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The Effect of Overwintering Site Temperature on Energy Allocation and Life History Characteristics of Anadromous Female Dolly Varden Char (*Salvelinus malma*), from Northwestern Canada

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by

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THE EFFECT OF OVERWINTERING SITE TEMPERATURE ON ENERGY ALLOCATION AND LIFE HISTORY CHARACTERISTICS OF ANADROMOUS FEMALE DOLLY VARDEN CHAR (Salvelinus malma), FROM NORTHWESTERN CANADA

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ABSTRACT

Overwintering sites used by Dolly Varden char (Salvelinus malma)(Walbaum) populations on the Yukon and Northwest Territories north slope are situated near thermal freshwater springs. These springs vary with respect to physicochemical characteristics (e.g., orifice water temperatures) which presumably place different environmentally driven energetic demands upon the fish. This study examined the possible effect of water temperature differences on energy allocation to competing life history demands of growth, reproduction and metabolism for adult female char from the Babbage and Big Fish Rivers (orifice water temperature is 4°C and 16°C respectively). Specifically, the study examined whether higher overwintering site water temperature increase the overwintering metabolic demands of adult female char, thereby compromising growth and/or reproductive effort.

Results indicated that prior to overwintering, post-spawned females from the two systems had similar muscle lipid reserves, whereas gut lipid reserves were only slightly higher in females from the Big Fish River. This similarity in somatic energy reserves suggests that, despite the physicochemical differences in the springs, adult char of both systems overwinter in similar thermal regimes. This may be due to the formation of ice tunnels within the *aufeis* field unique to the Big Fish River. Energy allocated to growth in length was not significantly different between stocks, however, Big Fish River females had significantly greater adjusted mean dressed weights (muscle mass) than Babbage River females. Big Fish River females allocated more energy to reproduction (gonad weight), when controlling for length, but not when controlling for dressed weight. Additional muscle mass in Big Fish River females may permit production of larger gonads either by providing greater somatic energy supply

available for gonad production, and/or by creating larger body cavities for gonads to occupy. Furthermore, Big Fish River females had larger adjusted mean egg diameters (30 % by volume), and consequently lower adjusted fecundities (opposing attributes). It was speculated that larger adjusted mean egg diameters in Big Fish River females compensate for the higher incubation temperatures experienced by eggs in this system. A longer feeding period for Big Fish River char may permit greater allocation of energy to muscle and germinal tissue production.

The higher water temperature (measured at the orifice) in the Big Fish River system does not appear to increase the metabolic demand of overwintering adult fish; consequently, growth and/or reproductive effort of females in this population are not constrained. However, the higher overwintering site temperature appears to lower the current reproductive potential of female char by requiring them to produce larger, and therefore fewer eggs.

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1. INTRODUCTION

1.1 Advantages of Anadromous Migration

In theory, anadromous life histories will evolve through natural selection only when migration across the freshwater-marine boundary provides a gain to individual fitness (lifetime reproductive success) that exceeds the costs of this behaviour (Gross, 1984). These costs may include adjustments to physiology, greater allocation of energy to swimming, and potentially higher mortality due to longer migrations. The fitness benefit is that anadromy enables individuals from the population to acquire more energy than would have been possible, in the same period of time in the riverine environment. This is because the coastal brackish environment has densities of prey items which can be on the order of four to five magnitudes (i.e., 10^5) greater than those available in the riverine environment (Craig, 1989). Greater net food accumulation results in individuals being able to attain a larger body size than they would if they were to have remained in the freshwater habitat. This increased body size not only results in an increased ability to avoid predators but also an increased reproductive capacity and thus an increased fitness, especially for the females in the population. In the case of the females, increased reproductive capacity associated with the larger body size manifests itself as greater fecundity (number of eggs), larger eggs (thus larger fry), greater selection of spawning sites where conditions (substrate, current, temperature, etc.) are optimal for incubation of eggs, greater success at securing a mate, and better preparation (deeper redds) and protection of spawning nests (thus increased survival of eggs) (McCart, 1980). For males, the major advantage in reproductive fitness of anadromous migration and the resulting larger body size is a greater success in securing mates through competition with other males. However, direct competition is not the only way by which male fish can succeed in reproducing. That is, a sneaker strategy favouring small mature non-anadromous males with juvenile external appearance has evolved in these fish (McCart, 1980). Thus, selection pressure for anadromous migration in males will not be as great as it is in females. As a consequence, the major fitness advantage to a population which undertakes an anadromous migration is increased reproductive potential of the female component.

