

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

A thesis
submitted to
the Faculty of Graduate Studies
University of Manitoba

In partial fulfilment
of the requirements for the
degree of Master of Science

by

Stephen J. Sandstrom

Winnipeg, Manitoba

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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),
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STEPHEN SANDSTROM

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba
in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

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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 post-

spawning 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

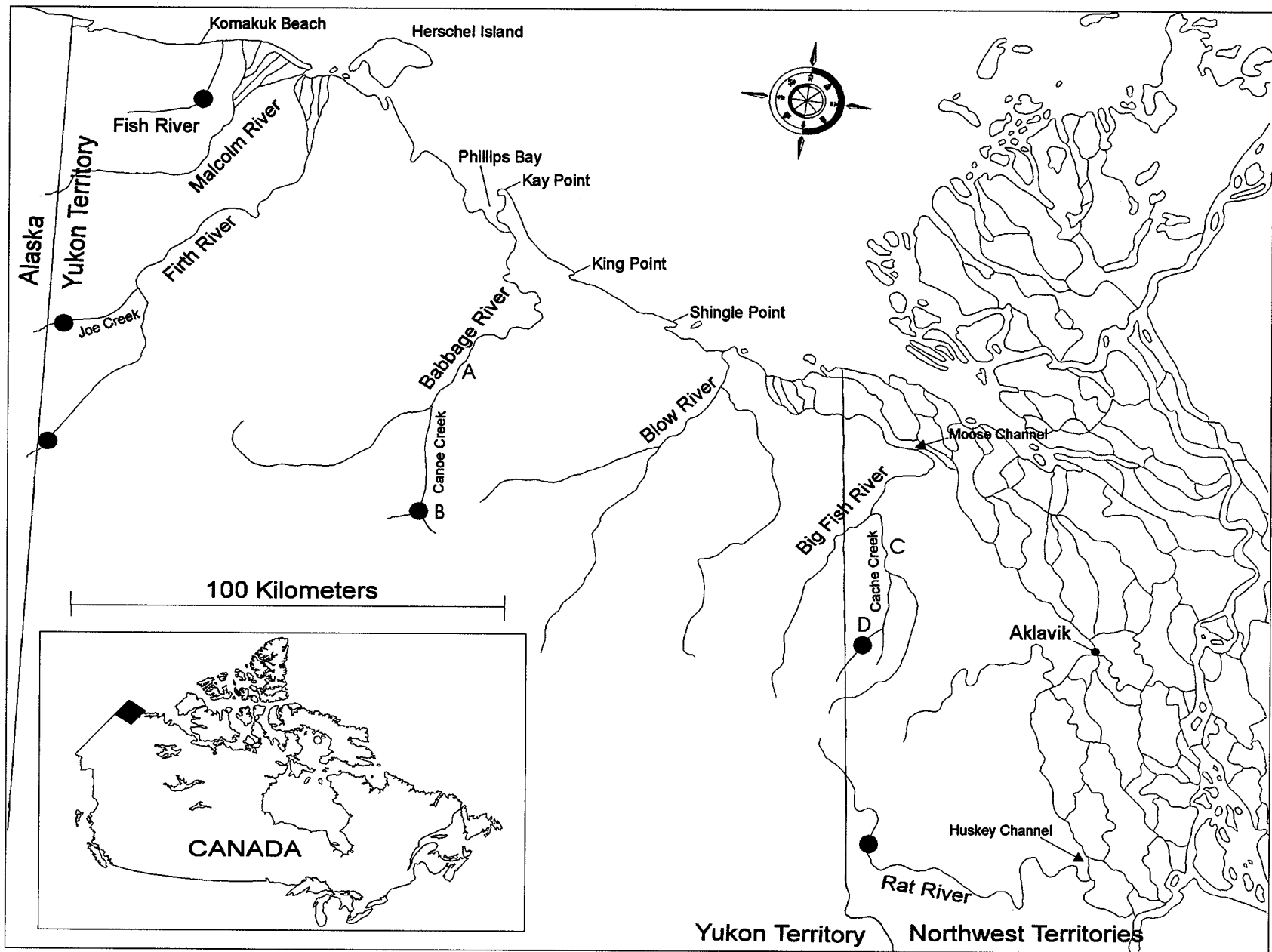
In the western arctic, which includes the Yukon north slope, the Mackenzie River forms the demarcation between two taxonomic forms of anadromous char (Reist et al., 1995 in press). To the east of the Mackenzie River are populations of Arctic char (*Salvelinus alpinus*)(Linnaeus), which utilize primarily 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.



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

movement to this system is uncertain, subsistence fisheries (recapture mechanism) for char have operated at both the Rat River and Big Fish River in 1992 and 1993. Also extensive seining surveys of the Big Fish River population in 1992 and 1993 failed to capture any fish tagged in river systems other than the Big Fish River. This evidence confirms that the individual populations of char inhabiting north slope rivers are indeed discrete genetic populations.

1.3.5 History of Exploitation of North Slope Char Populations

Only char from two north slope systems have faced significant exploitation in the recent past. Because of their relative proximity to the Mackenzie Delta, the populations of the Rat and Big Fish Rivers have both had a fairly active subsistence fishery. Also, for a span of 20 years (1965-85), a small commercial fishery occurred and in 1985 had a total quota of 900 kg for the Mackenzie Delta area (Gillman et al., 1985). The annual take of this fishery has been significantly higher in the past with as much as 7,300 kg of char being harvested in 1965 for local sale (Gillman et al., 1985).

The population in the Rat River has been fished annually and historically at the mouth of the river (Figure 1) and at different points downstream of the mouth along Husky Channel by residents of Fort McPherson. Some char from the Rat River are also removed each year by subsistence nets at the town site of Aklavik as the char migrate up the Husky and Peel Channel to their overwintering site in the Rat River.

The local subsistence harvest of the Big Fish River population occurred at two different times during the year. The first occurred during August and early September at

the mouth of the river and along the immediate coast where char were caught by gillnets as they migrated upstream (Gillman et al., 1985). The second, which was the major harvest, occurred later in October when seine and fine-mesh gillnets were used to "sweep" char from the fish holes on the spawning and overwintering site in the headwaters of Cache Creek, a tributary of the Big Fish River (Figure 1).

Since the early 1970s when the advent of the snowmobile provided a method of easy access to the overwintering site during the winter, the Big Fish River has supported an active subsistence harvest for char (J. Archie, Aklavik Hunters and Trappers Committee, personal communication). As many as 5,000 to 7,000 char were removed by the fishery in 1972 (Stein et al., 1973) but as the overall population size declined due to the exploitation, annual catches dropped each year until 1986, when only 1,860 char were removed (Fehr and Archie, 1989). In 1987, because of the declining catches, by mutual agreement of the Department of Fisheries and Oceans and the Fisheries Joint Management Committee, the river was closed to fishing for five years in order to allow the stock to recover. The char population of the Big Fish River has yet to experience significant levels of exploitation within the river itself since the re-opening of the fishery in 1992. About 20 char were taken by a subsistence fishery at the mouth of the river in the summer of 1992 and a quota of 200 char was issued for a fall fishery at the overwintering site in 1993. However, only 30 to 50 fish were taken that fall (L. Harwood, Dept. of Fisheries and Oceans, Inuvik, personal communication). No pre-impact data is available for the char population in the Big Fish River. Thus, it is not known whether the population is nearing stable equilibrium with its physical and biotic environment now that it has had between

five and eight years of recovery (prior to this research). However, it is assumed in this research that five to eight years is a reasonable period for recovery and, thus, the effects of past exploitation on observed life history parameters in this population should be minimal.

The populations of the Fish, Firth, and Babbage Rivers can, for all intents and purposes, be considered unexploited populations and have individually not been subjected to significant commercial, subsistence or sport fishing pressures due to their inaccessibility. Historically, a large number of char from the Babbage, Fish, and Firth Rivers were probably taken annually in the coastal waters around Herschel Island by local residents of the island up until the mid-1960s when the town site and island were abandoned (Figure 1). The relative contribution of these three stocks to this harvest is unknown. In the mid-1960s the Menzies Fish Co. harvested around 7,300 kg of char from Pauline Cove and Ptarmigan Bay off Herschel Island in a commercial venture to market north slope char (Baker, 1987). This proved to be a one-time event because logistical constraints, weather conditions, and high operation costs prevented it from becoming a successful economic venture. Sport fisherman and tourists rafting the Firth River have taken approximately one hundred char each summer from this population (D. Frandsin, Parks Canada, Inuvik, personal communication).

Each summer, between 200 and 500 char are harvested, primarily by residents Aklavik, at Shingle Point in conjunction with the summer beluga whale hunt that occurs there in July and August (Figure 1). The majority of these char are probably from the stocks of the Big Fish and Rat Rivers, but tag recaptures have indicated that Babbage River char are also taken there (Harwood and Sandstrom, unpublished data). Again, the

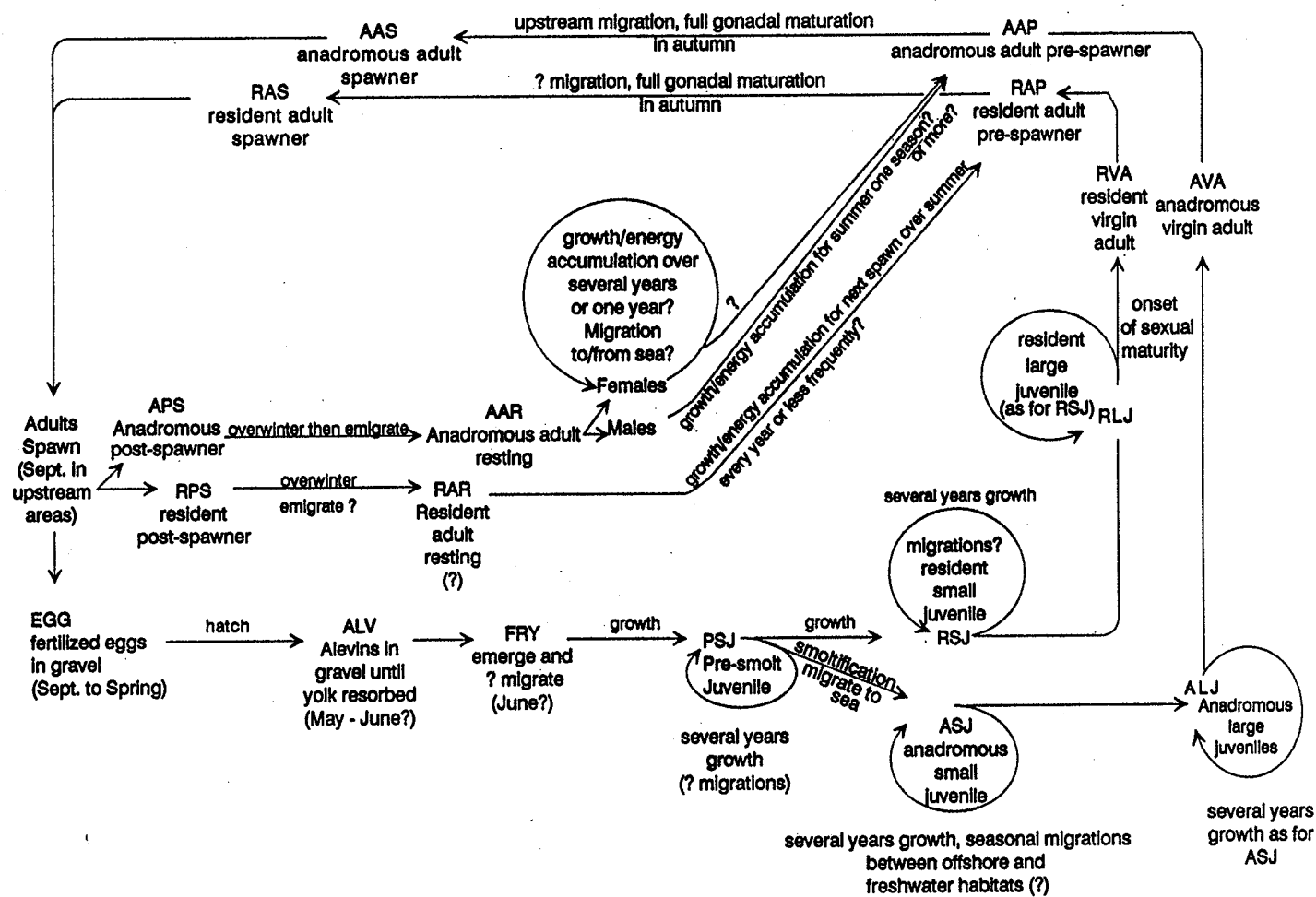
relative contribution of char from each system to the total catch has never been determined

1.3.6 General Life History of North Slope Dolly Varden Char

The general life history stages of north slope anadromous male and female char and the co-occurring residual male char are summarized in Figure 2. Spawning behaviour of the northern form of Dolly Varden char has not been described but is probably not significantly different from that documented for the southern form (Leggett, 1969; Armstrong et al., 1980). Spawning of north slope anadromous Dolly Varden char typically occurs between mid-September and early October at the spring-fed overwintering sites in a headwater tributary (Bain, 1973; Glova and McCart, 1974; McCart, 1980). Mature anadromous females are usually the first to arrive on the spawning grounds where they select a suitable site in the region of the orifice of the thermal springs to dig a shallow depression (redd) in which to deposit their eggs. Pairing with an anadromous male occurs during or shortly after the location for the redd is selected and both redd and female are defended by the male partner until spawning takes place. After spawning the male may either remain in the vicinity of the spawning site to spawn with other females or will move downstream to the lower limit of the overwintering site to prepare for the upcoming winter (Craig, 1977; DeCicco, 1989). The female will remain on the redd for several days defending the area from other females who are searching for spawning sites, but will later move downstream to overwinter with the rest of the population in the ice-covered lower reaches of the overwintering site.

Eggs incubate during the eight months of winter to hatch as alevins sometime in mid-

Figure 2. Summary of the life history stages for anadromous male and female Dolly Varden char and the co-occurring residual or resident male Dolly Varden char on the north slope. Abbreviations are for the life history stage also labelled on the figure (eg. AAR = Anadromous Adult Resting) (Reist, unpublished data).



May (Bain, 1974; Glova and McCart, 1974; McCart, 1980). The alevins will remain in the gravel for about one week, increasing in length and living off reserves in the yolk sack. Once the yolk sack is absorbed, the alevin works its way up to the surface of the gravel and becomes a free-swimming and now exogenously feeding fry. Those fry that are not washed downstream by the spring freshet will spend the first year in the vicinity of the overwintering site but may in later years, as parr, make limited downstream movements during the summer (Glova and McCart, 1974; Craig and Poulin, 1975; Armstrong et al., 1980). The overwintering habitat in these systems is spatially limited during the winter months to the area of the spring-fed overwintering site and a few deeper pools along the lower river channel. The exception to this is in the Firth River drainage where the presence of springs near the delta of the river maintain additional areas of open water capable of overwintering char. As a result, in order to survive the majority of parr that do move downstream must return to the overwintering site by late summer. After approximately three summers in the freshwater riverine environment, the parr will join the anadromous adults and move downstream in the spring to the river estuary. There the parr smoltify and feed, returning shortly after the adults to the overwintering site in the fall (Bain, 1974). The smolts probably do not undertake as extensive a coastal migration as the adults in their first years "at sea" and may simply remain in the estuary of the river system feeding and undergoing the necessary physiological adaptations needed for migrations in more marine waters in subsequent summers (Armstrong et al., 1980).

The seasonal downstream migration of the north slope stocks usually corresponds with the spring break-up of the river and the spring freshet, although downstream movement

can be impeded and char prevented from entering the sea during the freshet if winds move broken sea-ice onshore (DeCicco, 1989). Char move from the rivers to the coastal Beaufort Sea environment to feed, however, little information is known regarding the degree to which these north slope stocks migrate in the marine environment or what part of this environment they utilize most frequently. Several researchers have suggested that this movement is coastal in nature with the migrating fish preferring the narrow band of brackish water that lies relatively close to shore during the summer months (Johnson, 1980; McCart, 1980; Bond et al., 1989). However, DeCicco (1992) has documented movements of the northern form of Dolly Varden char across the Bering Sea from Alaska to Russia. Also, high seas fisheries in the Bering Sea regularly capture Dolly Varden char more than 200 km from the nearest land (Reist, unpublished data, personal communication). Tag recaptures of Firth River char at Barter Island and in the Canning River (250 km to the west of the Firth River) indicate that the coastal migration distance may be extensive for some stocks (Glova and McCart, 1974). Coastal migrations up to 485 km have been reported for some populations of the northern form of Dolly Varden char on the north west coast of Alaska (DeCicco, 1989). One Dolly Varden char tagged in a northwestern Alaskan river in September of 1988 was recaptured in a Russia River draining into the Gulf of Anadyr in August of 1989 (DeCicco, 1992). This represents a non-coastal migration of close to 1690 km in one summer.

The return upstream migration of adult and juvenile char from the sea is fairly consistent in its timing from year to year. In the case of the char population in the Babbage River, return migration commenced in the first week of August and tailed off

around the first week of September fairly consistently between 1990 and 1992 (Sandstrom, Harwood and Reist, unpublished data, Figure 3). Timing of the upstream run in the Big Fish River recorded in 1991 was similar to that recorded at the Babbage River (Harwood and Sandstrom, unpublished data, Figure 4). Thus, the duration of time char spend feeding at sea during a particular summer is dependent on the date of spring break-up, with char probably having a longer summer feeding opportunity in rivers or years in which break-up is earlier.

Current-year spawning adult char are usually the first to begin their upstream migration in late July and early August, followed by adult non-spawners in mid- to late-August and finally by smolt and post-smolt juveniles in the latter part of August and early part of September (Glova and McCart, 1974; Griffiths et al., 1975 and 1977 as cited in McCart, 1980; Sandstrom, Harwood and Reist, unpublished data).

The juvenile char will spend several summers migrating to the sea each spring to feed and put on length and weight as post-smolts, and may mature for the first time in the summer of their fifth year, but more usually in their sixth year (Bain, 1974; McCart, 1980). Love (1980) noted that fish in general tend to mature for the first time at a particular length rather than at a particular age. Because the relatively smaller male gonad requires a smaller body size, and fork length is positively correlated with age, anadromous male char are likely capable of maturing for the first time at a smaller size and thus younger age than female char.

The Dolly Varden char of the north slope are iteroparous and may spawn numerous times over their lifespan, which may be as long as 18 years in the northern form of Dolly

Figure 3. Numbers of Dolly Varden char enumerated each day at the weir on the Babbage River in (A) 1990, (B) 1991, and (C) 1992 (Sandstrom, Harwood, and Reist, unpublished data).

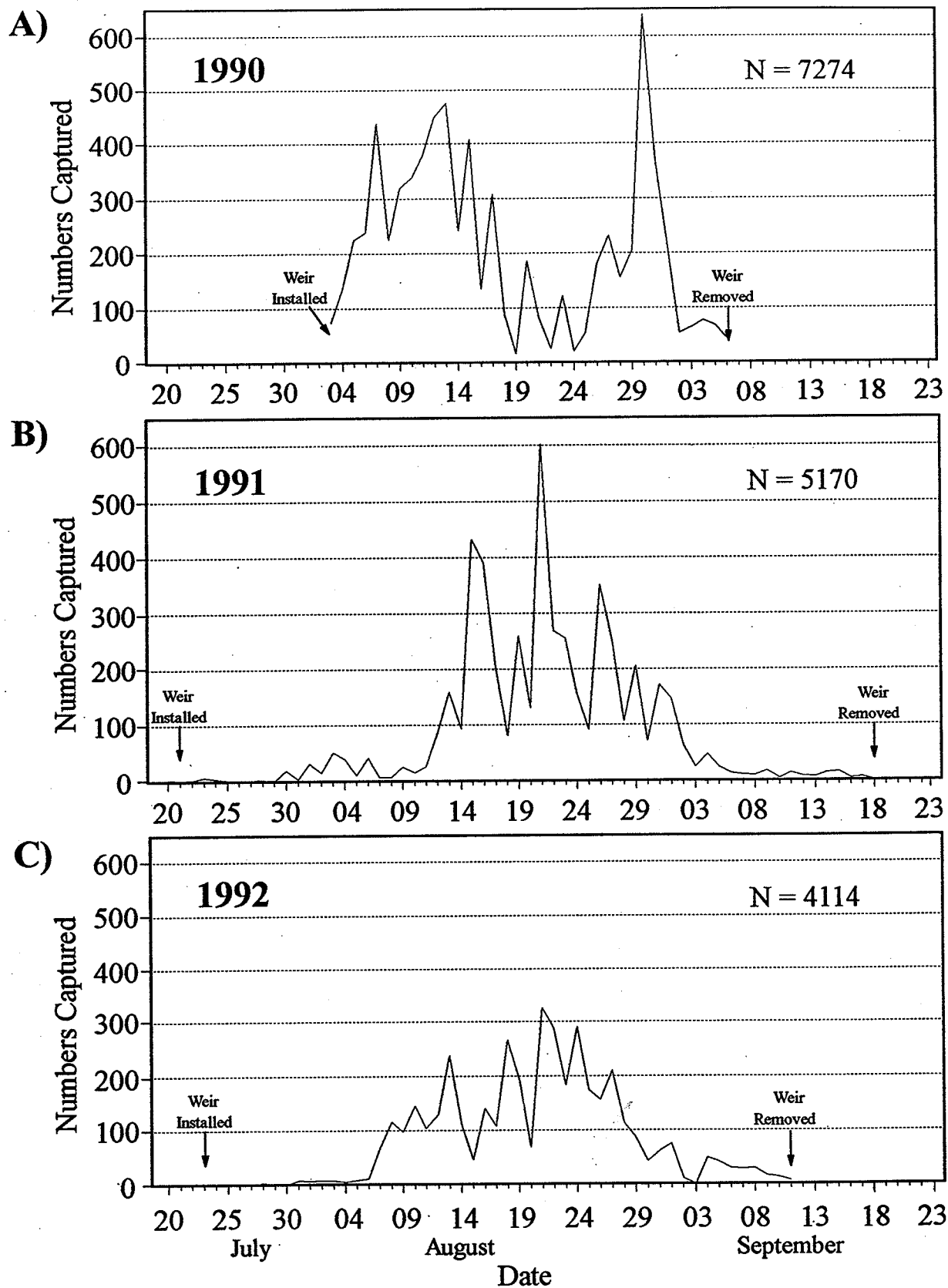
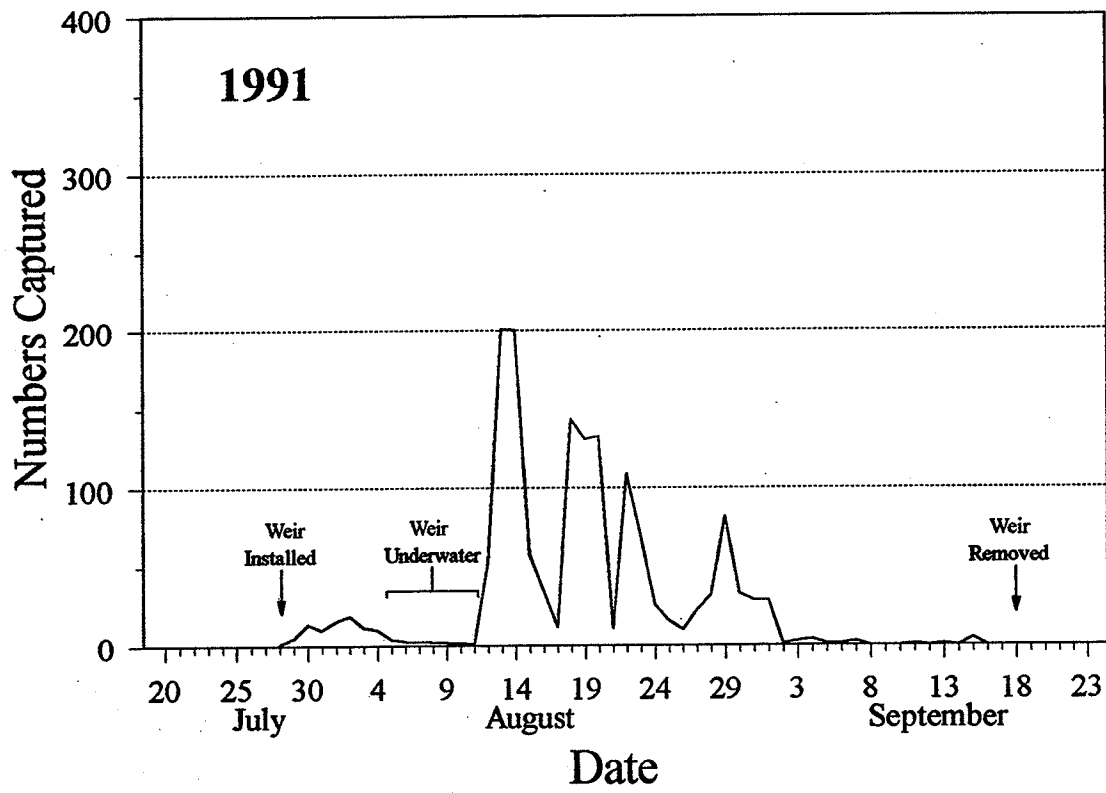


Figure 4. Numbers of Dolly Varden char enumerated each day at the weir on the Big Fish River in 1991 (Harwood and Sandstrom, unpublished data).



