Pool	Fa (1, 17)*		Su (11)	Fa, Wi, Sp (12, 16)	*Pools below rapids (1), often in the downstream end of the pool or in the run below (17)
Run	Fa (17)		Su (11)		
Riffle	Fa (4)*			All (12,14,16)**	*Spring areas above aufeis areas and at canyon mouths (4); **Shallow riffles (12).
Rapid					
River Margin		Su (5-10)			
Off-channel					
Groundwater inflow	Su, Fa, Wi (1,2,3,4)*	**	All (12, 15)	Wi, Sp, Su (12, 14)	*Eggs incubate in the gravel in areas fed by groundwater, **Not observed but likely present year-round.

- 1 = Stein et al. 1973b—Fish Creek on the Rat River system and Little Fish Creek (Fish Hole) on the Big Fish river system, Northwest Territories
- 2 = Hatfield et al. 1972—Fish Creek on the Rat River system, Northwest Territories
- 3 = Gillman et al. 1985—Little Fish Creek on the Big Fish River system, Northwest Territories
- 4 = Yoshihara 1973—Lupine River, Alaska
- 5 = Craig 1978—Canning River, Alaska
- 6 = Bain 1974—Babbage River, Yukon
- 7 = Glova and McCart 1974—Firth River, Yukon
- 8 = Armstrong and Morrow 1980—northern-form review
- 9 = McCart et al. 1972—Sagavanirktok River, Alaska
- 10 = McCart 1980—northern-form review
- 11 = DenBeste and McCart 1984—Sagavanirktok River system, Alaska
- 12 = Sandstrom and Chetkiewicz 1996— Fish Creek on the Rat River system, Northwest Territories
- 13 = Sandstrom et al. 2001— Fish Creek on the Rat River system, Northwest Territories
- 14 = Stephenson and Lemieux 1990—Rat River, Northwest Territories
- 15 = Netsch 1975—Yukon River headwaters, Alaska
- 16 = Sandstrom et al., in prep.—Rat River, Northwest Territories
- 17 = N. Mochnacz, unpubl. data—Rat River, Northwest Territories and Babbage River, Yukon