1.2 Types of Anadromous Salmonids - Iteroparous vs. Semelparous

In salmonid fish species two general patterns of reproduction can be identified: semelparity and iteroparity. In semelparous fish species such as the Pacific salmon (*Oncorhynchus spp.*) spawning takes place only once with the adult fish dying on completion of the spawning act. For iteroparous fish species such as the Atlantic salmon (*Salmo salar)*(Linnaeus), the lifetime reproductive effort is spread over several spawning attempts. In such fish on reaching maturity, the frequency of spawning may be annual or as infrequently as every third year. Semelparity is favoured in populations where adult post-spawned mortality is high and thus chances of a future reproductive attempt(s) are unlikely (Roff, 1992). It is also favoured in systems where egg and juvenile mortality is low and stable, and ample opportunity exists for juveniles to become established (i.e., density-independent juvenile mortality) (Calow, 1985). Glebe and Leggett (1981) concluded for American shad (*Alosa sapidissima*)(Wilson) that differences in the predictability of the reproductive environment, through its influence on juvenile mortality, were the principle regulators of whether populations exhibited semelparous or iteroparous life history patterns. They found semelparity was exhibited in southern populations with more temperature-stable rearing environments whereas iteroparity was exhibited in northern populations with more unpredictable environments. The Pacific salmon populations of the west coast of British Columbia utilize a semelparous reproductive strategy. In these populations mortality of spent adults is inevitable because many of the populations must undertake long and difficult migrations up fast rivers with many sets of falls and rapids. These migrations thus require the individual salmon to expend relatively large amounts of energy. This coupled with large amounts of energy needed for reproduction and the uncertainty of surviving a difficult downstream migration, makes a successful return to the sea following spawning extremely unlikely. Juveniles in these populations move to sea either immediately after hatching or within a couple of years depending on the species. Once in the marine environment, food resources and habitat are abundant and probably not limiting, thus the mortality of the juveniles is independent of density. Both density-independent mortality of juveniles and high mortality of post-spawners are expectations associated with a semelparous strategy for life history.

By contrast, iteroparity is favoured in populations where the likelihood of adult post-spawned mortality is low and/or egg and juvenile mortality is high and variable, with few opportunities for juveniles to become established (i.e., density-dependent juvenile mortality) (Calow, 1985). The salmonid species of *Salmo* and *Salvelinus* exhibit an iteroparous life history strategy with the char species of the genus *Salvelinus* exhibiting the greatest degree of iteroparity. Char exhibit delayed maturity and relatively high postspawning survival rates and thus are long-lived. Juveniles of these species can spend up to five years in the riverine environment before undertaking migration to marine environments (McCart, 1980). For arctic riverine populations of these species, like the northern form of Dolly Varden char (*Salvelinus malma*), the amount of food resources and suitable habitat within the rivers is limited by the severe climatic conditions. With average yearly air temperatures of well below zero and short cold summers, the majority (95%) of arctic freshwater riverine habitat freezes to the bottom during the eight months of winter (Craig, 1989). Thus, each river system can only adequately support a certain density of juveniles. Also, these riverine environments are susceptible to early and variable timings of freeze-up as well as unpredictable flow regimes. Thus, survival of eggs and juvenile survivorship will vary from year to year depending on the severity of the weather and competition with conspecifics. As a result, the young stages of arctic riverine species, like Dolly Varden char, are subjected to high levels of density-dependent mortality. The long life span of adults of these species enables them to spawn enough times such that, despite the high and variable mortality of the young, sufficient numbers survive for the population to maintain long-term stability. Multiple attempts at reproduction ensures that the loss of all progeny of an individual in one particular year due to bad weather, competition, or a combination of these will lessen the likelihood of the elimination of that individual's genotype from the population. Additional reproductive episodes will allow further opportunity for the individual to contribute to future generations.