Varden char (Yoshihara 1973a as cited in Armstrong et al., 1980). However, few north slope char appear to live past ten years of age and spawn more than twice (McCart, 1980). Because of the short feeding season and the extreme environmental demands placed on these populations, some individuals in a population are probably not able to accumulate enough energy the summer after spawning to both replenish depleted energy reserves, and build up sufficient reserves to spawn the following fall. As a result, the majority of adults in these populations probably spawn every second or third year. Gudkov (1991) concluded that the majority of Dolly Varden char populations from the Chukotka Peninsula and the rivers of the northern Sea of Okhotsk in northeast Siberia were able to accumulate sufficient energy the summer after spawning to spawn every year after first maturation. These conclusions were based on the cross-section analysis of the otoliths which revealed that spawning checks were present in sequential years in 87% of the otoliths examined. Armstrong (1975) determined that in the three populations of the southern form of Dolly Varden char he studied in south west Alaska, most of the population spawned annually once maturity was reached. On the contrary, Furniss (1975, as cited in McCart, 1980) determined by way of tagging studies that in the case of the northern form of Dolly Varden char in the Sagavanirktok River in northern Alaska, only 1.3% of the anadromous male char and 5.9% of the anadromous female char spawned consecutively. For northern populations of coregonids the proportion of the population which does not reproduce yearly increases (from 52° N northwards) up to 42% of females and 23% of males (Moreau, 1981 as cited in Dabrowski, 1985). The apparent reason for this reproductive discontinuity is energy insufficiency in the more northerly

populations. Thus, it appears for the northern form of Dolly Varden char that these populations are less likely to spawn in consecutive years. This is probably due to greater environmental demands being placed on the more northerly populations due to the shorter growing season.

In freshwater, char overwinter in headwater regions of the river where the presence of a thermal spring maintains a section of open water throughout the winter (Bain, 1973; Glova et al., 1974; McCart, 1980). These habitats are characteristically shallow (average depth of 0.5 meters), three to five meters wide and several kilometers long. In these overwintering sites the majority of the upper stretch remains relatively free of ice, with ice forming only along the edges of the river bank. The lower stretch of river is totally ice covered, which in sections can be over several meters thick. As the water travels downstream away from the spring orifice it slowly drops in temperature, thus, creating a thermal gradient spatially along the extent of the overwintering site. Significant movement of char along this temperature gradient is almost impossible once freeze-up has occurred. This occurs because many of the shallower riffle areas, which separate the deeper stretches, freeze almost to the gravel leaving usually less than an inch of free water flowing over the gravel. Decreased winter flow also lowers the depth of water in these riffle sections making it difficult for fish to traverse. At the downstream limit of the overwintering site the flowing water is forced to the surface where the flow is dispersed horizontally and freezes, forming a large field of ice. These areas of layered ice are known as *naleds* or *aufeis* fields and may reach a thickness of six meters in some systems (Keller et al., 1961 as cited in Craig, 1989). The majority of north slope rivers freeze to the

substrate during the winter, except for a few of the deeper pools, so the spring-fed overwintering sites represent the only substantial habitats available for the char to overwinter. To date there has been no overwintering habitat confirmed as being used by char, other than those at the spring site(s) for any of the Canadian north slope systems. Craig (1989), in a review of some Alaskan north slope systems, also found char only in the spring-fed habitat during the winter and none in the middle or lower sections of the rivers he investigated. Glova and McCart (1974) identified potential areas in the lower main stem of the Firth River where char could overwinter but were unable to substantiate this with the capture of fish in these areas. DeCicco (1989) did find that the lower regions of several rivers in northwest Alaska were used by some of the population for overwintering. However, because these systems are considerably larger than any found on the Canadian north slope, the lower reaches of the river are sufficiently deep enough that they do not freeze to the substrate in the winter, and some level of flow is maintained throughout the winter.

The majority of the char population, from egg to adult, is restricted during the fall and winter to the area of the river between the spring source and the *aufeis* field for up to nine months. The only documented exception to this is found at the Big Fish River overwintering site located in the headwaters of the Cache Creek tributary (Figure 1), where juvenile and adult char were caught in "ice tunnels" that form in the core of the *aufeis* field (Harwood and Sandstrom, unpublished data). These tunnels are approximately two meters in diameter with half meter of water flowing through them, and extend downstream throughout most of the *aufeis* field. The type of habitat found at the

Cache Creek overwintering site appears to be unique, because similar habitat has not been identified in the literature regarding other north slope overwintering sites. Similar habitats were not found during an investigation of the *aufeis* field at the overwintering site on the Babbage River in March of 1991 and May of 1992 and 1993 (Sandstrom and Reist, unpublished data). It is likely the result of the warmer orifice temperatures (i.e., 15° C) at the spring on the Big Fish River in comparison to those of the other systems (e.g., 4° C at the Babbage River).

There are twelve such thermal spring sites on the North Slope, seven of which are known to contain overwintering char, and several of which vary dramatically with respect to the physical and chemical composition of the spring's water (Craig and McCart, 1974; Mutch and McCart, 1974). For example, the two systems under investigation in this research - Babbage and Big Fish Rivers- have springs with marked physical and chemical differences (Table 1). The low mineral content of the Canoe River (Babbage River) spring water combined with a low water temperature at the orifice (4° C) and moderate oxygen concentrations indicate that this is a relatively shallow, rapid flow system with its origin in the solution channels of the underlying limestone (Mutch and McCart, 1974). In comparison, spring water from Cache Creek (Big Fish River) has a significantly higher water temperature (15° C) at the orifice, lower dissolved oxygen concentration, and higher dissolved solids content than the Canoe River spring (Mutch and McCart, 1974). This indicates that the water is being discharged from a deep slow flow system in which the water, during its movement up through the substrate, travels through sediments of recent marine origin or evaporitic rock (Mutch and McCart, 1974). As a result, the spring on

Table 1. Physical and chemical data for the springs at the Babbage and Big Fish Rivers, Yukon and N.W.T. north slope. Data collected in 1972 by Water Resources Branch, Environment Canada (van Everdingen, 1973 a, b as cited in McCart and Bain, 1974). Values are in mg per liter unless otherwise indicated. Capital letter in brackets for location is a cross reference to location on Figure 1.

River	Big Fish R.	Big Fish R.	Babbage R.	Babbage R.
Location	Cache Ck. (D)	Cache Ck.(D)	Canoe Ck.(B)	Canoe Ck.(B)
Sub-Location	Main Spring	Main Spring	Main Spring	Main Spring
Date	11/11/72	25/11/92	10/11/72	18/05/93
Temp.°C	15.5	13.0	4.0	4.0
D.O. (% sat.)	20	28	76	-
pH	7.8	7.9	7.8	8.6
Conductance (umhos/cm @25°C)	4546	3963	265	258
Ca	95	96	39	39
Mg	22.1	21.1	7.4	9.8
Na	824	705	0.3	0.7
K	17.5	19.7	0.4	0.5
Fe	<0.05	<0.01	<0.05	0.03
Mn	0.008	0.01	<0.005	0.01
Cu	<0.002	-	<0.002	-
Pb	<0.006	-	<0.006	-
Zn	0.56	-	0.19	-
HCO ₃	267.2	-	140.3	-
CO ₃	0.0	-	0.0	-
SO ₄	417	343	13.2	19.5
Cl	1036	985	0.2	0.7
F	1.2	-	0.12	-
NO ₃	0.04	-	0.06	-
PO ₄	-	-	<0.003	-
SiO ₂	17.6	-	4.3	-
Sum of Constituents	2698.1	-	205.5	-

Cache Creek is not only classified as a thermal spring because the temperature of the water lies significantly above the mean annual air temperature, but is also a mineral spring because the total amount of dissolved solids in the water is significantly higher than that found in the surrounding surface water of the region. This difference in freshwater environments may have significant implications for the char populations.

The suite of reproductive and growth-related life history traits (including the degree of iteroparity) expressed by Dolly Varden char populations, even within a relatively confined area such as the north slope, may vary significantly from one river system to the next. This is because a certain portion of the phenotypic variation seen in reproductive and growth characteristics between populations reflects evolutionary adaptation to the local circumstances, including energetic demands placed on the populations by their environment. Fry (1971) pointed out that all environmental variation is ultimately expressed at the metabolic level such that environmentally caused changes in metabolism result in changes in the growth or reproductive characteristics of the population. The resulting expressions of life history characteristics are population specific, with the potential for genetic changes due to gene flow between populations minimized by a strong "homing" instinct of maturing Dolly Varden char to their natal rivers. Presumably, the suite of life history characteristics specific to individual populations represents the combination which in the past has best maximized the reproductive fitnesses of the component fish over their individual life times. In this context, fitness of the individual is defined as the number of offspring reaching maturity relative to the number of maturing offspring produced by the other fish in the population (Wootton, 1985). The process

whereby natural selection increases the frequency of traits within a population that enhance the survival or reproductive success of individuals expressing them is called local adaptation (Taylor, 1991).

1.3.7 Energetic Consequences and Life History Models of the Iteroparous Dolly Varden Char

Anadromous Dolly Varden char of the north slope appear to restrict feeding to times while at sea, during the spring and summer, and probably fast during the fall and winter while at the freshwater overwintering sites (Bain, 1973; Glova and McCart, 1974; McCart 1980). Bain (1973) found that 81.7% of the juvenile char and 87.2% of the anadromous char captured in the fall (Oct.) at the Babbage River overwintering site had empty stomachs. Glova and McCart (1974) also found that a similar percentage (79.2%) of anadromous char in the Firth River had empty stomachs. For char that did have food in their stomachs in the freshwater environment, chironomid larvae were the most commonly found prey item in juvenile char stomachs and char eggs the primary food consumed by adults (Bain, 1973). This same study indicated that the freshwater feeding of anadromous char may be limited to the fall because the percentage of empty stomachs in this component of the population increased to 95.8% over the winter. Thus, following nine or ten months of residency in the freshwater riverine environment, char have only two or three months during the summer to accumulate sufficient energy reserves at sea to conduct the necessary life history activities until the following summer. In theory, Dolly Varden char life history strategy should evolve in such a way that there is an optimal

allocation of energy reserves to the combined fitness benefits of growth, maintenance and reproduction and, in the process, maximize the genetic contribution of an individual to the future populations (Cody, 1966).

Since biological systems conform to the law of thermodynamics, all energy accumulated during the brief summer feeding each year that is not lost as waste due to egestion (faeces) and excretion (urine), must ultimately be allocated between the competing life history activities of somatic growth and/or gonadal growth and metabolism. A basic energy budget can be put forward to demonstrate the partitioning of energy incorporated into the body into the major physiological components:

$$C_{\text{Total}} = M_{\text{Total}} + G_{\text{Total}} + W_{\text{Total}} \quad \text{Equation 1}$$

Where C_{Total} is the total food resources ingested, G_{Total} the total synthesis of tissues, and W_{Total} the total energy resources that are lost as waste. Of course, the required model is more complex than Equation 1 in the following ways.

a) Total metabolism (M_{Total}) of Equation 1 comprises a number of sub-

components: standard metabolism (M_s) or the minimal observed energy used by a fasting fish at rest; routine metabolism (M_r) or the energy involved in 'routine activities'; active metabolism (M_a) or the energy involved in migration, foraging, spawning activities (i.e., redd construction and defense), and overwintering movement, and; finally, feeding metabolism (M_f), sometimes called specific dynamic action metabolism, which is the energy involved in food processing and assimilation (Beamish, 1974). Thus, if all aspects are represented in the same energy units (i.e., joules; 4.2 J per cal) total metabolism can be expressed as such:

$$M_{\text{Total}} = M_s + aM_r + bM_a + cM_f. \quad \text{Equation 2}$$

Where a, b, and c are constants representing the fraction of time that each type of metabolism is used.

- b) The total synthesis of tissue (G_{Total}) can also be decomposed into a series of contributory factors. These are, energy allocated to somatic growth (both in lipid deposition (G_l) and protein synthesis (G_p)), and energy allocated to reproduction (G_r), such that:

$$G_{\text{Total}} = G_l + G_p + G_r. \quad \text{Equation 3}$$

- c) The total energy resources lost to Waste (W_{Total}) consist of the resources lost to faeces (W_f), urea (W_u) and miscellaneous secretions such as mucus (W_m).

These also include the proportion of the total food resources (C_{Total}) that are not assimilated, such that:

$$W_{\text{Total}} = W_f + W_u + W_m. \quad \text{Equation 4}$$

Thus, in summary and combining Equations 2, 3 and 4 into a single model, the total energy consumed and assimilated by an individual is partitioned to various activities as indicated in Equation 5:

$$C_{\text{Total}} = \underbrace{(M_s + aM_r + bM_a + cM_f)}_{\text{(metabolism)}} + \underbrace{(G_l + G_p + G_r)}_{\text{(growth)}} + \underbrace{(W_f + W_u + W_m)}_{\text{(waste)}}. \quad \text{Equation 5}$$

It should be noted that all components must be expressed in the same units.

For anadromous char of the north slope, resources available for allocation are finite and limited. Hence resources used in one aspect of metabolism will not be available for use in others. For example, energy used to support active metabolism (M_a), which

might increase the individuals ability to escape predators and enhance survival, would not be available for production of germinal tissue (G_r) and will have a negative effect on the reproductive output. Thus, there will exist trade-offs between the various components of metabolism and hence the components of fitness (i.e., survival and reproductive potential) influenced by them.

The energetic costs associated with reproduction include not just that energy allocated to the production of the gametes (G_r), but also energy expended in the reproductive behaviour (i.e., territory defense, redd construction, and courtship behaviour), as well as energy needed for the development of necessary secondary characteristics (spawning colouration and morphological adaptations). Both of these demands would, in part, comprise the active metabolism (M_a) component of the energy budget along with other metabolic activities such as migration, foraging and overwintering movement.

The particular way in which energy is partitioned between the various components of reproduction is also different for males and females. Jonsson et al. (1991) showed for Atlantic salmon that both male and female salmon invested approximately 50% of their total available energy to reproduction. However, 50% of the energy that females invested into reproduction consisted of gonadal tissue, whereas, males invested more than 90% of the energy to somatic investments (morphological adaptations) and metabolic costs (territorial defense). As noted above, Dolly Varden char of the north slope are an iteroparous species and may live to fifteen years of age and reproduce several times over their life span (McCart, 1980; Glova and McCart, 1974). Thus, the energy allocated to

active metabolism (e.g., migration, foraging, spawning activities, and overwintering movement), that used for routine metabolism, that which is used in feeding metabolism, and that necessary for overwintering metabolism (M_o , multiplied by the number of days in freshwater) for these stocks can be considered to be fixed energy expenditures and must come primarily (assuming no freshwater feeding) out of endogenous energy reserves of lipids (G_l). Endogenous protein (muscle) can also be oxidized to provide energy to conduct life history activities particularly overwintering metabolism. Dutil (1982) determined that fasting Arctic char derived 65% of their metabolic needs from lipids and 35% from proteins. However, because endogenous protein sources yield significantly less metabolizable energy (4.8 kcal per gm) than lipid sources (9.45 kcal per gm), proteins are usually only utilized after significant depletion of lipid reserves has occurred (Brett et al., 1979). Carbohydrates can also be used as an endogenous energy source. However, dietary carbohydrates are scarce in the foods ingested by arctic fish and are also poorly digested and metabolized. Because carbohydrates provide only 4.1 kcal per gm of physiologically useful energy, they are seldom used as an endogenous energy source (Love, 1980). Thus, once sufficient energy has been allocated for the fixed energy expenditures, any additional energy (G_i) can then be channelled into either somatic (G_p) or reproductive (G_r) tissues or some combination of the two. Somatic tissue growth can take the form of either growth in weight (muscle mass) and/or growth in length (bone and muscle mass).

The average amount of surplus energy available within individuals for growth and/or reproduction may vary from population to population because the energetic

demands associated with migration and overwintering in the respective systems may, in turn, vary. For example, populations with longer or more arduous migration distances will have higher energetic demands associated with the M_a component of the energy budget. As a result, assuming similar overall consumption, less energy will be available for growth of somatic and/or reproductive tissue. This has been substantiated by a study of anadromous American shad which found populations which allocated a greater proportion of their energy reserves to migration accomplished this by reducing the energy allocated to gonadal development (Leggett and Carscadden, 1978). Char from the Babbage and Big Fish Rivers likely have similar overall demands for migration (M_a), however, this is partitioned differently. Both rivers have similar lengths (Babbage River- 110 km, Big Fish River- 95 km) but their spawning and overwintering sites lie at a different elevations (Babbage River- 250 meters, Big Fish River- 380 meters). In comparison to those of the Babbage River, char from the Big Fish River likely have lower energy demands due to the slightly shorter migration distance. However, this is probably balanced by a larger energy demand associated with the slightly higher water velocity, due to the greater elevation of the Big Fish River spawning and overwintering site. Thus, assuming that energy required for foraging, spawning activities, and overwintering movement is the same for the populations, it is concluded that, in general, char from both systems likely experience similar energy demands for active metabolism. Establishing similarities in the energy demands for migration between the populations allows for a more accurate investigation of whether differences in environmental conditions at the spawning and overwintering sites have an effect on the degree to which energy is allocated between

the competing life history activities of growth (G) and metabolism (M) in these fish.

Fish are poikilotherms, thus, standard metabolism (M_s) is primarily a function of water temperature and body size. Populations that overwinter in systems with higher water temperatures will experience higher standard metabolic rates (Brett, 1979; Dodson et al., et al. 1985). Phillips et al. (1960) determined, by way of laboratory studies, that during starvation the body weight of brook char (*Salvelinus fontinalis*)(Mitchill) decreased by 10% for each degree Celsius increase in water temperature. As noted above, the spawning and overwintering site on the Big Fish River has significantly higher water temperature (measured at the spring orifice) than the site at the Babbage River. As a consequence, north slope char inhabiting systems with higher overwintering temperatures, like the Big Fish River, may allocate more of their assimilated energy to body reserves in the form of lipid deposition (G_l) for overwintering survival at the expense of protein synthesis (G_p) and reproduction (G_r). Some initial evidence to support this statement is available from the literature. MacDonnell (1987) noted that Big Fish River char had what appeared to be lower growth rates (observed a smaller mean size at age) and fecundity than other north slope char populations, although he was unsure why. The research described in this study sets out to examine whether the differing temperatures at the spawning and overwintering sites result in differences in fish from the two systems in the amount of energy allocated to growth in body length and body weight and/or reproduction (i.e., gonad weight).

1.4 Aims of this Study

In terms of the energy budget (Equation 5), male reproductive costs can be considered to be primarily associated with the metabolic component (M), while female reproductive costs are primarily associated with the growth component (G_r). Thus, in the case of males, it is extremely difficult to make an accurate assessment of the metabolic costs involved in the performance of the wide range of behavioural activities that contribute to a successful reproductive attempt. Because the energy demands associated with reproduction are more easily quantified and examined in females, this study will focus upon differences in females. The aim of this research was to determine whether higher overwintering site temperatures in the Big Fish River, in comparison to the Babbage River, have a significant effect on the annual growth and/or reproductive effort of female anadromous Dolly Varden char. The hypothesis tested was that higher water temperature at the spawning and overwintering site on the Big Fish River will require anadromous adult females from this system to allocate more energy to overwintering somatic reserves in order to address an increased metabolic demand. If this is so, it is expected that growth (length and/or weight) and/or reproductive effort will be decreased in females from the Big Fish River relative to those from the Babbage River. The specific predictions derived from the hypothesis are: 1) mature adult females from the Big Fish River will have significantly greater amounts of somatic lipids after spawning, and 2) in order to balance this, either lower annual growth rates and/or reproductive effort than mature adult females from the Babbage River. Dutil (1983) showed that protein (muscle) provides a large percentage (35%) of the required metabolizable energy for overwintering

Arctic char. However, because lipid oxidation appears to be the principle energy producing pathway in char species (Dutil, 1983), if differences exist between the two stocks in the amount of overwintering energy reserves then this should be detectable in the percent lipid composition of the tissue. Also, because lipid determination is relatively easier than protein determination, only lipid composition of the female char was examined in this study. Thus, it must be assumed that overwintering females from both the Big Fish and Babbage Rivers utilize protein reserves for metabolic needs to the same degree and that this usage is similar. Finally, several additional assumptions must be made with respect to the hypothesis. First, the energy accumulated by the two populations is assumed to be more or less finite, with the energy accumulated being limited to just that incorporated during the summer at sea. Second, the total energy accumulated (C_{Total}) is assumed to be similar for similar sized fish between populations. Third, the energy required for active metabolism (M_a - Equation 5) is also assumed to be similar for the two populations. Finally, it is more than likely that a thermal gradient of water temperatures exists at each overwintering site between the point where water first reaches the surface of the streambed and the point where it freezes downstream. Thus, it is possible that char can locate themselves in areas of the overwintering site at a specific, 'preferred' temperature. It is, however, assumed, because of the vast difference in orifice temperatures (over ten degrees Celsius) between the two sites, that the stretch of river in which the majority of the char population in the Big Fish River overwinters will be proportionately and significantly higher in temperature than the stretch of river that the majority of the population in the Babbage River uses for overwintering. Thus, the expected differences between the two populations should hold.

2. METHODS

2.1 Study Area

2.1.1 Physiographic Regions

The continental north slope of the Yukon and Northwest Territories west of the Mackenzie River, comprises three distinct physiographic regions (Bain, 1973). Running adjacent and parallel to the Beaufort Coast is the Arctic Coastal Plain, a narrow band of low lying tundra which varies in width from five km near the Alaskan border to 30 km at the Babbage River basin and slopes down gradually to the north from an elevation of 305 meters to sea level. Scattered along this zone are numerous shallow lakes and ponds which are remnants of former shoreline lagoons. To the south of the Arctic Coastal Plain is a narrow band of rolling foothills that rises from 305 to 610 meters in altitude and are referred to as the Arctic Plateau or the Arctic foothills. To the south of the Arctic Plateau is one of three distinct mountain ranges, the British Mountains which make up the most westerly range and rise to an elevation of 1665 meters in the Yukon Territory. In Canada this mountain range is drained to the north by tributaries of the Fish, Malcolm, Firth, and Babbage Rivers (Figure 1). Located to the east of the British Mountains and more centrally positioned on the Yukon north slope are the Barn Mountains. The Barn Mountains are the lowest of the three mountain ranges, reaching a maximum elevation of only 1195 meters. The western edge of these old, rounded mountains is drained to the north by the Canoe River (tributary of the Babbage River) and to the eastern side by western tributaries of the Blow River (Figure 1). The third mountain range on the north slope is the northern Richardson Mountains found between the Barn Mountains to the west and the Mackenzie Delta to the east, straddling the

border between the Yukon and Northwest Territories. These mountains rise to an elevation of 1753 meters in this region and are drained to the north and northwest by tributaries of the Blow and Big Fish Rivers and to the east into the Mackenzie Delta by tributaries of the Rat River.

Offshore and running the length of the north slope is the shallow Beaufort Sea continental shelf with an average depth of 37 meters and an average width of 72 kilometers (Sharma, 1979 as cited in Craig, 1989). The bathymetry off the northern Yukon coast west of Shingle Point is considerably different than that to the east of Shingle Point, due to the sedimentation effects of the Mackenzie River. The ten meter isobath lies approximately 30 kilometers offshore to the north of Shingle Point, only a few hundred meters offshore of King Point, which is to the west of Shingle Point, and two kilometers offshore of Kay Point near the Babbage River (Gulf Canada Resources, 1982)(Figure 1). Coastal currents driven by the clockwise Beaufort Sea Gyre in the offshore waters and winds in the inshore waters tend to contain the summer discharge of the north slope rivers to a narrow band of brackish/freshwater along the coast, which gradually increases in salinity as you move offshore (McCart, 1980). Bond *et al.* (1989) recorded water temperatures in the near shore zone around Phillips Bay reaching a summer high of 13° C in the early part of July. Ice usually begins to form along the north slope coast in late September and freezes to a thickness of two meters by late winter with underlying water temperatures dropping to -2° C and becoming hypersaline (McCart, 1980). Spring break-up of the coastal habitat occurs well after the north slope rivers begin to flow in late May and early June, with the spring discharge over the ice helping to speed the break-up of the shore-fast ice. The coast is usually totally

ice free by mid-June but drifting seasonal pack-ice and the more northerly permanent Beaufort polar pack ice remains year round, between 50 and 80 km offshore during the summer (Gulf Canada Resources, 1982).

2.1.2 Climatology

There has been little in the way of long-term climatic data recorded for the Arctic Plateau and Mountain regions of the Yukon north slope, but data were recorded between the late 1950s and the early 1990s at two coastal sites. Climatic data were collected as part of the daily operation of the Distant Early Warning (DEW) stations at Komakuk Beach and Shingle Point, which were established in 1957 and 1958, respectively (Figure 1) (Bain, 1973). Climatic data are also available from the town site of Aklavik, on the northwestern edge of the Mackenzie Delta collected as part of airport operations since the 1970s (Figure 1). Climatic conditions can vary considerably from east to west across the north slope with the mean yearly temperatures tending to be slightly warmer and precipitation levels higher in those regions of the north slope further to the east and closer to the Mackenzie Delta (Tables 2 and 3). Air temperature extremes along the north slope can range from -50°C in February to 28°C in July, with the mean daily air temperature only above 0°C during the months of June to September, inclusive (Bond and Erickson, 1989). Maximum and minimum yearly air temperatures are probably less extreme inland in the mountainous regions of the north slope, where a more continental climate predominates, than along the Arctic coast.

Table 2. Mean monthly temperatures recorded at three locations along the Yukon north slope (see Figure 1) (Environment Canada data). Numbers in brackets are the number of years upon which the monthly mean is based.

Month	Komakuk Beach Temp. °C (No. of Years)	Shingle Pt. Temp. °C (No. of Years)	Aklavik Temp. °C (No. of Years)
September	0.6 (24)	2.1 (24)	3.9 (12)
October	-9.7 (24)	-8.8 (24)	-8.8 (11)
November	-19.9 (24)	-20.2 (24)	-22.9 (13)
December	-23.7 (24)	-23.5 (24)	-25.3 (13)
January	-24.2 (25)	-24.9 (25)	-27.6 (12)
February	-26.0 (25)	-25.3 (25)	-26.2 (13)
March	-25.2 (25)	-24.0 (25)	-21.7 (13)
April	-17.6 (25)	-16.7 (24)	-13.2 (13)
May	-5.6 (25)	-4.6 (24)	-1.1 (12)
Winter Average	- 16.8	- 16.2	- 15.9
June	4.0 (25)	6.0 (24)	10.4 (8)
July	7.7 (24)	11.0 (24)	13.0 (6)
August	6.2 (24)	8.7 (24)	10.5 (13)
Summer Average	6.0	8.6	11.3
Yearly Average	- 11.1	- 10.0	- 9.1
	West	→ East	

Table 3. Mean monthly precipitation levels recorded at three locations along the Yukon north slope (see Figure 1) (Environment Canada data). Numbers in brackets are the number of years the monthly mean is based on.

Month	Komakuk Beach Millimeters (No. of Years)	Shingle Pt. Millimeters (No. of Years)	Aklavik Millimeters (No. of Years)
September	21.4 (24)	36.6 (24)	29.7 (12)
October	18.6 (24)	28.6 (24)	29.6 (11)
November	8.7 (24)	14.6 (24)	11.8 (13)
December	5.9 (24)	9.9 (24)	9.5 (13)
January	5.4 (25)	7.3 (25)	14.7 (12)
February	4.4 (25)	7.2 (25)	8.5 (13)
March	3.5 (25)	7.8 (25)	8.8 (13)
April	4.2 (25)	8.7 (24)	6.0 (13)
May	5.0 (25)	11.7 (24)	14.3 (12)
Winter Total	77.1	132.4	132.9
June	16.4 (25)	24.7(24)	6.5 (8)
July	25.8 (24)	31.8 (24)	30.2 (6)
August	35.3 (24)	54.6 (24)	36.0 (13)
Summer Total	77.5	111.1	72.7
Yearly Total	154.6	243.5	205.6
	West	→ East	

2.2 Sampling

Samples of mature Dolly Varden female char (hereafter unless specified otherwise the term mature/maturing will refer to those individuals that will spawn in the current year) were collected in the summer (August) of 1991 (Site C, Figure 1), and 1993 (Site D, Figure 1) and samples of ripe and spent females in the fall (late September and early October) of 1992 and 1993 (Site D, Figure 1) from the Big Fish River. Samples of maturing females were collected from the Babbage River in the summer (August) of 1991, 1992 (Site A, Figure 1), and 1993 (Site B, Figure 1) and samples of spent females in the fall (late September and early October) of 1992 and 1993 (Site B, Figure 1). Numbers of fish collected, date of collection and the methodology used to collect the samples are summarized in Table 4. An attempt was made to collect a sample of spent female char from both systems in the spring of 1991, 1992 and 1993. This sample was intended for comparison to the fall sample of spent females from the respective populations to determine whether the amount of energy utilized for overwintering is different between the two stocks. However, due to ice conditions at the Babbage River in 1992, and high water in both systems in 1991 and 1993, only a small sample of spent females was collected from the Big Fish River in the spring of 1992. As a result, it was not possible to directly compare the amount of energy used for overwintering between the populations. Thus, conclusions as to whether one population required greater amounts of energy to overwinter was made based on similarities or differences in the amount of energy reserves prior to overwintering. Additional information (e.g., length frequency distributions and maturity ratios of the populations, and Floy tag recapture data) regarding

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the structure of the populations was collected by the Department of Fisheries and Oceans in conjunction with summer weir operations (late July to mid-September) at the Babbage River in 1990, 1991 and 1992 (Sandstrom, Harwood and Reist, unpublished data) and at the Big Fish River in 1991 (Harwood and Sandstrom, unpublished data). The weirs that were utilized for the enumeration of the populations were floating deflection board weirs. These weirs are designed to impede movement of upstream migrating fish, funnelling them into a holding pen where they can be examined. Furthermore, this type of weir is not prone to wash out, unlike other fixed-weir designs (Kristofferson et al., 1986). When flow becomes too excessive the weir is pushed beneath the surface of the water, consequently relieving pressure and allowing debris to pass overtop. When flow recedes the weir floats to the surface and resumes its function. A 56 meter weir was installed in the Babbage River and a 31 meter weir was installed in the Big Fish River. Population data on the Big Fish River stock were also collected in the fall of 1992 and 1993 during seine and visual surveys at the spawning and overwintering site on Cache Creek.

Fork length for each fish was recorded to the nearest millimeter in the field prior to freezing and the frozen fish were shipped to the Freshwater Institute in Winnipeg where they were stored at -35° C until processed (within 12 months).

Water chemistry data collected during this and previous research (1972) are presented in Table 1.

2.3 Processing/Analysis

2.3.1 Biological Analysis

To compare certain life history parameters between the two stocks, a number of biological measurements were taken from the sampled fish. Initial processing in the lab recorded fork length to the nearest millimeter and, round weight, dressed weight (gills intact), and liver and gonad weight to the tenth of a gram from each freshly thawed fish. The degree of maturation of the gonad was identified as to one of the following categories: 1. maturing (gonads complete and egg still developing), 2. ripe (gonads complete and eggs expelled by slight pressure), 3. partially spent (at least 40% of gonad still remaining in body cavity), and 4. spent (less than 10% of gonad still remaining in body cavity). Egg diameters of mature fish were obtained from the average of two samples of ten randomly selected eggs lined up side by side on a measuring board (measurement (mm) \div 10). In the case of spent females from the fall samples, egg diameters were only taken from females that had at least ten or more residual eggs remaining within the abdominal cavity. Gonads of mature females were fixed in Gilson's solution or formalin for two weeks, then washed, any loose membrane removed and finally allowed to air dry. Absolute fecundity was estimated by dividing the total dry weight of eggs measured to three decimal places by the average weight of two approximately one-gram sub-samples of eggs (Rep. = replicate) and then multiplied by the average number of eggs in the two sub-samples:

$$\left(\left(\frac{\text{Total Dry Weight of Gonad}}{\left(\frac{\text{Weight of Rep. 1} + \text{Weight of Rep. 2}}{2} \right)} \right) \times \left(\left(\frac{\text{No. of Eggs in Rep. 1} + \text{No. of Eggs in Rep. 2}}{2} \right) \right) \right)$$

The accuracy of this method was tested by comparing nine estimated fecundities with their

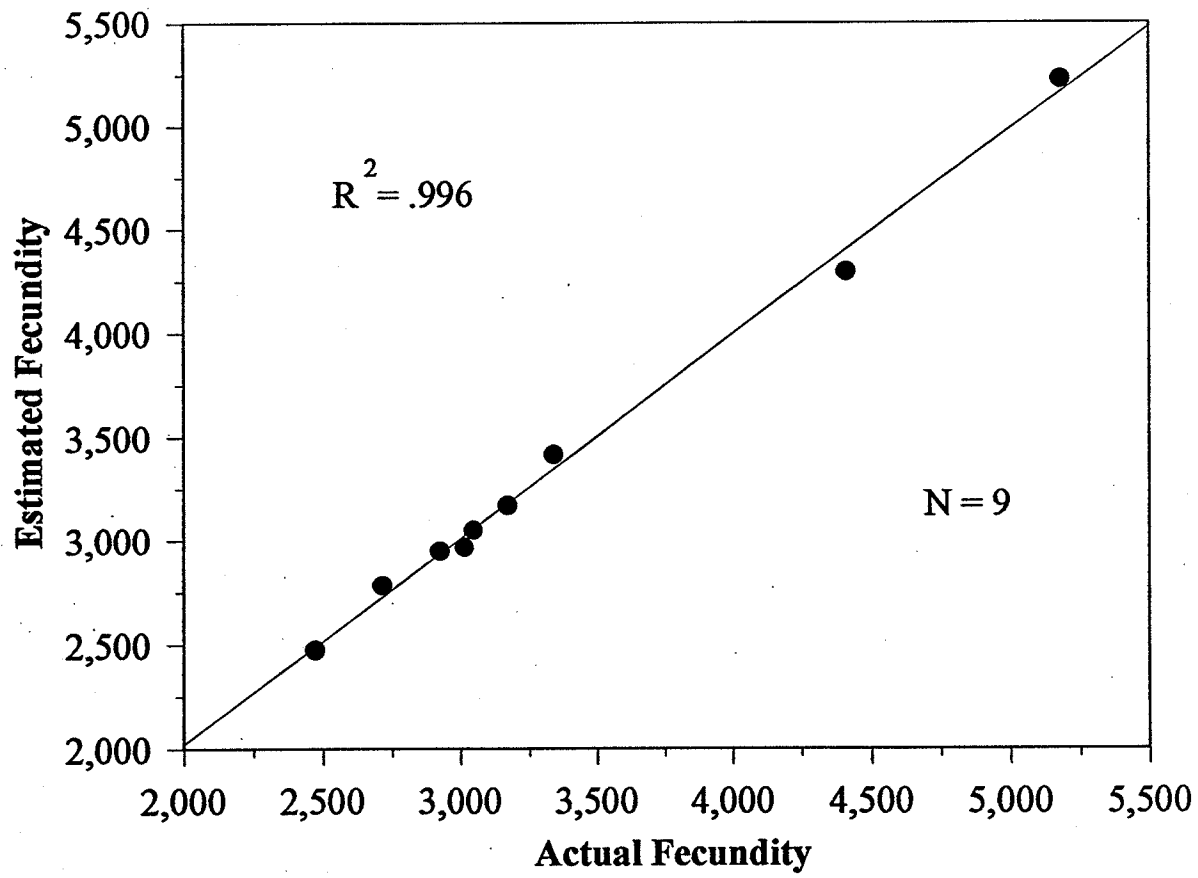
total counts. Results of this test showed this method of estimating the fecundity to be highly accurate. The estimates were on average within ± 35 eggs of the actual fecundity (Figure 5). Ages of the fish were determined from the otoliths by methodology outlined in Nordeng (1961).

2.3.2 Energetic Analysis

To establish whether differences in post-spawned pre-overwintered female energy reserves existed between the two stocks, several measurements were taken from the fall-sampled female char. The gut (esophagus, stomach, pyloric caecae, and intestine) was emptied of any contents, the nature of the contents identified, and the gut patted dry and weighed to three decimal places. After weighing, the gut was freeze-dried until a constant weight was obtained and then re-weighed to determine the percent dry weight ((gut dry weight \div gut wet weight) \cdot 100). Two muscle samples were taken from the area posterior to the dorsal fin, anterior to the operculum and between the lateral line and the dorsal midline. The muscle sample, which included light and dark muscle but not the skin, was weighed to three decimal places and then freeze-dried until a constant weight was obtained. Averages of the two replicates were used to obtain the percent dry weight of the muscle ((muscle dry weight \div muscle wet weight) \cdot 100). The liver functions as a minor and transient site of lipid storage. Furthermore, high blood content of the organ made it difficult to consistently weigh and freeze-dry the tissue. Therefore, the whole wet weight of the liver was used for the comparisons of relative lipid content of the liver for fish from the two systems.

Lipid extractions were performed on fourteen freeze-dried muscle and fourteen freeze-dried gut samples. The average of two extractions from each tissue sample was used for the

Figure 5. Correlation between the actual fecundity of Dolly Varden char and the estimated fecundity.



final percent lipid composition. The samples were selected from a combination of both rivers so that the range of percent dry weights obtained for the total sample from both populations was represented. A modified Bligh/Dyer micro-extraction method (1959) was used to determine total lipid in the tissue (Appendix 1).

2.3.3 Statistical Analysis

General life history parameters (fork length, round weight, dressed weight, age, growth rates, and maturity ratios), parameters of reproductive effort (gonad weight, egg diameter, and fecundity) and parameters of energy reserves (percent dry weight muscle, percent dry weight gut, and liver whole wet weight) were compared both between populations in the same year and within the same population between years. Fork length, maturity ratio, and for some of the comparisons egg diameter and also percent dry weight of the gut, were not shown to be correlated with the length of the individual fish. However, the majority of the parameters did exhibit a significant correlation with fork length. Thus, inter-year and inter-population comparisons of the regression relationship of these parameters with length were carried out by Analysis of Covariance (ANCOVA), using length as the covariate, in the Statistical Analysis System Version 5 (SAS Inc. 1985). The plots were checked for outliers and covariance was accounted for before main effects were tested by ANCOVA. This model assesses the variation in slope and the variation in elevation, calculated as adjusted means. A probability level of 0.05 was used to accept statistically significant differences. Where the regression relationship of the independent variable with length did not vary significantly between years, the data from these years were combined within the populations for inter-population comparisons. Logarithm to the base 10 transformations of the data were

done in cases where it was shown to significantly improve (change in $r^2 > 5\%$) the relationship. Due to the difficulty in consistently and accurately aging char of this species, as well as small annual sample sizes, inter-year comparisons of age could not be reliably done. Also, age was not included in any of the regression comparisons discussed above, because it was not shown to account for significantly more of the variance observed in each comparison beyond what was explained by fork length. Student's t-test, using Statistical Analysis System Version 5 (SAS Inc. 1985), was used to compare the unadjusted mean percent dry weight of the gut for populations and years in which it was shown not to have a significant relationship with fork length (Babbage Fall 1992 vs. Babbage Fall 1993; Babbage Fall 1992 vs. Big Fish Fall 1992).

To examine whether inter-population differences in growth rate existed between the two populations, all females aged during the research from each population were grouped and the slope and intercept of the regressions compared. An additional comparison of the annual growth rate for the two populations was done using Floy-tag recaptured females captured during this research that were larger than 425 mm at time of tagging. Returning (upstream migrating) modal length (10 mm size classes) of first-time-sea migrant char (smolts) was determined from the total measured catch at the weirs on the Babbage River in 1990 to 1992 and the Big Fish River in 1991. The length mode assigned to the smolt life-history stage was the smallest length mode observed in the returning anadromous populations.

Females sampled in the summer of 1991 and 1992 were collected over four to five weeks during the summer. Because gonad weight increases throughout the summer as the fish matures, and because insufficient numbers of fish were collected consistently over this time period to adequately control for date of capture, the comparison of gonad weight using

the summer 1991 or 1992 data could not be done. Therefore, gonad weight was compared between sites using the data from the summer in 1993 because this was the only sample of mature females collected at a single and similar point in time in both systems. Two separate inter-population comparisons of gonad weight were done (by ANCOVA) using the 1993 summer data, one using fork length as the covariate, and in the other, using dressed weight as the covariate.

Inter-year (1992 fall vs. 1993 fall) and inter-season (1993 summer vs. 1993 fall) comparisons of egg diameter within systems was also done using ANCOVA for samples collected from the Big Fish River. The absence of a significant relationship between length and egg diameter in both the fall samples from the Babbage River precluded using ANCOVA to compare egg diameter. For this population, inter-year and inter-season comparison (within system) of egg diameters was done on unadjusted means using Student's t-test using Statistical Analysis System Version 5 (SAS Inc. 1985). Gonadosomatic index ((GSI = gonad wt (g) \cdot 100) \div total body wt (g)) was used to compare the degree of sexual maturity of the individuals in the 1993 summer sample. Because the relationship of GSI and fork length was not observed to vary (Babbage River GSI = 16.78, Big Fish River GSI = 17.98; $F_{3,55} = 2.55$, $P = 0.1156$) between stocks, it was concluded that females in the two stocks were at the same stage of gonadal maturation at the time the sample was collected. Furthermore, because both ripe and spent females were collected in the fall samples from the two systems, it was concluded that spawning occurs at approximately the same time in both populations. Thus, for better inter-population comparison of egg diameters, 1993 fall sample sizes were increased by adjusting 1993 summer egg diameters and combining these with the 1993 fall

egg diameters. This was done by adding the difference in mean egg diameter observed between the summer and fall sample for each population to each of the summer egg diameters. Inter-system comparison of the combined 1993 egg diameter data was done using ANCOVA.