1. 3 Iteroparous Dolly Varden Char

1.3.1 Geographical Distribution

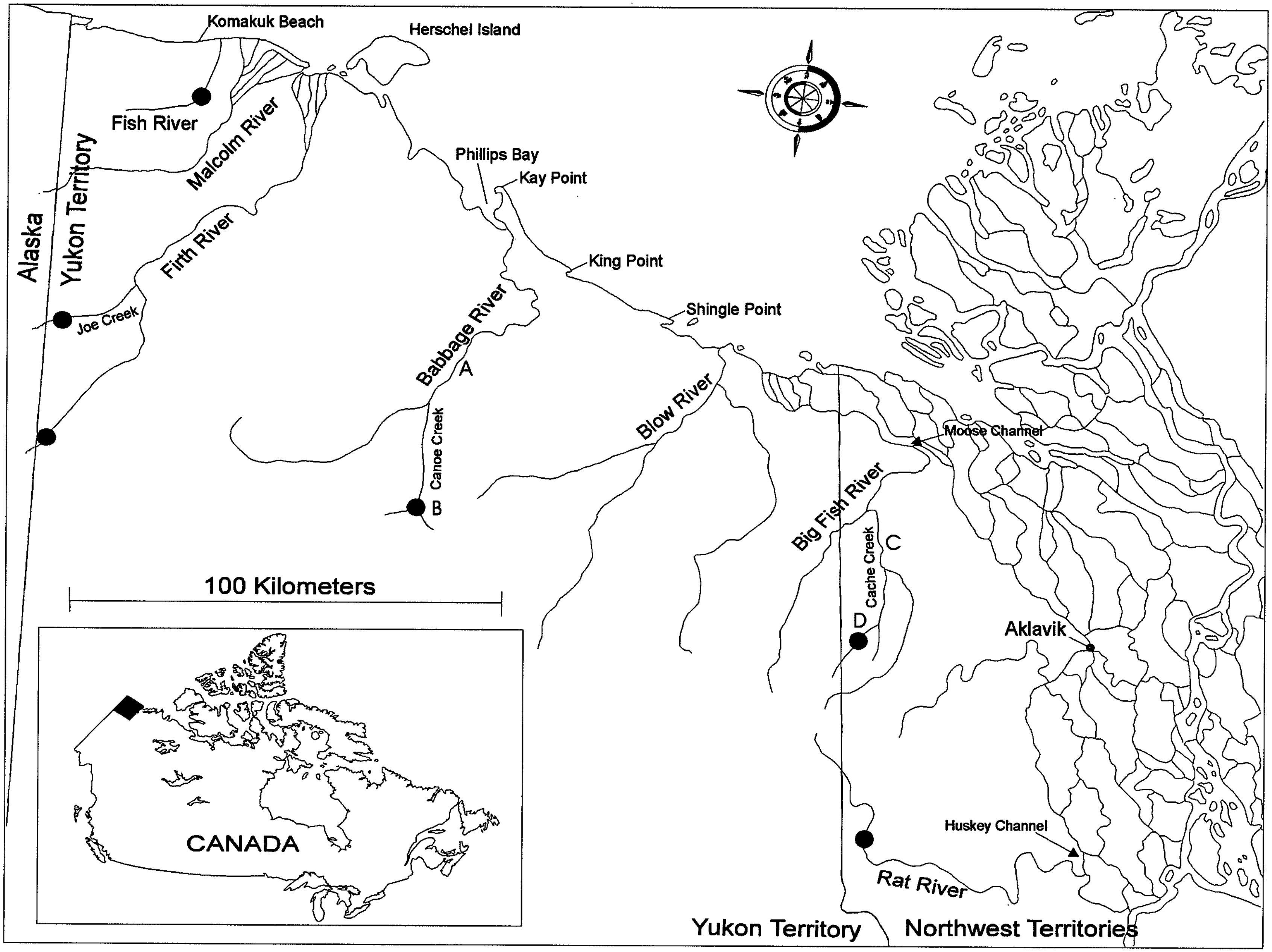
In the western arctic, which includes the Yukon north slope, the Mackenzie River forms the demarcation between two taxonomic forms of anadromous char (Reist et aL., 1995 in press). To the east of the Mackenzie River are populations of Arctic char (*Salvelinus alpinus*)(Linneaus), which utilize primarily lacustrine habitats for spawning, rearing, and overwintering. To the west of the Mackenzie River are populations of Dolly Varden char. These two groups are taxonomically distinct (McPhail, 1961; Morrow, 1980; Reist et al., 1995 in press). For the anadromous Dolly Varden char west of the Mackenzie River, two forms exist: a northern form, with 21-23 gill rakers, 25-30 pyloric caeca and 66-68 vertebra ranging from the Alaskan Peninsula to the Mackenzie River; and a southern form, with 16-18 gill rakers, 20-30 pyloric caeca and 62-64 vertebrae, found in coastal rivers south of the Alaskan Peninsula (DeCicco, 1991). The southern form of Dolly Varden char, like *S. alpinus,* is usually associated with lakes, using lacustrine environments for spawning, rearing and overwintering. In contrast, the northern form of Dolly Varden char almost exclusively utilizes riverine habitats for spawning, rearing, and overwintering.