The mean length of the spawning females, both between years and between sites, was compared by Student's t-tests for those samples that were collected randomly by weir and seine. Samples collected by electroshocking were omitted from any analysis of mean length, because this collection technique tended to be biased towards larger fish and thus would not be representative of the population on the whole. Evidence of this collection bias is apparent when a comparison is made of the mean length of the 1993 Big Fish River summer sample and the actual mean length of the female spawning population determined later that same year. The summer sample was randomly collected on the spawning grounds in August by electroshocking, because high water that time of year prevented sampling by other, less selective, methods such as seining. The actual mean length of the female spawning population was determined by extensive seining on the spawning grounds in the fall of 1993. The mean length of the summer sample (498 ± 44 mm, $n=28$) was found to be significantly larger (t-test (equal variance): d.f.= 124, $t = -3.48$, $P= 0.0007$) than the actual mean length of the female population (459 ± 54 mm, $n=98$).

3. RESULTS

3.1 General Population Parameters

Several general life history parameters were examined within and between populations to determine whether females from the Big Fish River compromise their growth in fork length and/or body weight in order to allocate more energy to overwintering metabolic demands. The parameters examined were mean fork length of the spawning populations, round and dressed weights, and growth rate as determined from Floy-tag recaptured individuals and that estimated from the slope of the length on age regression.

3.1.1 Mean Fork Length of the Mature Female Char Populations

3.1.1.1 Within Populations Between Years

The length frequency distributions of the Dolly Varden char populations in the Babbage River (1990 to 1992) and Big Fish River (1991 and 1993) are presented in Figures 6 and 7. The modal returning smolt length, determined from these figures, was 270 mm in the Babbage River for all sample years, but varied between 300 mm (1991) and 320 mm (1993) for the population in the Big Fish River.

There was no significant change in the mean fork length of spawning female char over the duration of the research (1991 to 1993) in either of the populations. The mean fork length of the Babbage River spawning female population did not vary significantly over the three-year period from 1990 to 1992, remaining around 480 mm (t-test: Babbage 1990 vs. 1991 (equal variance), d.f.= 82, $t = -0.0517$, $P = 0.9589$; Babbage 1991 vs. 1992 (unequal variance), d.f.= 88, $t = -0.0096$, $P = 0.9924$; Babbage 1990 vs. 1992 (unequal variance), d.f.= 38, $t = -0.0592$, $P = 0.9531$) (Figure 8). Comparison of the mean fork length of female char

Figure 6. Length distributions for the Dolly Varden char population in the Babbage River recorded in 1990 (A), 1991 (B) and 1992 (C) from randomly live-sampled char caught by the weir during the upstream migration of the stock. The weir was in place from early August to early September (Sandstrom, Harwood and Reist, unpublished data).

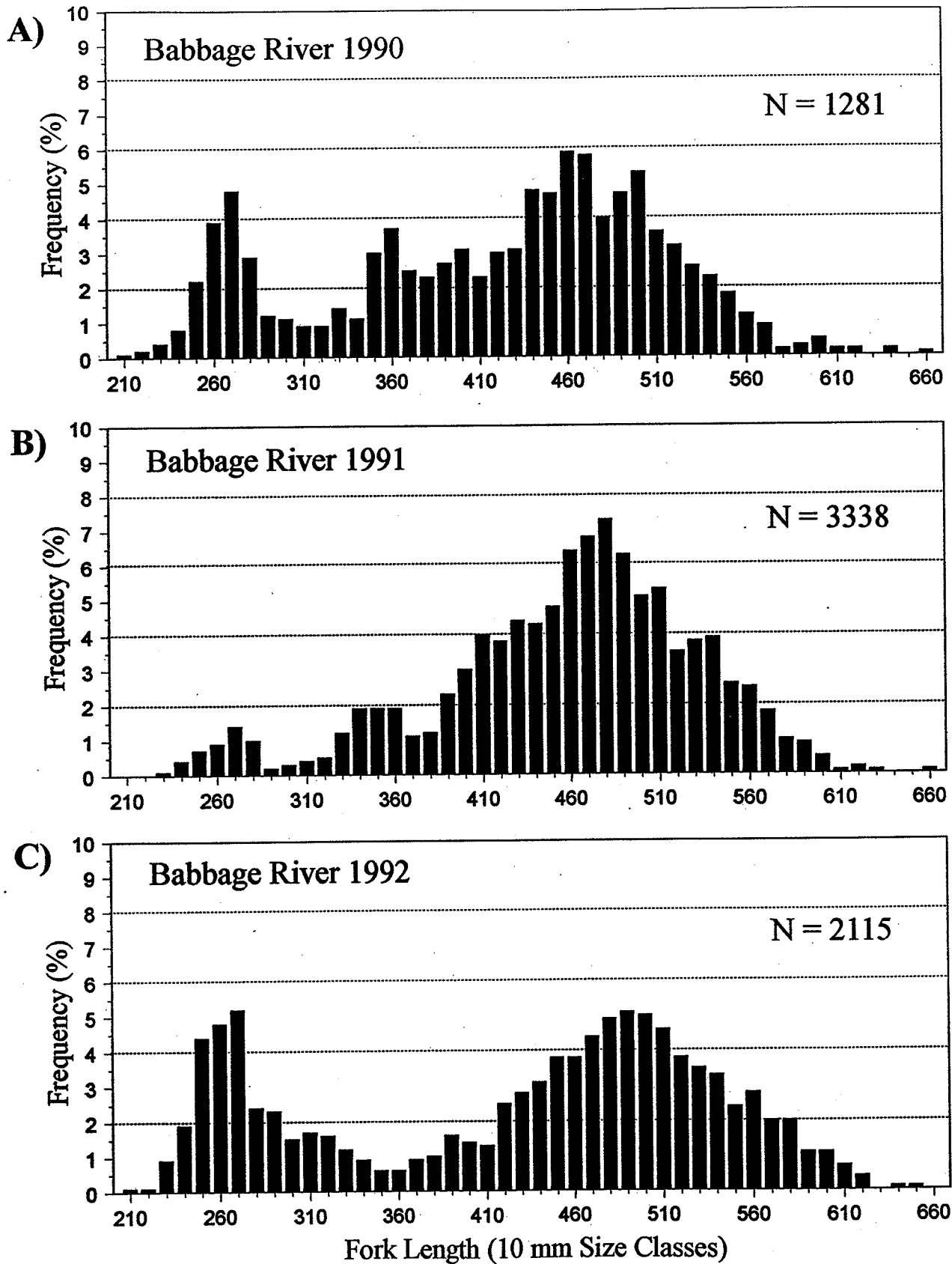


Figure 7. Length distributions of the Dolly Varden char population in the Big Fish River determined from randomly live sampled char caught in (A) by the weir during the upstream migration of the stock in 1991 and (B) during seine hauls at the overwintering site in 1993. The weir was in place from early August to early September and the seining survey was conducted in early-October (Harwood and Sandstrom, unpublished data)..

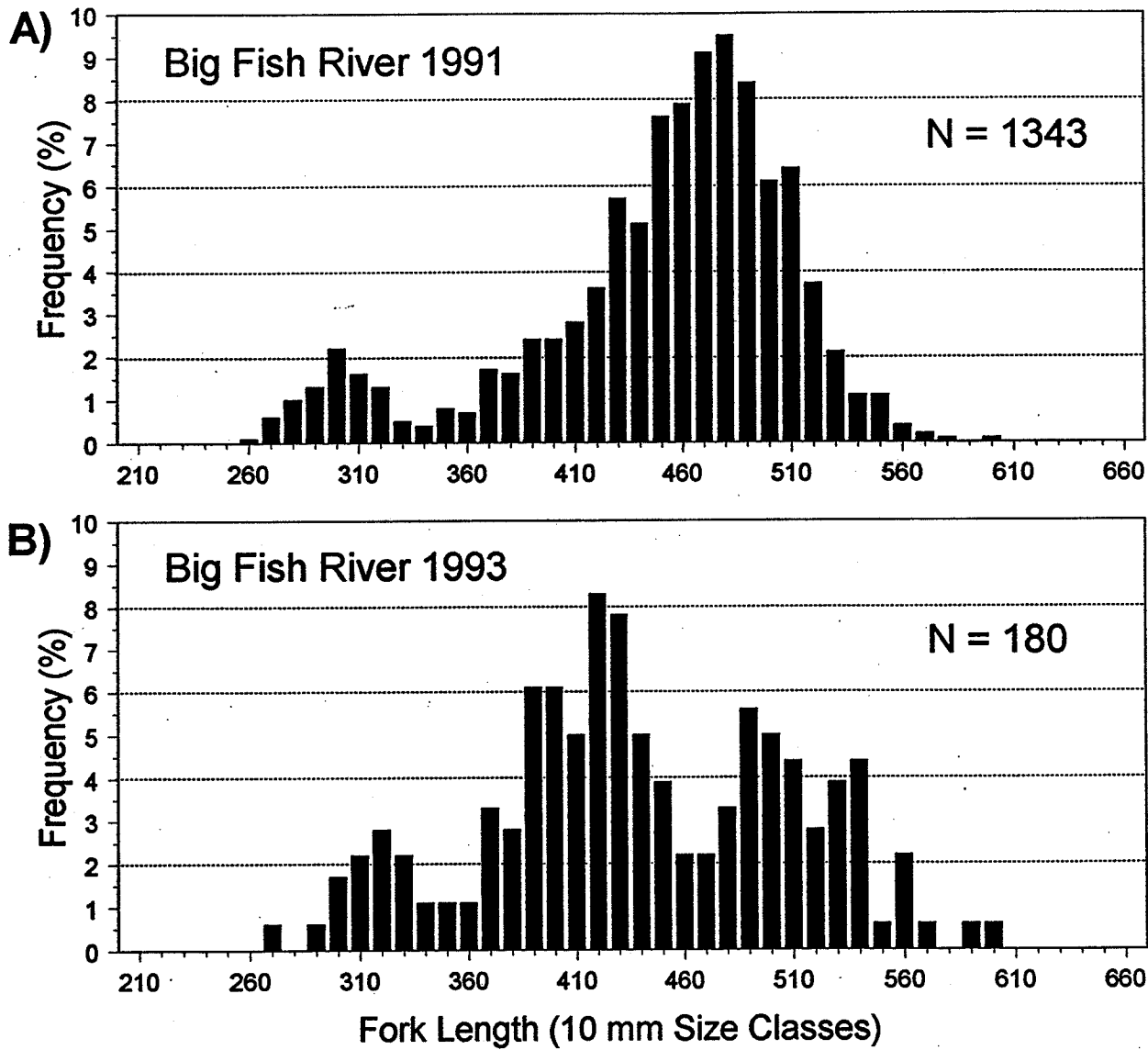
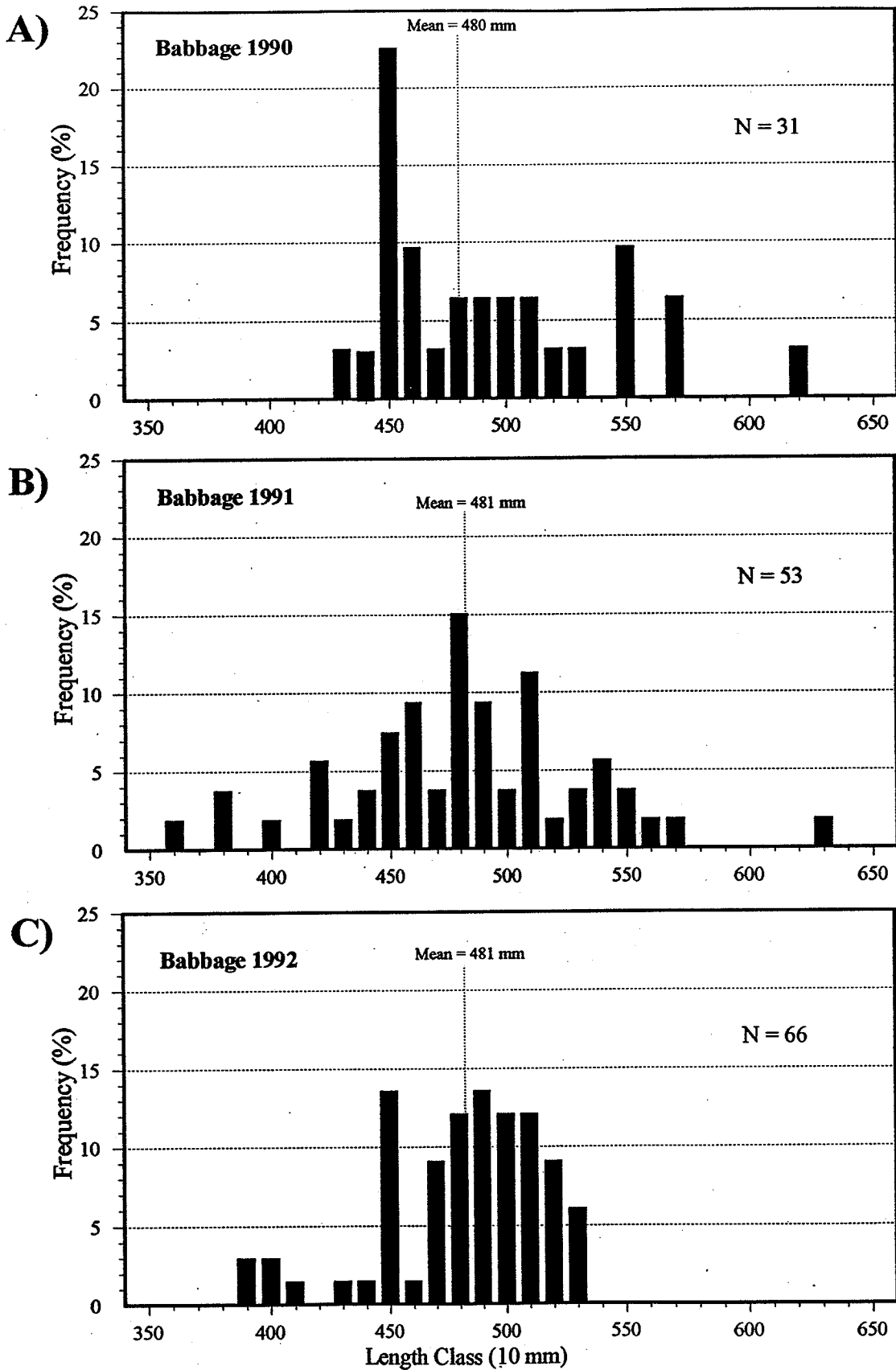


Figure 8. Length distributions for spawning female Dolly Varden char from the Babbage River population in 1990 (A), 1991 (B) and 1992 (C). Length distributions were obtained from a random dead sample collected from the weir, during the upstream migration of the stock.

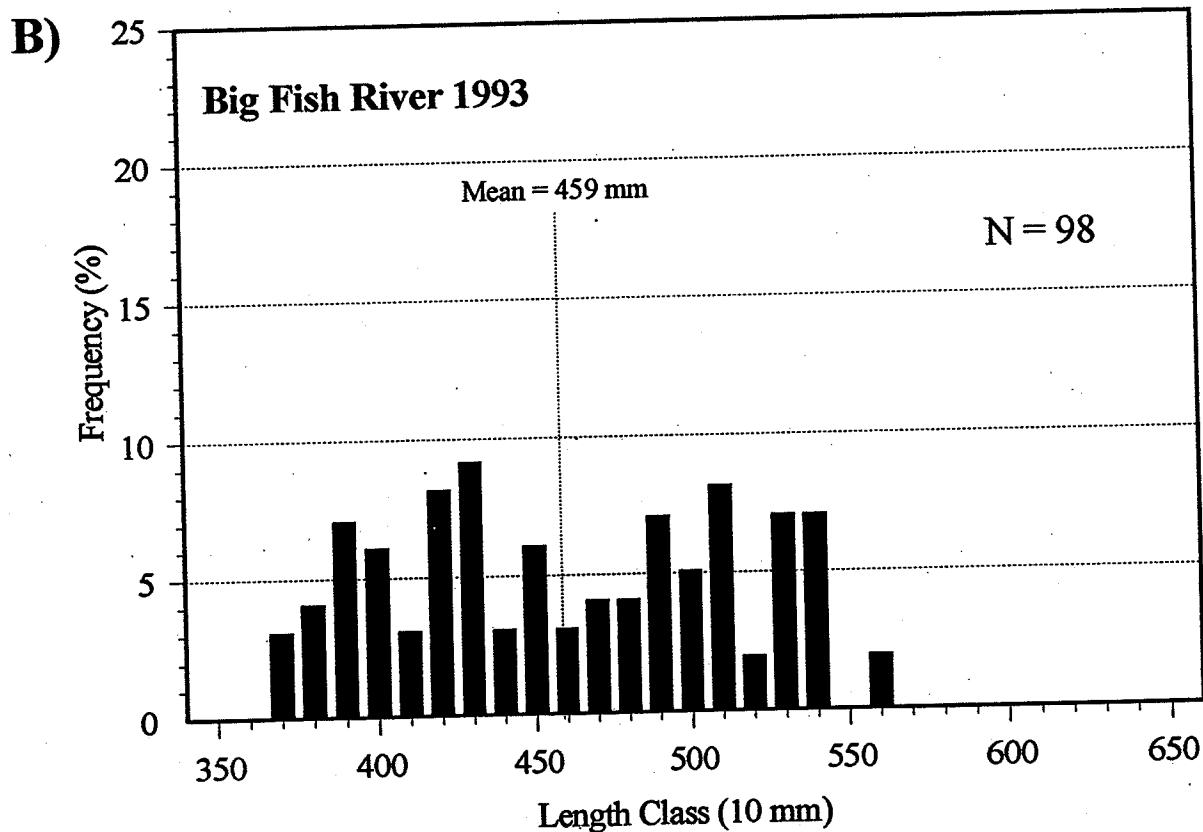
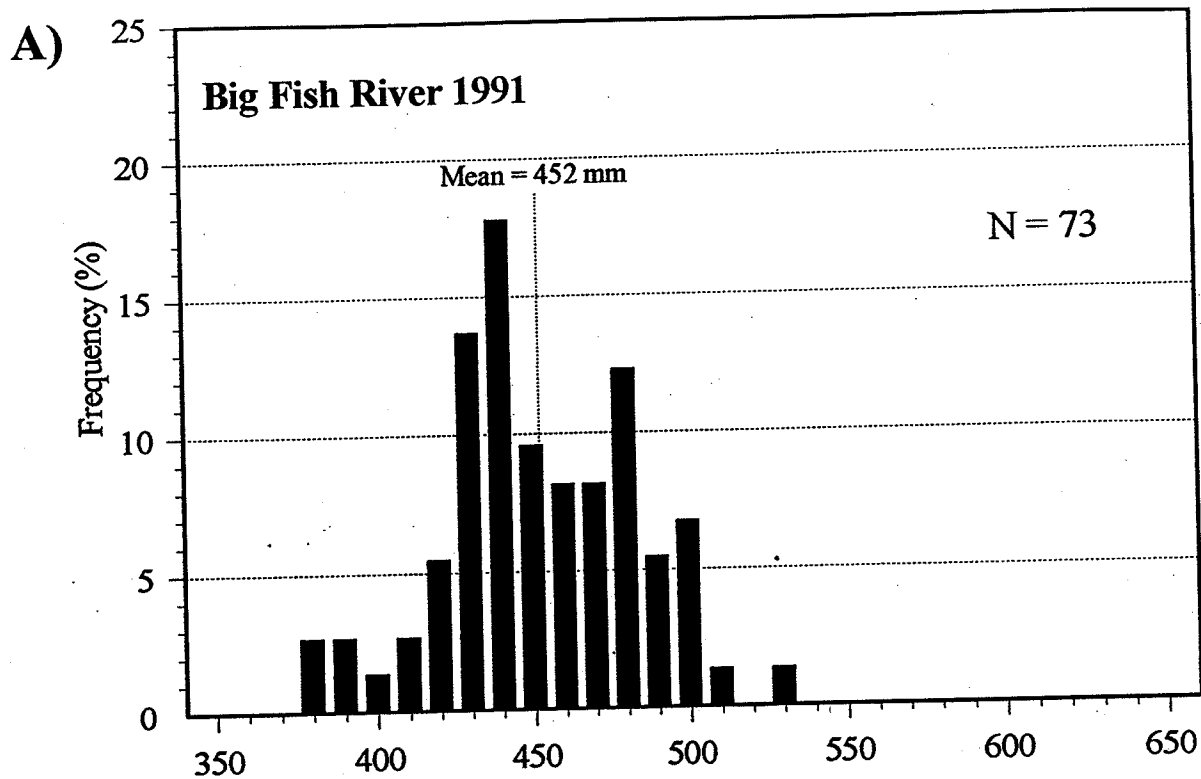


from the Big Fish River in 1991 and 1993, the only two years when a representative sample of the female population was obtained, indicated that the mean length had increased over the three-year period, although non-significantly, from 452 mm to 459 mm (t-test: Big Fish 1991 vs. 1993 (unequal variance), d.f. = 160, $t = -1.1377$, $P = 0.2569$)(Figure 9). However, the length distributions of female spawning char from the Big Fish River population was noticeably different between comparison years (Figure 9a and b). The distribution of lengths of spawning female char for the Big Fish River population was visibly wider in size range and more platykurtotic (i.e., flattened) in the 1993 sample compared to the 1991 sample. The distributions of lengths obtained for the Babbage River were also somewhat irregular between the sample years. This was probably due in part to small sample sizes. However, some similarities were visible between the 1990, 1991 and 1992 spawning female length distributions in the Babbage River. The distributions were similar in the width of size range and also, in all sample years the majority of spawning females were found above a fork length of 430 mm.

3.1.1.2 Between Populations

Although the mean fork length of the female spawning populations did not vary between years within populations, it did vary significantly between the Babbage River (1990, 1991 and 1992 samples combined, $n = 150$) and the Big Fish River (1991 and 1993 samples combined, $n = 171$). The female spawning population of the Big Fish River was found to have a mean fork length of 459 ± 38 mm, which was significantly smaller by 24 mm, than the mean fork length of the Babbage River female population (483 ± 43 mm)(t-test: Babbage vs. Big Fish (equal variance), d.f. = 319, $t = 4.6953$, $P = 0.0001$).

Figure 9. Length distributions of spawning female Dolly Varden char from the Big Fish River population. Length distribution recorded in 1991 (A) was from a random dead sample collected from the weir during the upstream migration of the stock and the distribution in 1993 (B) was from a random live sample collected by seine at the spawning grounds in early October.



The smallest mature female captured in the Big Fish River was 366 mm (1993), whereas the smallest mature female captured in the Babbage River was 357 mm (1991). The largest mature females captured in the Big Fish and Babbage Rivers were 563 mm and 632 mm, respectively.

3.1.2 Round Weight

3.1.2.1 Between Populations

Inter-system comparisons of the relationship of round weight and length was only possible between spawning females from the Babbage and Big Fish Rivers in the summer of 1993 (see Methods for explanation). The slopes of the regressions of round weight on fork length (8.30 and 8.26 respectively) were not significantly different (Table 5). However the intercepts of the regressions were significantly different. As a result, in 1993 females from the Big Fish River had a significantly heavier mean round weight adjusted for length (1489 g) than did females from the Babbage River (1403 g) (Table 5). The adjusted mean round weight of females from the Big Fish River was approximately 86 grams greater than that for females from the Babbage River.

3.1.3 Dressed Weight

Dressed weight was used as a proxy for amount of muscle mass on a particular fish, assuming that the head, bones, fins and skin make up a similar percentage of the dressed weight in both stocks. Dressed weight was moderately correlated with fork length (r ranged from 0.83 to 0.91) in both populations in both sample years and the variance accounted for was moderately light (r^2 ranged from 0.70 to 0.83) (Table 6).

Table 5. Analysis of Covariance statistics for round weight comparisons between systems within years

Comparisons	Classification Variable	Sample Size	Correlation r	P-value	Fitted Model	S.E. of Intercept	S.E. of Slope	LSMEAN	Std Err of LSMEAN	P-Value (Slope ; Intercept)
Between Systems (1993 Summer Data)	Babbage	31	0.90	0.0001	Round Wt = -2730.46 + 8.30 Fork Length	311.6823	0.6243	1403.0354	15.7504	} 0.0004 (0.9679 ; 0.0004)
	Big Fish	28	0.98	0.0001	Round Wt = -2632.37 + 8.28 Fork Length	194.0168	0.3884	1488.9213	16.5726	

Table 6. Analysis of Covariance statistics for dressed weight comparisons: (A) between years within systems; and (B) between systems within years

Comparisons	Classification Variable	Sample Size	Correlation r	P-value	Fitted Model	S.E. of Intercept	S.E. of Slope	LSMEAN	Std Err of LSMEAN	P-value (Slope ; Intercept)
A. Within System - Babbage R. - Fall	1992	33	0.84	0.0001	Dressed Wt = -1526.71 + 4.77 Fork Length	358.5816	0.7374	789.4715	11.9552	0.0012 (0.4604 ; 0.0011)
	1993	31	0.85	0.0001	Dressed Wt = -1202.05 + 4.21 Fork Length	245.6490	0.0157	847.8390	12.2755	
Within System - Big Fish R. - Fall	1992	31	0.91	0.0001	Dressed Wt = -1120.13 + 4.02 Fork Length	190.0400	0.4042	765.3449	11.4509	0.0134 (0.1354 ; 0.0138)
	1993	28	0.91	0.0001	Dressed Wt = -1364.72 + 4.63 Fork Length	119.1230	0.2517	807.8364	12.0438	
Within System - Babbage R. - 1993	Summer	31	0.89	0.0001	Dressed Wt = -1712.22 + 5.54 Fork Length	219.4924	0.4398	1031.7293	14.2142	0.0001 (0.0807 ; 0.0001)
	Fall	31	0.85	0.0001	Dressed Wt = -1202.05 + 4.22 Fork Length	368.0844	0.7428	887.5066	14.2499	
Within System - Big Fish R. - 1993	Summer	28	0.97	0.0001	Dressed Wt = -1750.04 + 5.73 Fork Length	139.9157	0.2801	1025.1219	12.4152	0.0001 (0.0052 ; 0.0001)
	Fall	28	0.91	0.0001	Dressed Wt = -1364.72 + 4.64 Fork Length	183.2360	0.3754	879.8598	12.5307	
B. Between Systems - Summer 1993	Babbage	31	0.89	0.0001	Dressed Wt = -1712.22 + 5.53 Fork Length	286.7110	0.5743	1044.7330	14.4885	0.0076 (0.7380 ; 0.0076)
	Big Fish	28	0.97	0.0001	Dressed Wt = -1750.04 + 5.73 Fork Length	178.4726	0.3573	1103.3886	15.2449	
Between Systems - Fall 1992	Babbage	33	0.84	0.0001	Dressed Wt = -1526.72 + 4.77 Fork Length	309.3235	0.6485	729.0188	12.1731	0.0022 (0.2570 ; 0.0030)
	Big Fish	31	0.91	0.0001	Dressed Wt = -1120.13 + 4.02 Fork Length	155.9980	0.3332	784.2229	12.2454	
Between Systems - Fall 1993	Babbage	31	0.85	0.0001	Dressed Wt = -1202.05 + 4.22 Fork Length	259.3950	0.5301	832.5828	12.1829	0.0266 (0.4337 ; 0.0171)
	Big Fish	28	0.91	0.0001	Dressed Wt = -1364.72 + 4.64 Fork Length	115.9346	0.2450	871.6265	12.0546	

3.1.3.1 Within Populations Between Years

The adjusted mean dressed weight was observed to increase significantly within each system between 1992 and 1993. Females from the Big Fish River had an adjusted mean dressed weight in the fall of 1993 approximately 40 grams heavier than that seen in 1992 (765 vs. 808 g)(Table 6). The increase in the adjusted mean dressed weight from 1992 to 1993 for females from the Babbage River was approximately 60 grams (789 vs. 848 g) (Table 6). In both cases these observed increases were the result of significant differences in intercepts of the regressions rather than slopes. Comparison within a year and within system was also possible in 1993. Comparison of adjusted mean dressed weights in the Babbage River between the summer (1032 g) and the fall (888 g) showed a significant decrease of 144 g. The same comparison for the Big Fish River showed a similar significant decrease (145 g) between the 1993 summer and 1993 fall sample (Table 6).

3.1.3.2 Between Populations

The post-spawned adjusted mean dressed weight was significantly heavier in females from the Big Fish River than females from the Babbage River, by approximately 40 to 50 grams, in both of the fall comparison samples (1992 and 1993) (729 vs. 784 and 833 vs. 872, respectively) (Table 6). As previously, in both cases these observed differences were the result of significant differences in intercepts rather than slope. The post-spawned adjusted mean dressed weight was also significantly heavier in females from the Big Fish River than those from the Babbage, by approximately 60 grams, in the 1993 summer comparison sample (1103 vs. 1045, respectively) (Table 6).

3.1.4 Estimation of Adult Female Growth Rates

Growth rates of adult female char were calculated, from Floy-tag recaptured data and the length-on-age regressions, for the two populations in order to examine whether adult females from the two populations were allocating similar amounts of energy annually to growth in length. Inter-year comparisons within populations were not possible due to small annual sample sizes. As a consequence, all Floy-tag recapture data collected within a river system during the course of this research was combined for an inter-population comparison of growth.

3.1.4.1 Between Populations

Inter-system comparison of the growth rate of adult female char, that were larger than 425 mm at time of tagging, based upon Floy-tag recaptured fish showed that there were no significant differences between the populations in the annual estimated growth rates (Table 7). Floy-tag recapture data indicated that the annual adjusted mean growth rate was approximately 21 and 18 mm a year for adult females from the Babbage and Big Fish Rivers, respectively.

Comparison of the length-on-age regressions for the adult female populations showed Babbage River char to have larger fork lengths at all ages (Table 7). This was due to significantly different intercepts rather than significantly different growth rates (i.e., the slopes were similar). The slope of the length-on-age regressions indicated that the annual mean growth rate was approximately 17 mm a year for adult females from the Babbage River and 15 mm a year for adult females from the Big Fish River. This comparison also showed that the adjusted mean fork length of adult females from the Babbage River (486 mm) was

Table 7. Analysis of Covariance statistics for comparisons between systems of (A) yearly growth rate as determined from Floy-tag recaptured fish that were larger than 425 mm at time of tagging and were identified as female at time of recapture, and (B) regression of the age on fork length for adult females (i.e., randomly caught spawning females of all sizes and non-spawning females that are larger than 425 mm).

Comparisons	Classification Variable	Sample Size	Correlation r	P-value	Fitted Model	S.E. of Intercept	S.E. of Slope	LSMEAN	Std Err of LSMEAN	P-Value (Slope; Intercept)
A. Between Systems (Floy Tag Recapture Data)	Babbage	81	0.40	0.0002	Yearly Growth = 81.92 + -0.13 Fork Length	35.53	0.08	21.29	1.05] 0.1983 (0.6628; 0.2257)
	Big Fish	23	0.54	0.0079	Yearly Growth = 94.65 + -0.16 Fork Length	32.19	0.07	18.17	2.17	
B. Between Systems (Female Age Data)	Babbage	193	0.62	0.0001	Fork Length = 367.68 + 16.75 Age	15.99	2.13	486.33	2.64] 0.0001 (0.4320; 0.0001)
	Big Fish	141	0.69	0.0001	Fork Length = 349.29 + 15.06 Age	12.10	1.51	455.87	3.05	

approximately 30 mm larger at a given age than female char from the Big Fish River (456 mm).

3.2 Parameters of Reproductive Effort

A number of reproductive parameters were examined in the two populations to determine whether females from the Big Fish River compromise their reproductive effort, in some way, in order to allocate more energy to overwintering metabolic demands. The parameters examined were gonad weight, fecundity, egg diameter and the maturity frequency (incidence of sequential spawning) of the female populations.

3.2.1 Gonad Weight Comparisons

Gonad weight was used as a proxy for reproductive effort, that is, the greater the mean gonad weight of a stock adjusted by fish length, the greater the amount of energy devoted to reproduction by the stock. Gonad weight was positively correlated with both length and dressed weight in both populations in the 1993 summer sample, with larger and heavier fish able to produce and physically accommodate larger gonads (Table 8).

3.2.1.1 Between Populations

Females from the Big Fish River had significantly heavier adjusted mean gonad weights by approximately 34 grams (or 13 %) when fork length was used as a covariate (273 g compared to 239 g, Table 8). This resulted from significant differences in the intercepts of the regression rather than differences in slopes of the relationship. Thus, based solely on this it would appear that female char from the Big Fish River exhibited a greater reproductive effort than did female char from the Babbage River. However, gonad weight

Table 8. Analysis of Covariance statistics for gonad weight comparisons between systems using the 1993 summer data.
Gonad weight is regressed in (A) upon fork length and in (B) upon dressed weight.

Comparison	Classification Variable	Sample Size	Correlation r	P-value	Fitted Model	S.E. of Intercept	S.E. of Slope	LSMEAN	Std Err of LSMEAN	P-Value (Slope ; Intercept)
A) Between Systems (1993 Summer Data)	Babbage	31	0.88	0.0001	Gonad Wt = -789.13 + 2.06 Fork Length	126.15	0.25	239.19	6.37	0.0006 (0.7192 ; 0.0006)
	Big Fish	28	0.94	0.0001	Gonad Wt = -709.72 + 1.97 Fork Length	78.53	0.16	273.13	6.71	
B) Between Systems (1993 Summer Data)	Babbage	31	0.75	0.0001	Gonad Wt = -58.99 + 0.28 Dressed Wt	59.71	0.06	247.16	8.46	0.1950 (0.5106 ; 0.1986)
	Big Fish	28	0.91	0.0001	Gonad Wt = -81.72 + 0.32 Dressed Wt	39.46	0.03	263.25	8.88	

was not observed to vary significantly between the populations when dressed weight was used as the covariate (Big Fish River = 263 g compared to 247 g for the Babbage River, Table 8). For the 1993 summer sample, approximately $16.9 \pm 3.2\%$ of the total body weight in females (averaged over the regression) from the Babbage River and $17.9 \pm 2.5\%$ of the total body weight (averaged over the regression) in females from the Big Fish River was comprised of gonads.

3.2.2 Fecundity Comparisons

In both populations, and in all comparison years, fecundity was shown to be positively correlated with length, with larger females having greater fecundity than smaller females ($P < 0.0001$) (Table 9). In general the correlations (r) ranged from 0.57 to 0.82, and the variance (r^2) accounted for by the regression equation ranged from 0.32 to 0.67.

3.2.2.1 Within Populations Between Years

The average adjusted mean fecundity for the Big Fish River population in 1991 was not observed to vary significantly from that recorded for the population in 1993 (Table 9). However, the adjusted mean fecundity of females from the Babbage River in 1992 was shown to be significantly higher, due to significantly different intercepts but not slopes, than that recorded for the population in 1991, but was not significantly different for that recorded for 1993 (Table 9). Similarly, the adjusted mean fecundity of females from the Babbage River in 1991 was not different from that recorded in 1993.

3.2.2.2 Between Populations

Because there was no 1992 fecundity sample from the Big Fish River and also because

Table 9. Analysis of Covariance statistics for fecundity comparisons: (A) between years within systems; and (B) between systems within years.

Comparisons	Classification Variable	Sample Size	Correlation r	P-value	Fitted Model	S.E. of Intercept	S.E. of Slope	LSMEAN	Std Err of LSMEAN	P-Value (Slope ; Intercept)
A. Within System - Babbage R.	1991	44	0.82	0.0001	Fecundity = -3444.52 + 13.48 Fork Length	2054.88	4.22	3095	93.90] 0.0190 (0.2763 ; 0.0179)
	1992	42	0.57	0.0001	Fecundity = -5366.99 + 18.11 Fork Length	1826.97	3.75	3417	96.19	
Within System - Babbage R.	1991	44	0.82	0.0001	Fecundity = -3444.52 + 13.48 Fork Length	1730.01	3.48	3165	80.85] 0.6398 (0.0211 ; 0.4025)
	1993	30	0.78	0.0001	Fecundity = -7406.92 + 21.69 Fork Length	1532.09	3.06	3226	101.12	
Within System - Babbage R.	1992	42	0.57	0.0001	Fecundity = -5367.00 + 18.11 Fork Length	2773.19	5.62	3537	106.50] 0.0957 (0.5263 ; 0.0990)
	1993	30	0.78	0.0001	Fecundity = -7406.92 + 21.69 Fork Length	1942.97	3.88	3258	126.78	
Within System - Big Fish R.	1991	63	0.67	0.0001	Fecundity = -2574.69 + 10.55 Fork Length	1219.91	2.55	2329	59.56] 0.8923 (0.1624 ; 0.8159)
	1993	28	0.81	0.0001	Fecundity = -4259.32 + 14.14 Fork Length	951.76	1.91	2313	102.61	
B. Between Systems (1991 and 1993 combined)	Babbage	74	0.79	0.0001	Fecundity = -4402.19 + 15.55 Fork Length	858.79	1.79	3003	59.41] 0.0001 (0.0697 ; 0.0001)
	Big Fish	91	0.77	0.0001	Fecundity = -3350.20 + 12.29 Fork Length	568.36	1.22	2501	52.82	

the fecundity on fork length relationship was not observed to vary significantly between the 1991 and 1993 sample in either population, inter-population comparison of fecundity was done using the combined 1991 and 1993 fecundity data. The adjusted mean fecundity was significantly higher for females from the Babbage River, by approximately 500 eggs in the combined sample (Table 9). The two regressions differed significantly in intercept but not in slope, although the latter was approaching the statistically significant level (i.e., $P \approx 0.07$).

3.2.3 Egg Diameter Comparisons

Egg diameter had a moderately strong and positive correlation with fork length (r ranged from 0.67 to 0.83) in females from both of the 1992 and 1993 fall samples and the 1993 summer sample from the Big Fish River. The variance (r^2) accounted for by these regression equations ranged from 0.45 to 0.69 (Table 10). For fall sampled females from the Babbage River, egg diameter was not correlated with length in either of the two comparison years (r ranged from 0.14 to 0.00). The variance (r^2) accounted for by these regression equations was 0.02 and 0.00 (Table 10). However, egg diameter was shown to have a weak correlation ($r = 0.45$) with fork length for the Babbage River 1993 summer sample. The variance (r^2) accounted for by this regression was 0.20 (Table 10).

3.2.3.1 Within Populations Between Years

The adjusted mean egg diameter of females from the Big Fish River was significantly larger in 1993, compared to 1992, by approximately 0.3 mm (Table 10). Inter-year comparison of the unadjusted mean egg diameter in females from the Babbage River by Student's t-test indicated that the mean egg diameter in the fall of 1992 (4.1 ± 0.3 , $n = 8$).

Table 10. Analysis of Covariance statistics for comparisons of egg diameters (egg dia.): (A) between years or seasons within systems; and (B) between systems within years. The egg diameters of females sampled in the summer are not of final diameter as they are in the females sampled in the fall. Analysis of Covariance could not be done on the within system comparison of fall egg diameters in the Babbage River due to the absence of a significant correlation between the dependent variable and the covariate in one or more of the samples.

Comparisons	Classification Variable	Sample Size	Correlation r	P-value	Fitted Model	S.E. of Intercept	S.E. of Slope	LSMEANof	Std Err LSMEAN	P-Value (Slope ; Intercept)
A. Within System - Babbage R. - Fall	1992	8	0.14	0.7279	-	-	-	-	-	-
	1993	18	0.00	0.8642	-	-	-	-	-	
Within System - Big Fish R. - Fall	1992	25	0.77	0.0001	Egg Dia. = 2.25 + 0.005 Fork Length	0.72	0.001	4.50	0.04	-0.0001 (0.0562 ; 0.0002)
	1993	19	0.83	0.0001	Egg Dia. = 1.11 + 0.008 Fork Length	0.47	0.002	4.77	0.05	
Within System - Big Fish R. - 1993	Summer	27	0.67	0.0001	Egg Dia. = 1.55 + 0.006 Fork Length	0.66	0.001	4.54	0.06	-0.0001 (0.3727 ; 0.0001)
	Fall	19	0.83	0.0001	Egg Dia. = 1.11 + 0.008 Fork Length	0.92	0.002	4.92	0.06	
B. Between Systems - Summer 1993	Babbage	31	0.45	0.0124	Egg Dia. = 2.20 + 0.004 Fork Length	0.98	0.002	4.06	0.05	-0.0001 (0.2311 ; 0.0001)
	Big Fish	27	0.67	0.0001	Egg Dia. = 1.55 + 0.006 Fork Length	0.62	0.001	4.59	0.05	
Between Systems - 1993 (Adjusted Summer Data + Fall Data)	Babbage	49	0.32	0.0224	Egg Dia. = 3.02 + 0.003 Fork Length	0.75	0.002	4.37	0.04	-0.0001 (0.0072 ; 0.0001)
	Big Fish	46	0.76	0.0001	Egg Dia. = 1.52 + 0.007 Fork Length	0.41	0.001	4.93	0.04	

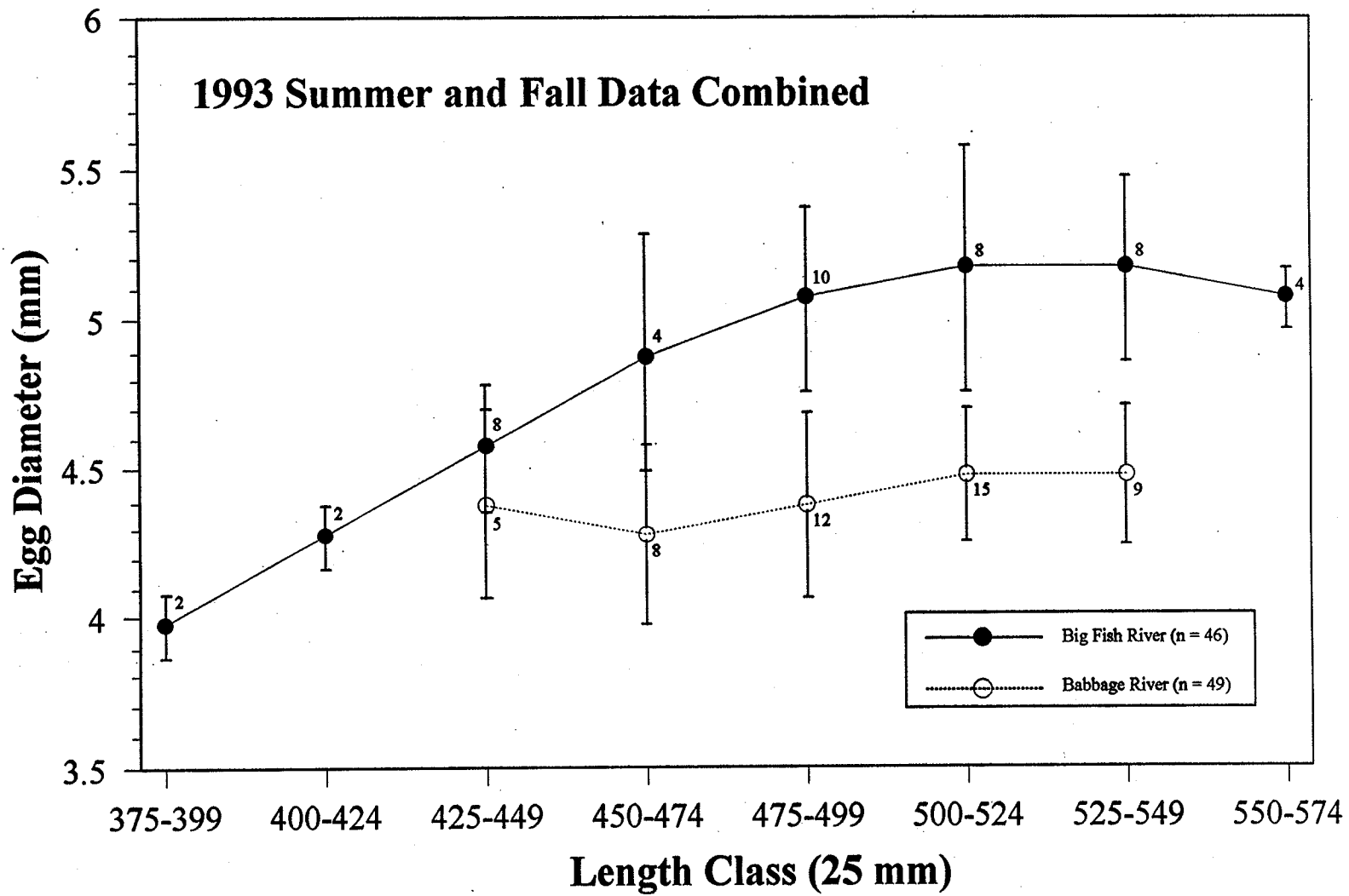
was significantly smaller by approximately 0.3 mm than the mean egg diameter recorded in the fall of 1993 (4.4 ± 0.2 , $n = 18$) (t-test: 1992 vs. 1993 (equal variance), d.f. = 24, $t = -3.0044$, $P = 0.0061$).