1.3.2 Yukon and Northwest Territories North Slope Dolly Varden Stocks

There are five known spawning stocks of anadromous Dolly Varden char on the Yukon north slope and the adjacent north west corner of the Northwest Territories (hereafter unless specified otherwise the phrase north slope will refer to the Yukon

Territory and the northwestern corner of the Northwest Territories of Canada) (McCart, 1980). The most easterly and southerly of these stocks is the population in the Rat River. The Rat River flows 90 km to the east from the spawning and overwintering site on Fish Hole Creek, in the Richardson Mountains, to the mouth at Husky Channel near the southern limit of the Mackenzie River Delta (Figure 1). The coast lies another 180 km north of this point down the channels of the Mackenzie River Delta. North of this system and on the western edge of the Mackenzie River Delta is the char stock in the Big Fish River. The Big Fish River flows 65 km northeast from the spawning and overwintering site on Cache Creek at an elevation of 380 m, to the river mouth at Moose Channel (Figure 1). From the mouth of the Big Fish River it is another 30 km down Moose Channel to Shallow Bay on the Beaufort Sea coast. Further west along the north slope is the stock in the Babbage River. The Babbage River flows approximately 110 km from the spawning and overwintering site in the headwater tributary of Canoe River at an elevation of 250 m, to the river mouth at Phillips Bay on the Beaufort Sea Coast (Figure 1). To the west of this, the largest stock of Dolly Varden char on the Yukon north slope, the Firth River stock occurs. The Firth River has two spawning and overwintering sites, one located on Joe Creek at an elevation of 550 m and approximately 110 km from the river mouth, and a second in the upper reaches of the Firth River at an elevation of 520 m and approximately 125 km from the river's mouth on the Beaufort Sea coast (Figure 1). The last and probably the least studied stock of Dolly Varden char on the Yukon north slope is the stock in the Fish River which is situated between the Malcolm River to the east and the Alaskan border to the west. This river is the shortest of the five river systems in

Figure 1. Map of the Yukon and Northwest Territories north slope showing the five rivers known to contain populations of anadromous Dolly Varden char (*Salvelinus malma*). These rivers are (from left to right) the Fish River, Firth River, Babbage River, Big Fish River, and Rat River. Solid circles on each river indicate the location of documented spawning and overwintering sites for anadromous fish. (A) is the location of the weir on the Babbage River 1990 to 1992, (B) collection location of fall samples from the Babbage River, (C) is the location of the weir on the Big Fish River in 1991, and (D) collection location of fall samples from the Big Fish River.


Komakuk Beach
Herschel Island
Fish River
Malcolm River
Alaska
Yukon Territory
Firth River
Joe Creek
Phillips Bay
Kay Point
King Point
Shingle Point
Babbage River
A
Canoe Creek
B
Blow River
Moose Channel
Big Fish River
Cache Creek
C
D
Aklavik
Huskey Channel
Rat River
100 Kilometers
CANADA
Yukon Territory
Northwest Territories

Canada that contain Dolly Varden char, stretching only 21 km from the spawning and overwintering site, at an elevation of 180 m, to the mouth on the Beaufort Sea coast near Komakuk Beach (Figure 1).