3.2.3.2 Between Populations

The 1993 field season was the only period in which samples had been collected from each system over a narrow time frame (two days) in both the summer and the fall. Because a significant correlation between egg diameter and fork length was found in both the summer and fall sample in the Big Fish River, it was possible in this system to determine the adjusted mean growth (mm) in egg diameter from the end of August up to the point of final ripening and subsequent spawning in mid- to late-September. The total increase in adjusted mean egg diameter in females from the Big Fish River during this interval, rounded to two decimal places, was 0.37 mm. The increase was shown to be significant, with the difference between the regression being due to differences in intercept and not slope. Similar slopes of the regressions suggests that the total growth in diameter was the same for both large and small eggs in females from the Big Fish River. Comparison of egg diameter growth between the 1993 summer and 1993 fall sample in the Babbage River was done using unadjusted means due to the lack of any correlation of egg diameter with fork length in the fall sample. Student's t-test comparison of the means showed that the eggs in this population increased significantly in diameter between the summer (4.06 ± 0.28) and fall sample (4.38 ± 0.24) by 0.32 mm (Babbage Summer vs. Fall (equal variance), d.f. = 47.0, $t = 4.1401$, $P = 0.0001$). Thus, for better inter-population comparison of egg diameters, 1993 fall sample sizes were increased by adjusting 1993 summer egg diameters and combining these with the fall egg diameters.

This was done by adding 0.37 mm to summer egg diameters from the Big Fish River, and 0.32 mm to summer egg diameters from the Babbage River. Inter-population comparisons of the combined 1993 egg diameter data from the Babbage and Big Fish Rivers indicated that females from the Big Fish River had significantly greater adjusted mean egg diameters, by approximately 0.56 mm (4.93 mm compared with 4.37 mm, Table 10). If the eggs are considered to be spheres, then the calculated volumes of the adjusted mean egg diameters are 43.70 mm^3 (Babbage River) and 62.74 mm^3 (Big Fish River). This indicates that the volume of an egg from a female in the Big Fish River is approximately 30 % greater than the volume of an egg in a similarly sized female from the Babbage River. The combined summer (adjusted) and fall egg diameter data are presented in Figure 10, by fork length groups of 25-mm. At all size classes, where mean egg diameters were obtained for both populations, females from the Big Fish River had larger mean egg diameters. Furthermore, females from the Big Fish River showed a definite increase in mean egg diameter with increasing fork length over the size interval of 375-499 mm. At sizes greater than 500 mm, the relationship of egg diameter with fork length for females from the Big Fish River asymptotes at an egg diameter of approximately 5.0 to 5.1 mm. In contrast, the relationship between egg diameter and fork length for females from the Babbage River is, more or less, linear and horizontal, with mean egg diameter remaining around 4.3 to 4.4 mm over all fork length classes. Furthermore, for fork lengths greater than 475 mm, the standard deviations of egg diameter did not overlap between the samples from the two rivers. The general trends discussed above were also visible in separate plots of the summer and fall egg diameter data. Inter-population comparison of fall egg diameters was not done on the 1992 data due to the small sample size

Figure 10. Relationship of mean terminal egg diameter (\pm one standard deviation) and fork length for mature female Dolly Varden char (grouped by 25 mm size classes) collected in 1993 from the populations from the Babbage and Big Fish Rivers. Numbers by each mean represent sample sizes for that length class. Both fall egg diameter data (collected in late September) and summer egg diameter data (collected in late August) were combined. In order to do so, summer egg diameter data was adjusted to expected egg diameters in the fall using a conversion factor: Big Fish River- summer egg diameter + 0.37 mm, and Babbage River- summer egg diameter + 0.32. This was derived from the difference in adjusted mean egg diameters in the Big Fish River population and the difference in the summer and fall unadjusted mean egg diameters in the Babbage River. This allowed for an increase in sample size, thus improving the final resolution of the relationships.



and the absence of any correlation with fork length in the sample obtained from the Babbage River.

3.2.4 Maturity Frequency of the Adult Female Populations.

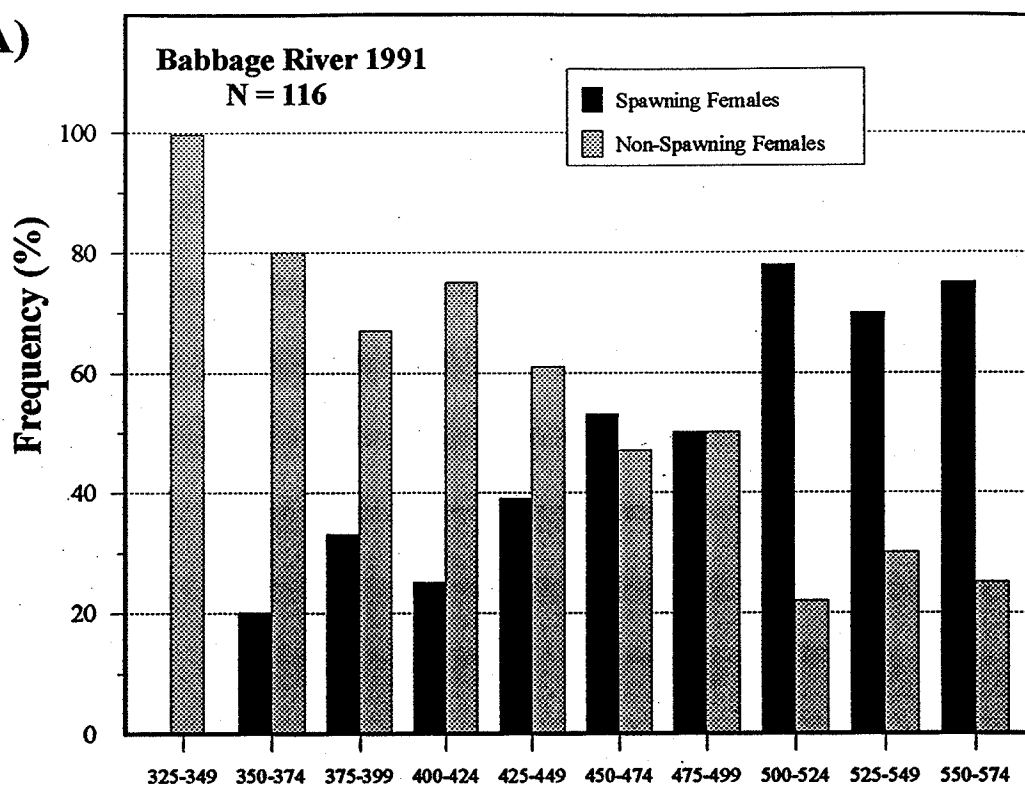
It was not possible to determine the percentage of females maturing at a given age due to the difficulty in consistently aging char of this species, combined with a small random dead sample of the entire female component (spawning and non-spawning) of each population. However, samples were sufficient to examine the percentage of females maturing in each of 10 - 25 mm size classes (intervals). The assumption inherent in this comparison is that the smaller the size class the younger the fish. This comparison was not possible on the 1990 Babbage River dead sample because few females ($n=7$) smaller than 425 mm in length were dead sampled that year. However, due to a larger sample size of adult fish larger than 425 mm ($n=43$), it was possible from the 1990 sample to determine the percentage of adult female char that were not spawning (resting) that year.

3.2.4.1 Within Populations Between Years

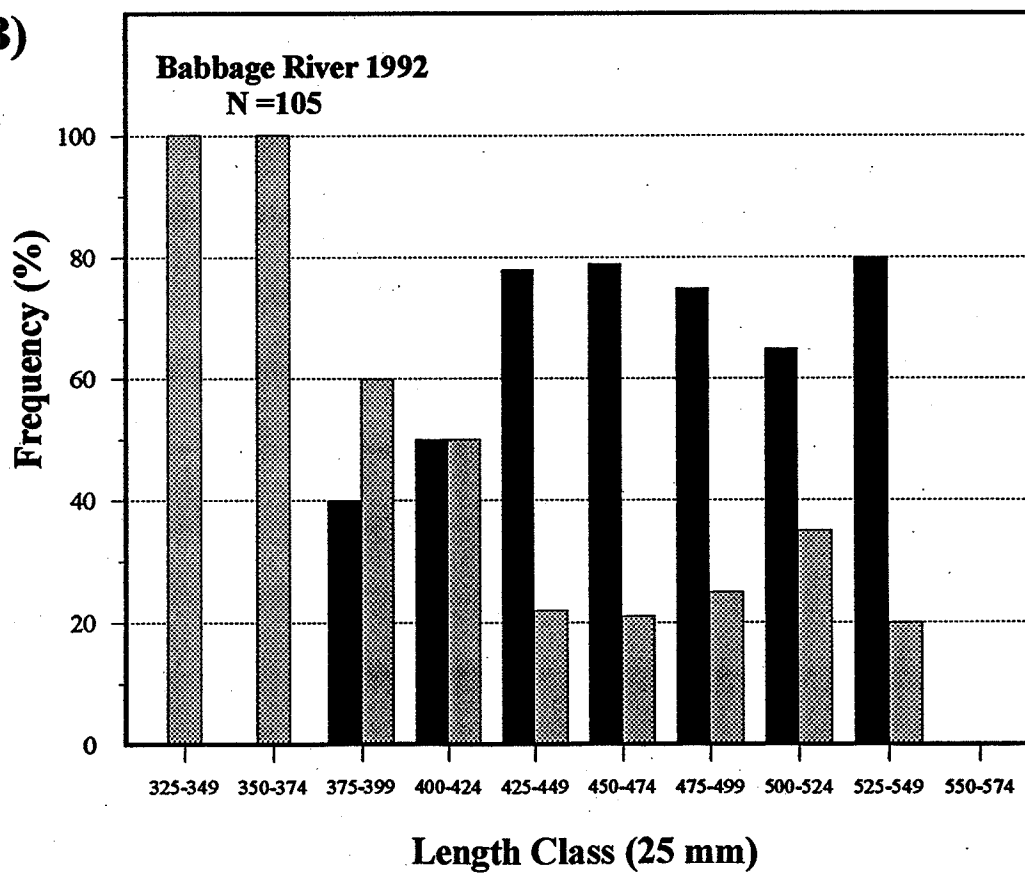
The maturity frequency for the female component of the population in the Babbage River was determined during weir enumerations in 1991 and 1992 (Figure 11 a and b). In 1992 in comparison to 1991, non-spawning females in the Babbage River were observed to make up a noticeably smaller percentage of each of the 25 mm size classes below 500 mm. Non-spawning char in the Babbage River made up 33 % of the adult (>425 mm) female population in 1990, 44 % in 1991, and 27 % in 1992. Inter-year comparison of the female maturity frequency in the Big Fish River population was not possible as a random dead

Figure 11. Maturity frequency of female Dolly Varden char, grouped by 25 mm size class, recorded from a random dead sample at the Babbage River in 1991 (A) and 1992 (B). Samples from both years were collected by similar weir operations over the duration of the upstream migration (Sandstrom, Harwood, and Reist, unpublished data).

A)



B)



sample of the entire (spawning and non-spawning) female component of the population was only obtained in 1991.

3.2.4.2 Between Populations

Maturity frequency of the female char populations from the Big Fish and Babbage Rivers were determined in 1991 during identical weir enumerations. No non-spawning (resting) adult female char larger than 475 mm were captured in the Big Fish River in either 1991 (Figure 12) or during the course of this research. Over all size classes greater than 425 mm, non-spawning adult female char accounted for only 5% of the adult females caught in the Big Fish River in 1991. The majority of non-spawning female char in this system were classified as either smolt or post-smolt juveniles (<425 mm). In comparison, non-spawning char in the Babbage River comprised between 27 % (1992) and 44 % (1991) of the adult (>425 mm) female population. The smallest size class in which the majority (>50%) of females from the Big Fish River were mature was the 375-399 mm size class in 1991. For the Babbage River the comparable size class was the 450-475 mm size class in 1991 and 400-424 mm size class in 1992.

The percentage of spent post-spawned females collected in the fall samples varied considerably between 1992 and 1993 in the Big Fish River but not in the Babbage River (Table 11).

3.3 Parameters of Energetic Reserves

In order to examine whether females from the Big Fish River allocate more energy to overwintering metabolic demands than do females from the Babbage River a number of

Figure 12. Maturity frequency of female Dolly Varden char, grouped by 25 mm size class, recorded from a random dead sample at the Big Fish Rivers in 1991 (Harwood and Sandstrom, unpublished data). The sample was collected over the duration of the upstream migration by weir.

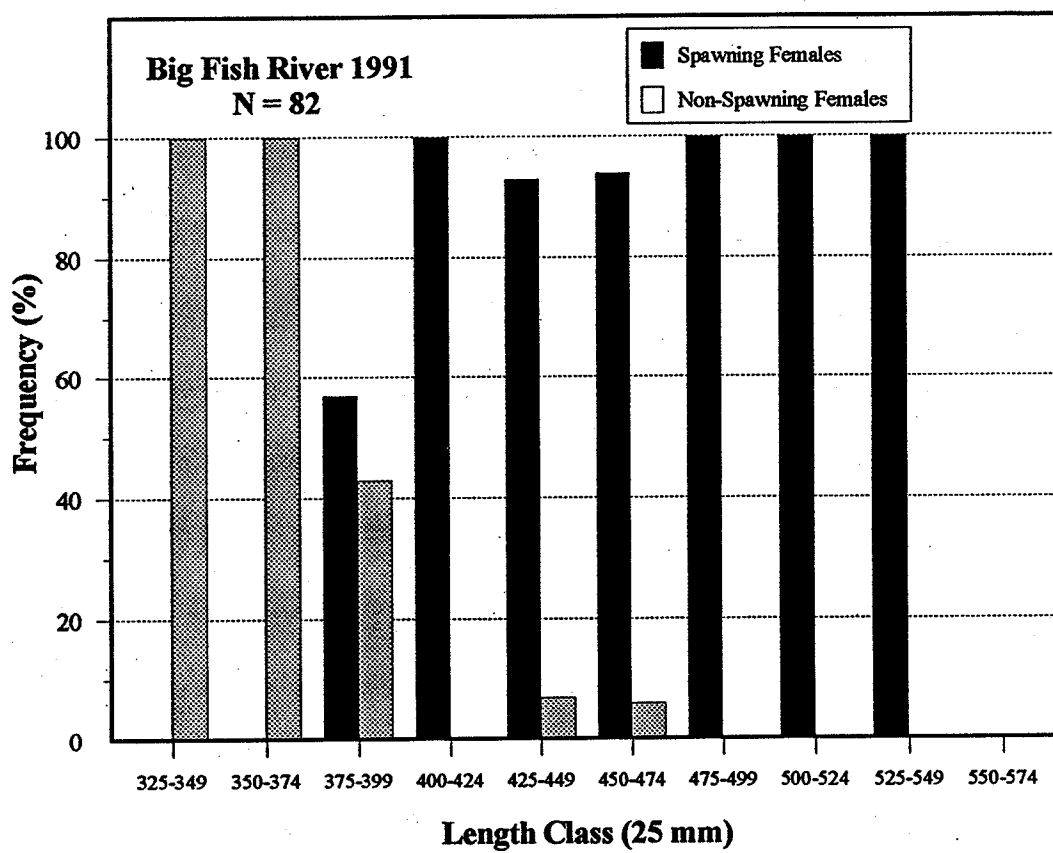


Table 11. Composition of the fall samples of mature females from the Babbage and Big Fish Rivers. Classification (see methods for criteria) was based on internal examination of the gonad.

River	Date (dd/mm/yr)	Condition	Number Sampled	Percentage of Sample
Babbage River	03/10/92	Ripe	6	18 %
		Partly Spent	3	9 %
		Spent	24	73 %
		TOTAL	33	100 %
Babbage River	30/09/93	Ripe	3	10 %
		Partly Spent	9	29 %
		Spent	19	61 %
		TOTAL	31	100 %
Big Fish River	01/10/92	Ripe	16	52 %
		Partly Spent	7	22 %
		Spent	8	26 %
		TOTAL	31	100 %
Big Fish River	30/09/93	Ripe	6	21 %
		Partly Spent	6	21 %
		Spent	16	58 %
		TOTAL	28	100 %

energetic parameters were examined between the populations. Maturing females draw heavily from endogenous energy stores throughout the summer to complete gonad maturation. As a result, the actual percent lipid in the tissues will vary depending on the date of sampling. Fish sampled "early" (i.e., prior to final maturation) will not have a lipid composition representative of what those same fish would have at the start of the winter (i.e., after spawning). Thus, to avoid the possibility that observed variation in lipid composition was due to the samples being collected from the populations at different points during the maturation of their gonads, only fall-sampled females that had spawned or were in the process of spawning (gonad fully matured) were used for the comparison of energetic parameters.

3.3.1 Liver Wet Weight Comparisons

The liver is known to be a minor storage site of energy in salmonid fish, thus it was included in the examination of whether there were differences in energy reserves within populations between years and between populations within years. Difficulty in freeze-drying the tissue prevented analysis for lipid content based on a dry weight/wet weight ratio and thus the whole wet weight was used as an alternative measure. Liver wet weight was correlated with fish length in both female populations and in both sample years (ranged from 0.45 to 0.82). The variance accounted for by the regressions ranged from 0.20 to 0.67 (Table 12).

3.3.1.1 Within Populations Between Years

The adjusted mean liver whole wet weight (\log_{10} -transformed) did not vary significantly within the Babbage River population between 1992 and 1993 (1.32 in both years, Table 12). However, this parameter was significantly lower for the Big Fish River population

Table 12. Analysis of Covariance statistics for liver weight comparisons: (A) between years within systems; and (B) between systems within years.

Comparisons	Classification Variable	Sample Size	Correlation r	P-value	Fitted Model	S.E. of Intercept	S.E. of Slope	LSMEAN of LSMEAN	Std Err	P-Value (Slope; Intercept)
A. Within System - Babbage R. - Fall	1992	33	0.45	0.0098	LogLiver Wt = -5.39 + 2.50 LogFork Lth	3.02	1.12	1.32 (21.07)	0.02] -0.9662 (0.9591; .9669)
	1993	31	0.57	0.0007	LogLiver Wt = -5.54 + 2.56 LogFork Lth	2.04	0.76	1.32 (21.12)	0.02	
Within System - Big Fish R. - Fall	1992	31	0.59	0.0005	LogLiver Wt = -3.67 + 1.88 LogFork Lth	1.44	0.54	1.35 (22.12)	0.01] -0.0025 (0.7973; 0.0025)
	1993	28	0.82	0.0001	LogLiver Wt = -4.11 + 2.01 LogFork Lth	0.91	0.34	1.28 (19.00)	0.02	
B. Between Systems - Fall 1992	Babbage	33	0.45	0.0098	LogLiver Wt = -5.387 + 2.50 LogFork Lth	2.71	1.01	1.29 (19.67)	0.02] -0.0160 (0.5425; 0.0185)
	Big Fish	31	0.59	0.0005	LogLiver Wt = -3.67 + 1.88 LogFork Lth	1.32	0.49	1.35 (22.62)	0.02	
Between Systems - Fall 1993	Babbage	31	0.57	0.0007	LogLiver Wt = -5.54 + 2.56 LogFork Lth	1.86	0.69	1.3138(20.60)	0.02] -0.6530 (0.4400; 0.5355)
	Big Fish	28	0.82	0.0001	LogLiver Wt = -4.10 + 2.02 LogFork Lth	0.83	0.31	1.3047(20.17)	0.01	

in 1993 compared to 1992 (1.28 compared with 1.35, Table 12). In this case, the difference resulted from a difference in the intercepts of the regression rather than the slope.

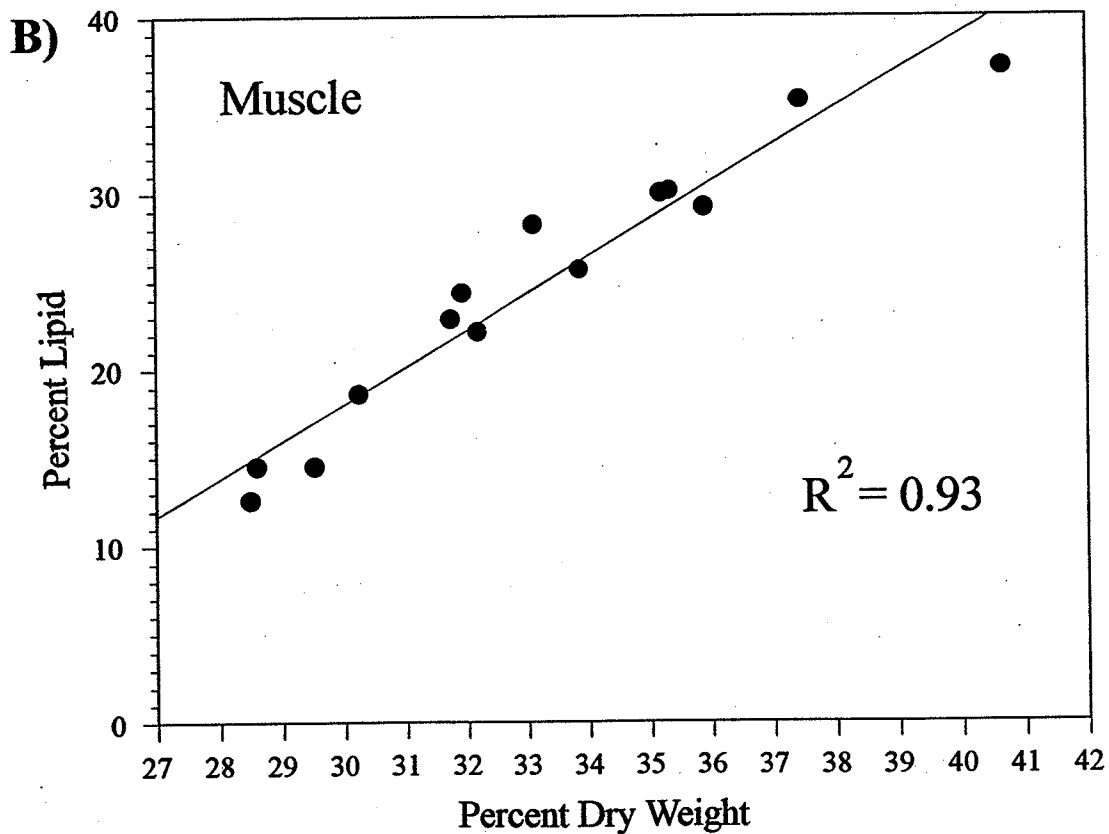
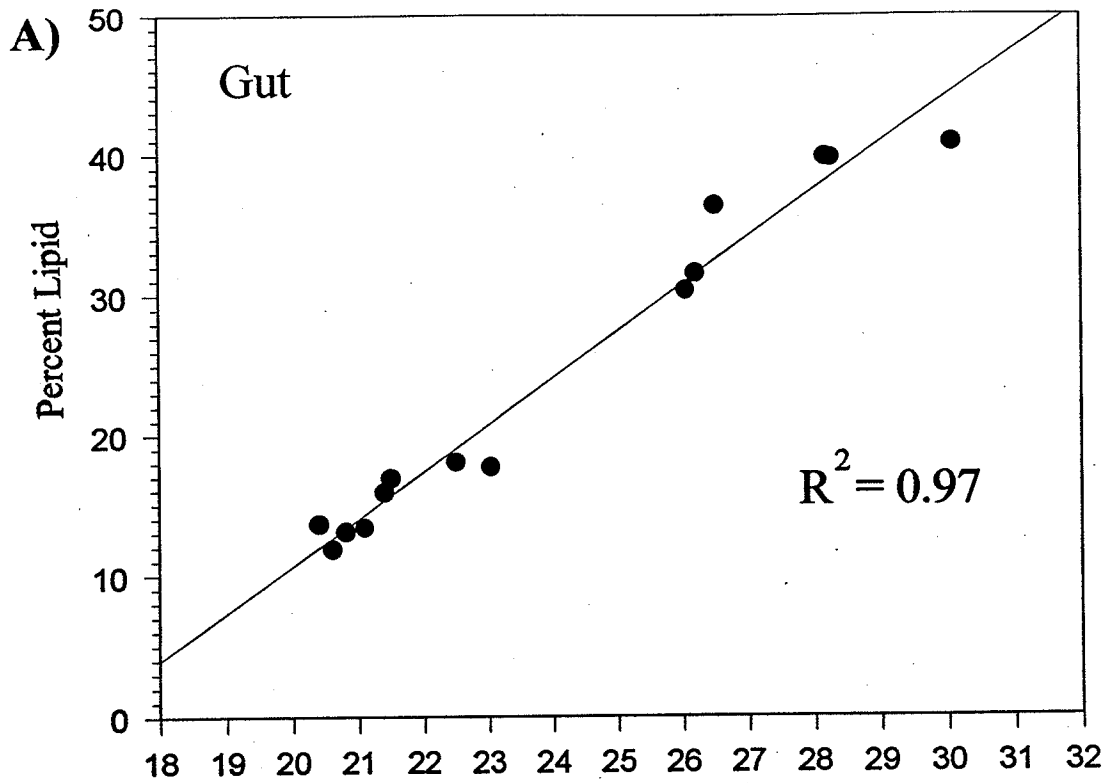
3.3.1.2 Between Populations

Adjusted mean liver whole wet weight (\log_{10} -transformed) did not vary significantly between the two populations in the 1993 post-spawned females of the fall sample, but did vary significantly in the comparable 1992 sample (Table 12). In 1992, females from the Big Fish River had significantly greater adjusted mean liver wet weight than did females from the Babbage River (1.35 compared with 1.29 respectively, Table 12). In this case, the difference resulted from a difference in the intercepts of the regression rather than the slope.

3.3.2 Comparisons of the Percent Lipid in the Gut

The gut (esophagus + stomach + pyloric caeca + intestine) is an important storage site of energy in salmonid fish. The percent dry weight of the gut ($\text{dry weight} \div \text{wet weight} \cdot 100$) was found to be a reliable estimator of the percent lipid of the gut ($r^2 = 0.97$, $n = 14$, $F = 115.74$, $P = 0.0001$; Figure 13). Therefore, this parameter was used for the determination of whether differences in the relative amounts of gut lipid reserves existed between the populations, and within the populations between years. The percent dry weight of the gut was either not correlated (Fall 1992 Babbage River: $r = 0.20$, $P = 0.4883$) or only weakly and negatively correlated with length (Fall 1993 Babbage River: $r = 0.37$, $P = 0.0442$ and Fall 1993 Big Fish River: $r = 0.37$, $P = 0.0529$), except for the Big Fish River 1992 fall sample where a moderately strong correlation was observed ($r = 0.69$, $P = 0.0044$).

Figure 13. Correlations found between the percent dry weight ((dry wt ÷ wet wt) • 100) and the percent lipid composition of (A) gut tissue and (B) muscle tissue in spent female Dolly Varden char collected prior to overwintering in the Babbage and Big Fish Rivers.



3.3.2.1 Within Populations Between Years

The gut energy reserves of females from the Big Fish River, as indicated by adjusted mean percent gut dry weight, were significantly higher in 1993 compared to 1992 (26.7 % compared with 23.4 %, Table 13). This difference resulted from a difference in the intercepts of the regressions rather than the slopes. A similar comparison of females from the Babbage River by analysis of covariance was not possible due to the non-significance of the relationship between the independent and dependent variable in the 1992 sample ($r^2 = 0.04$, $P = 0.4883$, Table 13). Thus, comparison between years in this system was done using unadjusted means (Student t-test). This comparison revealed that mean percent dry weight of the gut was not significantly different in spent spawning females in Babbage River in the fall for either 1992 (23.5 ± 2.44 %) or 1993 (24.7 ± 1.7 %) (1992 vs. 1993 (equal variance) d.f. = 41.0, $t = -1.880$, $P = 0.067$).

3.3.2.2 Between Populations

For post-spawned females from the two systems prior to overwintering, the adjusted mean gut energy reserves (percent dry weight) were significantly greater for females from the Big Fish River in the fall of 1993 (26.4 % compared with 25.0 %, Table 13). In this case, difference resulted from a difference in the intercept of the regression rather than the slope. The comparison of the 1992 fall unadjusted mean gut percent dry weights between the Babbage (23.50 ± 2.44 %) and Big Fish Rivers (23.66 ± 2.04 %) was found to be non-significant (Babbage vs. Big Fish (equal variance) d.f. = 27.0, $t = -0.1965$, $P = 0.8457$).

Table 13. Analysis of Covariance statistics for gut energy comparisons: (A) between years within systems; and (B) between systems within years. Analysis of Covariance could not be run on the within system comparison of Babbage River fall data due to the absence of a significant correlation between the dependent variable and the covariate in one or more of the samples.

Comparisons	Classification Variable	Sample Size	Correlation r	P-value	Fitted Model	S.E. of Intercept	S.E. of Slope	LSMEANof LSMEAN	Std Err	P-Value (Slope ; Intercept)
A. Within System - Babbage R. - Fall	1992	14	0.20	0.4883	-	-	-	-	-	-
	1993	29	0.37	0.0442	-	-	-	-	-	
Within System - Big Fish R. - Fall	1992	15	0.69	0.0044	Gut % Moisture = 39.91 + (-0.04) Fork Length	7.55	0.02	23.42	0.55	0.0001 (0.3158 ; 0.0001)
	1993	27	0.37	0.0529	Gut % Moisture = 35.50 + (-0.02) Fork Length	3.93	0.01	26.71	0.40	
B. Between Systems - Fall 1993	Babbage	29	0.37	0.0442	Gut % Moisture = 37.70 + (-0.03) Fork Length	8.44	0.02	25.01	0.41	0.0173 (0.6659 ; 0.0123)
	Big Fish	27	0.37	0.0529	Gut % Moisture = 35.49 + (-0.02) Fork Length	3.75	0.01	26.41	0.40	

3.3.3 Comparisons of the Percent Lipid in the Muscle

The muscle is an important storage site of energy as lipid in salmonid fish. The percent dry weight of the muscle ($\text{dry weight} \div \text{wet weight} \cdot 100$) was shown to be a good estimator of the percent lipid of the muscle ($r^2 = 0.935$, $n = 14$, $F = 172.65$, $P = 0.0001$; Figure 13). Thus this measurement was used in the inter-river comparisons to determine whether differences existed in the relative amounts of muscle lipid reserves. The percent dry weight of the muscle was shown to be negatively correlated (e.g., regression slopes ranged from -0.05 to -0.08) with length in both populations and in both sample years (Table 14). This suggests that in general larger fish had less energy reserves in the muscle than did smaller fish.

3.3.3.1 Within Populations Between Years

The average adjusted mean percent dry weight of the muscle for females from the Big Fish River was significantly higher in the fall of 1993 than in the fall of 1992 (37.65 % compared with 36.40 %, Table 14). In this case, the difference resulted from a difference in the intercept of the regression rather than the slope. There was no significant difference observed for females from the Babbage River for this same time period (Table 14).

3.3.3.2 Between Populations

No significant difference existed between the adjusted mean percent dry weight of the muscle between females from the Babbage and Big Fish Rivers in either the fall of 1992 or the fall of 1993 (Table 14).

Table 14. Analysis of Covariance statistics for muscle energy comparisons: (A) between years within systems; and (B) between systems within years

Comparisons	Classification Variable	Sample Size	Correlation r	P-value	Fitted Model	S.E. of Intercept	S.E. of Slope	LSMEAN of LSMEAN	Std Err	P-Value (Slope ; Intercept)
AW ithin System - Babbage R. - Fall	1992	33	0.41	0.0155	Muscle % Dry Wt = 59.17 + (-0.05) Fork Length	11.28	0.023	35.06	0.38	0.1807 (0.2668 ; 0.1748)
	1993	31	0.75	0.0001	Muscle % Dry Wt = 72.54 + (-0.08) Fork Length	7.73	0.016	35.79	0.39	
Within System - Big Fish R. - Fall	1992	31	0.71	0.0001	Muscle % Dry Wt = 59.85 + (-0.05) Fork Length	6.40	0.014	36.40	0.39	0.0293 (0.9756 ; 0.0293)
	1993	28	0.72	0.0001	Muscle % Dry Wt = 61.30 + (-0.05) Fork Length	4.01	0.009	37.65	0.41	
B. Between Systems - Fall 1992	Babbage	33	0.41	0.0155	Muscle % Dry Wt = 59.17 + (-0.05) Fork length	9.82	0.021	35.70	0.39	0.3883 (0.9839 ; 0.3868)
	Big Fish	31	0.71	0.0001	Muscle % Dry Wt = 59.85 + (-0.05) Fork Length	4.95	0.011	36.16	0.39	
Between Systems - Fall 1993	Babbage	31	0.75	0.0001	Muscle % Dry Wt = 72.55 + (-0.08) Fork Length	8.69	0.018	36.06	0.41	0.1249 (0.1621 ; 0.0709)
	Big Fish	28	0.72	0.0001	Muscle % Dry Wt = 61.30 + (-0.05) Fork Length	3.88	0.008	36.96	0.41	

4. DISCUSSION

Energy accumulated by a fish must be partitioned between various competing life history demands. Simplified, these demands can be classified under one of three general headings: growth, metabolism and reproduction. An energy budget or bioenergetic model is simply a balanced energy equation in which consumption is balanced by total metabolism (standard, active, and specific dynamic action [food digestion and assimilation]) and somatic and gonadal growth. It is expressed as follows:

$$\text{Energy Accumulated} = \text{Metabolism} + \text{Growth} + \text{Reproduction} + \text{Waste}.$$

It would appear that feeding of anadromous char during the freshwater period of the life history (i.e., migration, spawning and overwintering) is very limited and may not occur with some individuals. McCart (1980) noted that the majority (79%) of the anadromous component in north slope char populations, examined during the freshwater period of the life history, did not have any food in their stomachs. For those individuals that did have food in their stomachs, it is questionable whether it could have been adequately digested at the low water temperatures these fish are known to occupy during the winter. Thus, it was assumed the energy that these char accumulate from the anadromous phase of the life history and which is then allocated to differing demands in a particular year can be considered finite. As a result, a trade-off must exist between components of the energy budget. For example, energy used for growth in fork length cannot be available for use in metabolism or reproduction. That is, the energy budget must balance between intake and expenditure. Furthermore, because Yukon north slope char populations are an iteroparous species, survival throughout the winter is necessary. To do so, sufficient

somatic energy reserves must remain after spawning in order to survive the nine or ten months they spend in freshwater prior to the downstream migration in the following spring. Thus, populations which must allocate more energy to overwintering metabolism will have proportionately less energy available for allocation to reproduction and/or growth. In the case of the char populations in the Babbage and Big Fish Rivers, significantly different water temperatures, measured at the spring orifice, exist between the two overwintering sites for these populations. Because a positive relationship exists between the standard metabolic rate of a fish and the surrounding ambient temperature, it was hypothesized that char from the system with the higher water temperature (Big Fish River) would exhibit greater metabolic rates. Thus, because these populations spend up to ten months fasting at these sites, char in the Big Fish River which occupy the warmer habitat, should have considerably larger somatic energy reserves in order to successfully overwinter in comparison to char from the Babbage River. If the total amount of energy available for allocation is the same, and other energetic demands (i.e., migration) are similar between the two populations, the greater need to devote energy to metabolic activities should result in the char population of the Big Fish River having less energy available for allocation to either growth and/or reproduction. This research set out to determine whether differences in overwintering site temperatures have an effect on the annual growth and/or reproductive effort of female anadromous Dolly Varden char on the north slope. Specifically, it was predicted that mature adult females from the Big Fish River would have significantly greater amounts of somatic lipids after spawning and, to balance this, lower annual growth rates and/or reproductive effort than mature adult

females from the Babbage River. The first step for testing these predictions was to look at whether differences existed between the populations in those parameters that should be compromised by the greater allocation of energy to somatic reserves (i.e., growth and reproductive effort) in fish of the Big Fish River.

4.1 Growth

Growth rates of the adult female populations were compared by two methods in this study. The first method determined growth rate from Floy-tag recaptured char and showed that the mean adult female growth rate, adjusted to account for differences due to fork length, did not differ significantly between the populations. Females of both populations increased in fork length by approximately 16 mm per year.

The second test compared for differences in the linear regressions of fork length at age. Both slopes and intercepts were examined. The regressions of fork length-on-age showed that although the intercepts were significantly different (discussed in section 4.4.1) the slopes were equal. This indicated there was no significant difference in the annual growth rate of adult female char between the two systems. This test also determined that the average annual growth rate of adult females was around 20 mm, similar to the findings of the Floy-tag recapture comparisons. These results are contrary to what was predicted by the original hypothesis. It was predicted that Big Fish River females should exhibit lower annual growth rates than females in the Babbage River due to a greater allocation of energy to somatic reserves for overwintering. Thus, it appears from these results that growth in fork length is not compromised by a potentially greater allocation of energy to

overwintering reserves in females from the Big Fish River.

In addition, only five percent of adult char in the Big Fish River were classified as non-spawning adults compared with 27 to 44 % of adult females in the Babbage River. Thus, a large proportion of the samples of aged and Floy-tagged females from the Babbage River comprised both spawning and non-spawning adults. However, annual growth was not significantly different from that found in the Big Fish River, where females are predominately spawners. This suggests that the annual growth rate of 'resting' (non-spawning) and maturing (spawning) adult female Dolly Varden char from the Babbage River is probably similar. This is consistent with Lambert and Dodson (1990) who found that the annual growth increment of spawning and non-spawning males and females of the same age did not vary significantly for lake cisco (*Coregonus artedii*)(Lesueur) and lake whitefish (*Coregonus clupeaformis*)(Mitchill).

As noted earlier, the annual growth of a fish can take the form of not only growth in fork length (mm) but also growth in weight or muscle mass (grams). The mean round weight in the summer of 1993 adjusted for fork length was approximately 90 grams heavier in females from the Big Fish River than in females of the Babbage River. Additional analysis indicated that 35 to 40 grams of this difference was due to significantly heavier mean gonad weight adjusted for fork length. The remaining 50 grams was due to significantly greater mean dressed weight adjusted for fork length in females from the Big Fish River.

Assuming that the skeleton and gills made up a similar percentage of the dressed weight in both stocks, then the total dressed weight should be a reasonable estimator of

muscle mass if controlled for the effect of fork length. Therefore, in order to examine differences in weight, the mean dressed weight adjusted to a common fork length was compared both within systems between years and between systems within years. Inter-year comparisons revealed that the adjusted mean dressed weights in both populations were significantly higher in the fall of 1993 compared to the fall of 1992 (Babbage River females by 60 grams and Big Fish River females by 40 grams). The reason for this increase is not known. However, because several other energetic variables also increased significantly from 1992 to 1993 (discussed below), it can be speculated that the feeding opportunity for the stocks may have been better in 1993. This increased feeding opportunity would have enabled females from both stocks to accumulate a greater amount of energy, and thus would have allowed more energy to be allocated to muscle production in that year. The adjusted mean dressed weight was also observed to be significantly greater in females from the Big Fish River than in females from the Babbage River in both comparison years by approximately 50 grams. These results, like the growth in fork length results, are contrary to what was predicted for females from the Big Fish River. The expectation was that energy available for growth, either in fork length or weight, would be reduced in the Big Fish River stock due to the greater allocation of energy to somatic reserves, necessitated by a higher temperature-induced metabolic rate. However, it appears that not only can females at the Big Fish River grow in fork length at a similar annual rate to the females from the Babbage River, they can also produce more muscle at a given fork length than those of the Babbage River. Thus, it appears that the higher water temperatures at the Big Fish River overwintering site, as measured at the

spring orifice, do not compromise the annual growth in fork length or weight of adult females from this stock. Possible reasons for this are discussed below.

4.2 Reproductive Effort

Reproductive effort is defined as the proportion of total energy, procured over a specified and biologically meaningful time, that an organism devotes to reproduction (Hirshfield and Tinkle, 1975 as cited in Roff, 1992). The reproductive effort in Dolly Varden char comprises three separate components, each requiring varying degrees of energy expenditure: the reproductive product (gonad/eggs); mating behaviour (mate selection, redd construction and redd defense), and; necessary secondary characteristics (spawning colouration and morphological adaptations). It was not possible in this research to determine the energy requirements for the latter two demands. It was possible however, to compare whether the stocks differed in the energy allocated to the reproductive product by comparing the total weight of the gonad. Because no measurements of egg lipid were done in this study, it was assumed that the total energy content of an egg was dependent on its size (i.e., diameter), and that this relationship did not vary between the study populations. Kazakov (1981) showed that for Atlantic salmon large and small eggs did not differ in their biochemical properties, but differed only in the amount of nutrient available to the embryo. Kamler and Kato (1983) found similar results for rainbow trout (*Salmo gairdneri*) (Richardson), with the caloric value (cal per mg) not changing with the size of the individual egg. Finally, Smirnov et al. (as cited in Fleming and Gross, 1990) also found that the egg size of members of the genera *Oncorhynchus*

and *Salmo* was highly representative of the energy content and chemical composition of the egg. Thus, egg size appears to be a reasonable estimate of the energy investment by the female. It was also assumed that the energy required to produce an egg of similar volume or diameter (and energy content) were not different between the populations. Thus, if energy requirements of mating, development of secondary characteristics, and production of an egg of a particular diameter do not vary significantly between the populations, then the weight of the gonad should be a fairly representative measure of the total energy devoted to the reproduction by the female.

Comparison of the linear regressions of gonad weight versus fork length for each of the populations indicated that, although females from the Big Fish River face potentially higher metabolic rates and as a consequence a greater allocation of their finite energy reserves to somatic energy reserves, they have significantly heavier gonads than females of a similar fork length from the Babbage River. However, the adjusted mean gonad weight did not vary significantly between the two populations when dressed weight was used as the covariate. This suggests that the significantly greater dressed weight observed in females from the Big Fish River may be partly responsible for the significantly greater gonad weights in this stock in comparison to the Babbage River stock. Thus, increased muscle mass in a female char of a certain fork length may allow that individual to produce a larger gonad. This may result from either of two causes. First, by physically creating a larger body cavity and thus a greater volume that the gonad can occupy, the female can create a greater number of eggs. Second, because the muscle is an important site of energy storage, the increased muscle mass may provide a greater storehouse of energy necessary

for the production of a larger gonad. Further insight into factors behind why females from the Big Fish River have heavier gonad weights than females from the Babbage River was gained by examining the two components of gonad weight (i.e., egg size and egg number).

The total weight of the gonad depends upon, first, the number of eggs (fecundity) that make up the gonad and second, on the weight of an individual egg. The weight of an individual egg is dependent on its diameter; the larger the diameter of the egg the heavier the egg. Egg diameter and fecundity are negatively correlated. That is, holding gonad weight constant, observed fecundity will decrease as individual egg diameter increases (Duarte et al., 1989; Egar, 1990; Fleming and Gross, 1990; Roff, 1992). During their investigation of the variation in reproductive parameters of coho salmon (*Oncorhynchus kisutch*) (Walbaum) with latitude, Fleming and Gross (1990) observed that although egg number increased with latitude, egg diameter and gonad weight decreased with latitude. They suggested the lower reproductive investment in more northerly stocks may be the result of an increased energy cost of packaging the reproductive investment into more small eggs than into fewer larger eggs. A similar relationship between egg diameter, fecundity and gonad weight was found in mature female char from the Babbage and Big Fish River populations in 1993. Although females from the Babbage River had significantly higher mean fecundities (by approximately 500 eggs), they had significantly lower mean egg diameters (by approximately 0.5 mm) and gonad weight (by approximately 35 grams). According to Fleming and Gross, it may be that although females from the Babbage River have a lower measurable reproductive investment (i.e.,

gonad weight), the actual reproductive investment for the two populations (including the energetic costs of packaging) may be similar.