1.3.3 Life History Types of North Slope Char Populations

McCart (1980) indicated that four life history types of Arctic char are found in waters of the north slope. These are: 1) anadromous char, exhibiting a life history typical of anadromous fish; 2) stream-resident char (residuals or precocious parr) that are almost exclusively males, associated with anadromous fish, but which mature without going to sea; 3) lake-resident char that pass their entire life history in close association with lakes; and 4) isolated stream-resident char that are isolated from other char populations by impassable barriers to migration such as falls. Of these, the residual and anadromous forms co-occur spatially in riverine habitats usually near the spawning and overwintering locations and elsewhere as small juveniles. Resident males participate in spawning with the larger anadromous pair by utilizing a sneak spawning behaviour (McCart, 1980). During spawning resident males hide in the vicinity of the anadromous pair until the female releases her eggs, at which time the resident male(s) rush in under the female and release their milt at the same time as the anadromous male. The lacustrine life history type is known to only occur on the north slope in two small lakes associated with the lower Firth River. Reist et al. (1995 in press) found in a morphological and genetic comparison of char from locations in the western Arctic that the lacustrine north slope char exhibited a greater similarity to Arctic char than to Dolly Varden char. They conclude that lacustrine char from the Canadian north slope may in fact be relictual Arctic char. At least two populations of isolated stream-resident char are known from the north slope, one found in the upper Babbage River and the other in the upper Cache Creek. Both populations are found above an impassable water fall. Reist et al. (1995) concluded that these fish are Dolly Varden char. Reist (1989) concluded that isolated stream-resident fish are not members of the anadromous genetic stock found downstream in the same basin. So far as is known the only distributional overlap of life history types is between the anadromous and residual forms.

1.3.4 Stock Discreteness of North Slope Char Populations

1.3.4.1 Genetic Stock Structuring

Reist (1989) found significant genetic differences between samples of anadromous spawners from four north slope char populations (Firth, Babbage, Big Fish, and Rat River populations). He also found differences between spawning and overwintering locations within the Firth River drainage (Joe Creek and upper Firth River). These differences were observed in the two polymorphic enzymes examined, and genetic results were generally substantiated by a comparison of a small set of meristic data. This finding indicates that north slope char populations are structured into discrete genetic stocks or biological populations. Thus, the sexually mature and spawning adults of a particular population show a high degree of site fidelity by homing to their natal system for spawning and/or overwintering. For the limited samples available, no differences between the anadromous spawners and other life-history stages were found, also implying a high degree of site fidelity for migratory but non-reproductive individuals (e.g., non-reproductive juveniles, and resting anadromous adults). Also, no differences were found between the anadromous and residual life history types. The presence of genetic structuring into discrete stocks suggests that there is little inter-river wandering of reproductive adults between the stocks.

1.3.4.2 Degree of Inter-River Movement as Determined by Floy-Tagging Results

Tagging studies conducted on the north slope char populations between the mid-1970s and the present have failed to demonstrate any more than an incidental movement of anadromous (likely non-spawning) char between systems. Out of 641 char tagged during the seaward migration in the Firth River in 1972, only two were subsequently recaptured in other drainages, one in the Kongakut River and another in the Canning River, two systems found to the west along the Alaskan north slope (Glova and McCart, 1974). Both of these fish were non-spawners at the time of their capture (mid- to late-September, 1972) which suggests that there may be some inter-river movement of non-spawning individuals who would not necessarily be committed to their natal system in a non-spawning year. Between 1990 and 1992 over 1500 Floy tags were placed on anadromous char during summer weir operations in the Babbage River drainage and over 500 Floy tags were deployed during a similar weir operation on the Big Fish River in 1991 (Harwood and Sandstrom, unpublished data). To date no tagged char have been recaptured in any of the systems other than the one in which the fish was tagged. Although no recapture mechanism has operated at the Firth River during the intervening years, and thus