Females from the Big Fish River not only have similar growth rates to similarly sized females from the Babbage River but also exhibit an equivalent, if not greater, amount of reproductive effort. As a consequence, the original null hypothesis, that spawning females from the Big Fish River do not have to allocate more energy to overwintering somatic reserves at the expense of growth and/or reproductive effort can not be rejected. Thus, the explanation of effects of differences induced by the environment must be developed further to adequately explain these results.

4.3 Overwintering Energy Reserves

Comparisons of the life history characteristics of growth and reproductive effort have shown that higher overwintering water temperatures do not compromise the energy allocated to these parameters. However, females from the Big Fish River may still have to allocate more energy to somatic reserves for overwintering because of the higher water temperatures.

Salmonid fishes accumulate energy, digest, assimilate and store it in three primary locations within the fish: in the gut (externally around the pyloric caecae and within the intestinal wall); in the white and dark musculature, and; in the liver (Love, 1980). Jensen (1980) found that Arctic char stored some of the energy reserves as fat in the muscle, however, a considerable portion of energy reserves were deposited as fat in and around the gut, and only a small and varying amount was stored in the liver. Dutil (1986)

determined that the liver contributed less than 2% of the total energy storage in a 600 mm immature Arctic char in Nauyuk Lake, N.W.T. In the present study, percent dry weight of the gut and muscle tissue was found to be an accurate indicator of the percent lipid in that tissue. Because the liver probably only functions as a minor and temporary site of lipid storage in this species, and because of the difficulty in determining dry weight of this tissue, only whole liver wet weight was used for comparisons. Thus, it was predicted that if females from the Big Fish River must allocate more energy to somatic reserves, they will have significantly higher adjusted mean gut and/or muscle dry weights and perhaps liver whole wet weights than would females from the Babbage River. However, it appears from the results that little difference exists between the populations in energy reserves available to individual females after spawning. Females from the Big Fish River had only marginally higher gut lipid reserves immediately following spawning in one of the two sample years than did females from the Babbage River.

Inter-year comparisons of liver whole wet weight determined that the estimated relative mean liver whole wet weight was significantly higher in the Big Fish River, but only in 1992. However, this may have been the result of differences in the number of spent females collected in the Big Fish River in 1992. Spent females made up only 26% of the Big Fish River sample in that year, whereas in all other fall samples, both in the Babbage and Big Fish Rivers, spent females accounted for 60% or more of the sample. The liver is the location where endogenous energy reserves are converted to various compounds (i.e., vitellogenin) which are transported to the gonad by way of the bloodstream and used for production of yolk in the developing oocytes (Love, 1980;

Jobling, 1994). Thus, it is assumed that the liver in a maturing female char is largest and heaviest during the summer and early fall as the eggs mature, and diminish in size during and following spawning. The higher liver wet weight in the 1992 sample from the Big Fish River was probably due to the greater proportion of ripe fish in this sample. Liver activity (in association with gonad maturation) in these ripe fish may either had not ceased or had ceased but had not had similar recovery time prior to being collected, as had fish collected in 1993.

Inter-system comparisons of the adjusted mean whole liver wet weight found that significant differences only existed between the 1992 samples, with females from the Big Fish River having significantly higher liver weights than females from the Babbage River. Again, this was probably due to the high numbers of ripe fish in the 1992 sample from the Big Fish River. The reason for the larger number of unspawned females in the Big Fish River in 1992 is unclear. Because this sample was collected at approximately the same time of the year (October 1, 1992) as the 1993 sample (September 30, 1993), differences in time of sample collection were probably not responsible. It may have been that in 1992, spawning had been delayed to some extent, however, there is no corroborating evidence to support this. In summary, the energy content of the liver, if correlated with the wet weight of the organ, appears to not have been significantly different between the two stocks prior to overwintering. These results are in contradiction to the hypothesis in question, that char from the Big Fish River would have greater somatic reserves in this tissue due to higher water temperatures and metabolic rates requiring a greater somatic reserve.

The mean percent dry weight of the gut was not observed to vary significantly between years for fall-sampled spent females in the Babbage River. However, a significant difference was observed in the adjusted mean percent dry weight of the gut for fall-sampled females from the Big Fish River between 1992 and 1993. This may have been an artifact of the natural variability in gut lipid reserves experienced by these populations, compounded by the small sample sizes. Alternatively, this difference may have been due to better feeding opportunities for the Big Fish River population in the summer of 1993. Significant differences between the two populations in the adjusted (1993 sample) or unadjusted (1992 sample) mean percent dry weight of the gut were found in only the 1993 fall sample. These results, although inconclusive, are (in the case of the 1993 data) consistent with the hypothesis that females from the Big Fish River allocate more energy to somatic reserves because of an elevated metabolic rate due to environmental temperature.

Inter-year comparisons of the adjusted mean percent dry weight of the muscle showed significant differences only in the Big Fish River population with the adjusted mean weight higher in 1993 than 1992. This, like the differences seen in adjusted mean dry weight of the gut, may have been an artifact of the natural variability in muscle lipid reserves experienced by these populations. Alternatively, this difference may have been due to better feeding opportunities for the Big Fish River population in the summer of 1993.

Inter-system comparisons of the adjusted mean muscle dry weight showed that the female populations of the Babbage and Big Fish Rivers did not vary significantly in either of the two sample years. However, because females from the Big Fish River have

significantly greater dressed weights (muscle mass) than similar-sized females from the Babbage River, they may have a greater total amount of lipid reserves. A female char from the Babbage River appears to have the same amount of lipid per gram of muscle as a similar-sized female from the Big Fish River. However, because the female from the Big Fish River has significantly more grams of muscle (between 40 and 55 g) than one from the Babbage River, the total amount of lipid available to the female from the Big Fish River will be greater. Also, because the oxidation of muscle tissue is used for energy production in overwintering and fasting fish (Dutil, 1986; Lambert and Dodson, 1990), the greater amount of muscle in females from the Big Fish River could provide an additional reserve of resources that could potentially be utilized for energy production. This speculation, if confirmed by future research, would be consistent with this researches hypothesis of char from the Big Fish River requiring more energy reserves to overwinter due to increased metabolic requirements induced by the environment. However, at this point, it is not known whether females from the Big Fish River allocated more energy to muscle production in order to produce larger gonads or to a greater somatic energy reserve or perhaps for a combination of these two activities. To examine what the causal reason is, would require samples of spent females to be collected from each system in the spring (i.e., May) and energy values compared to those obtained from samples collected in the fall.

The inability to consistently identify significant differences in the amount of lipid reserves between the populations in either of the two sample years suggests that female char from the Big Fish River have similar, or perhaps slightly higher, overwintering energy

demands than do female char from the Babbage River. Because spawning female char from the Big Fish River do not allocate proportionately more energy to overwintering lipid stores (muscle and gut) than do spawning female char from the Babbage River, it can be concluded that spawning female char from the Big Fish River probably do not face a significantly increased overwintering metabolic rate as a result of higher thermal spring temperatures at that site. In order to do this, females from the Big Fish River must be able to locate themselves, for the better part of the winter, in energetically optimal areas of their overwintering site. In such areas temperatures and conditions are likely relatively ideal for the fish. Such locations in the Big Fish River would be similar in environmental parameters that require energy expenditure to those used by Babbage River overwintering females. The water at the site on the Big Fish River is around 15° C when it finally reaches the surface of the stream bed at the spring orifice. As it flows north downstream from this point the temperature of the water slowly drops until it finally reaches the freezing point. Thus, a temperature gradient will be set up spatially along the length of the overwintering site, with water temperatures highest at the upstream (south orifice end) and lowest at the downstream (north end). Because such a gradient exists, presumably individuals can choose amongst habitats. The areas used by overwintering char in the Big Fish and Babbage Rivers are probably those sections of the stream nearest the top of the *aufeis* field (farthest from the spring source) because water temperatures are closest to 0° C and thus least metabolically demanding. Also, char in the Big Fish River system may be able to escape the higher water temperatures by utilizing ice tunnels which form within the *aufeis* field itself and which appear to be unique to this system (Sandstrom and Harwood,

unpublished data).

Spring water at the overwintering site used by the Babbage River char population is significantly lower in salinity in comparison to the overwintering site at the Big Fish River ($[Na] = 0.3 \text{ mg} \cdot \text{l}^{-1}$ measured at Babbage River spring orifice, $[Na] = 824 \text{ mg} \cdot \text{l}^{-1}$ measured at Big Fish River spring orifice, McCart and Bain, 1974). The concentration of sodium in the spring water at the site in the Big Fish River is around 1 %, however, if other trace minerals and chemicals also contribute to the osmotic gradient, the surrounding ambient concentration may be as high as 2.5 % (Table 1). In comparison the concentration of sodium in the spring water at the site in the Babbage River is more or less zero, with an overall ambient concentration of approximately 0.2 % (Table 1). These differences may even be greater in winter at the lower end of the overwintering site where the flowing water begins to freeze and salt concentrations would begin to increase. One possible alternative explanation for the similarities in post-spawned energetic reserves between the two stocks is that although char from the Big Fish River may face increased temperature-induced metabolic rates, they may have lower osmotic demands (which also require the expenditure of energy) than do char from the Babbage River. This would be due to the overwintering site at the Big Fish River having water with a salinity that is closer to being isotonic with the internal environment of the fish than water from the Babbage River site. Thus, if this is true, although females from the Big Fish River may be faced with increased temperature induced metabolic rates, that would require them to utilize greater amounts of energy than char from the Babbage River, they may expend less energy on osmoregulatory demands. In this way then the net difference in energy

demands between the two systems is reduced and thus the energetic reserves are similar in contrast to the original predictions.

4.4 Additional Observations

A number of additional observations were made in the process of testing the hypothesis that provide further insight into the mechanisms controlling the observed energy allocation and life history characteristics of females from the Babbage and Big Fish Rivers.

4.4.1 Smaller Mean Size of Adult Females in the Big Fish River

The prediction from the hypothesis that growth in fork length would be compromised in females from the Big Fish River by a greater allocation of energy to somatic reserves was tested by comparing the slope of the fork length-at-age regressions. Although not different in slope, they were significantly different in intercept. These results indicated that at all ages mature adult female char from the Babbage River were approximately 30 mm larger than females from the Big Fish River. MacDonell (1987) also presented data showing that in 1987 char from the Big Fish River had smaller mean fork lengths at a specific age in comparison to other char populations in the region. The difference in size of females from the two populations was also noticeable in the t-test comparison of the mean fork length of the female populations. This test showed that not only were the mean fork lengths of the female populations different by approximately 24 mm, but that the mean fork length of the female population from the Babbage and Big Fish Rivers did not vary over a three-year period (Babbage 1990 to 1992; Big Fish 1991 to 1993). Thus

the mean fork length of spawning female char in both populations remained fairly constant from year-to-year. The stability of the mean fork length of the population is an important observation, particularly in the case of the Big Fish River. Exploitation has been shown in other species to decrease the mean fork length of the population because fisheries tend to select for the larger size classes of fish (Schaffer and Elson, 1975). The Big Fish River has faced significant exploitation in the past (as recent as 1986) and continues to do so to some extent (coastal fisheries). If the smaller mean size of this population observed during this research is due to past heavy exploitation removing the larger fish, then it would be expected that the mean size of the population should have increased over the three years of the study with little exploitation operating. Thus, as the fish grew and were recruited into the larger size classes, which would no longer be removed by a fishery, it would increase the mean size and thus increase the mean fork length of the population. Because the mean fork length for the female component of the Big Fish River population was not shown to increase significantly over the duration of this research, it suggests that the mean size observed is fairly representative of what the mean size of this component of the population is under normal (unexploited) conditions. Thus, past exploitation is probably not the cause of the smaller mean size of adult females in the Big Fish River. Although the mean fork length of the adult female populations was not significantly different between years in either population, the length distributions were observed to vary considerably within populations between years. This was probably due to a combination of small sample sizes, particularly for the Babbage River samples, and in the case of the Big Fish River population differences in the sample methodology. The 1991 sample from the Big

Fish River was collected by weir along the lower river in August and September, while the 1993 sample was collected by seine at the spawning grounds at the beginning of October. Both methods may have had their own biases regarding size of fish captured, although the actual occurrence and nature of these biases is not known. Some sampling bias may have taken place in 1990 during the Babbage River weir operations with larger fish tending to be preferentially dead sampled by the sampling crew. This would explain the absence of smaller females (<430 mm) in the 1990 Babbage River sample.

If not due to residual effects of past exploitation, why are spawning females from the Babbage River larger at a given age than females from the Big Fish River? This is especially unusual, considering that it was established that spawning adults from the two populations have similar annual growth rates once reaching maturity. Furthermore, the modal fork length of the returning smolt component of the populations is approximately 30 mm larger in the Big Fish River. Thus, it would be expected that adult char from the Big Fish River would tend to be larger resulting from the larger smolt size and similar adult growth rates. It is not known whether the larger smolt size in the Big Fish River is due to greater freshwater growth rates in this system producing a larger downstream migrant smolt size or whether it is because smolts from the Big Fish River population can accumulate more energy and thus exhibit greater growth rates during their first summer at sea. Although beyond the scope of this research, insight into which factor accounts for the larger smolt size could be gained by examining the fork length-at-age distributions of the freshwater juvenile component of each population. Similarities would suggest that it was differences in summer energy accumulation while at sea their first summer and not

freshwater growth rates that account for the larger smolt size in the Big Fish River. Back calculations done on the otoliths of returning smolts may also shed some light on whether it is differences in freshwater or marine growth rates that is responsible for the size difference.

Whereas females from the Big Fish River appear to spawn annually, a large percentage of females from the Babbage River appear to spawn biannually. That is, 5% of females larger than 425 mm in the Big Fish River were classified as resting and between 27% and 44% of females larger than 425 mm in the Babbage River were classified as resting. These non-spawning adults in the Babbage River population, because they are spared the energetic demands of spawning, are likely able to put more energy into growth in fork length in a non-spawning year than would be possible in a spawning year. The higher incidence and the higher growth rates of non-spawning adult females in the Babbage River could provide an explanation for the larger mean fork length of spawning females at a given age in this population. However, the similarity in growth rates of adult females from the two populations suggests that non-spawning adult females in the Babbage River do not have significantly different growth rates than spawning females. Lambert and Dodson (1990) also found that the annual growth increment of spawning and non-spawning male and female lake cisco and lake whitefish of the same age did not vary significantly, suggesting that non-reproductive fish do not devote more energy to growth in fork length than do reproductive fish. Thus, the higher proportion of non-spawning adults in the Babbage River population is probably not responsible for the larger size-at-age of this population.

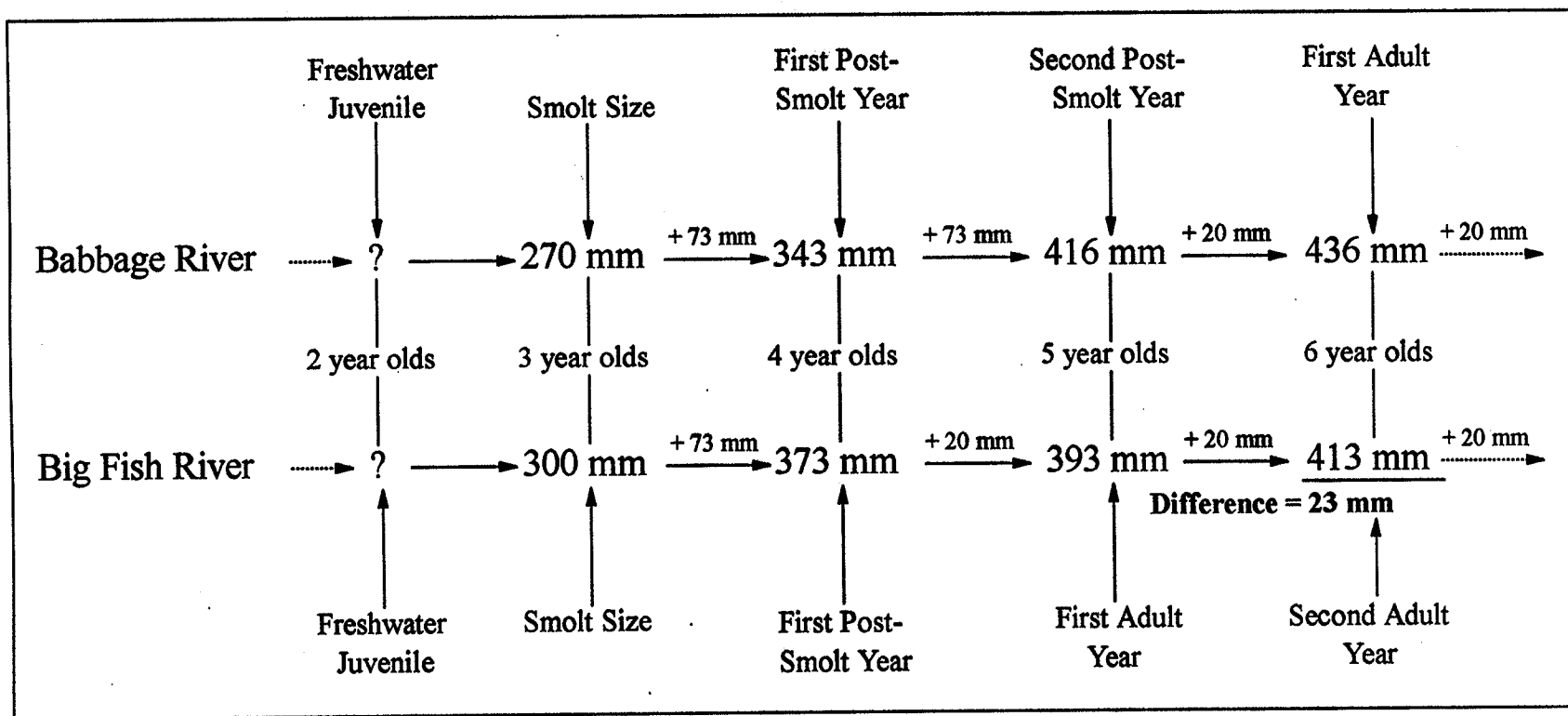
Several studies have shown that the mean fork length of some anadromous fish species increases with increasing migration distance in fresh water and also with increasing altitude of the natal spawning area (e.g., brown trout (L'Abée-Lund et al., 1990), Atlantic salmon (Jonsson et. al., 1991; Schaffer et. al., 1975), sockeye salmon (Blair et. al., 1993, and a review of 15 species (Bernatchez and Dodson, 1987)). It is theorized that as swimming ability and efficiency increase with increasing body size, a larger mean body size is needed to successfully migrate up long rivers or short, fast-flowing rivers (Trump and Leggett, 1980). However, Fleming and Gross (1989) found that for coho salmon female body length decreased with migration distance, although they did not offer an explanation for the negative relationship. In the present study it is unlikely that river length or river velocity was responsible for the large differences observed in female mean fork length between the Babbage and Big Fish Rivers. Although the Babbage River is slightly longer (Babbage River = 110 km, Big Fish River = 95 km), the higher elevation of the Big Fish River natal site (Babbage River = 250 m, Big Fish River = 380 m) and resulting faster flow, probably balances out to some extent the migration energy requirements of the stocks. However, the two stocks may have significantly different marine migration differences.

It is possible that char from the Big Fish River do not have to migrate in the coastal marine environment as far as char from the Babbage River in order to procure food. The decreased overall (freshwater + marine) migration distance for char from the Big Fish River would permit a greater allocation of energy to germinal and somatic growth. This hypothesis still remains to be tested.

Alternatively, the smaller average size of females from the Big Fish River may be the result of the majority of females from this system spawning a year earlier than females from the Babbage River. Maturation in fish comes at the expense of growth in fork length due to the trade-off effect when energy is allocated between these two parameters. Floy-tag recapture data indicates that mean growth of post-smolt juveniles and virgin adults from the Big Fish River is around $73 \text{ mm} \pm 13 \text{ mm}$ ($n=34$, $\text{max} = 102 \text{ mm}$, $\text{min} = 51 \text{ mm}$) (Harwood and Sandstrom, unpublished data). Similar Floy-tagged data for post-smolt juveniles and virgin adults in the Babbage River is not available. However, differences in modal fork lengths of first (smolt) and second summer sea-run (post-smolt) char from the Babbage River in 1991 indicate a similar annual growth rate of around $80 \text{ mm} (\pm 10 \text{ mm})$ for this life history stage in this system (Figure 6 b). Thus, an additional summer feeding and growing at this rate prior to first maturation would allow females from the Babbage River to make up the 30 mm size difference seen between the modal smolt fork lengths of fish from the two systems. It would also allow the mean fork length of adult females from the Babbage River to surpass that of adult females from the Big Fish River by the observed 20 to 24 mm. This difference could then be maintained over the life of the adult fish by the similar adult female growth rates documented in the two stocks by this research. Figure 14 summarizes how this pattern of growth and maturation is hypothesized to account for the size difference seen between the adult female populations.

There is evidence from the present research that lends support to the above hypothesis of an earlier age of maturation in females from the Big Fish River. Unfortunately, due to the difficulties in aging char of this species and the small number of female char (spawning

Figure 14. The hypothesized pattern of growth and maturation of female Dolly Varden char in the Babbage and Big Fish Rivers that would account for the significantly different mean fork lengths at a given age observed between the populations. Mean growth rates for post-smolt juveniles and adult females were determined from Floy-tag recaptured char from these life history stages. Fork lengths listed, except for the smolt life history stage, represent an estimated upstream migrant mean fork length for that life history stage (estimated standard deviation of 20 mm). Mean length of the smolt life history stage is the actual modal length for the upstream migrant smolts determined during weir enumerations in 1991.



and non-spawning) dead sampled in the 325 mm to 450 mm size classes it was not possible to accurately determine the percentage of females maturing at a given age. However, it appears that the proportion of females that mature in the smaller size classes (and presumably younger ages) is considerably higher in the Big Fish River than in the Babbage River. Evidence of this becomes apparent when examining the maturity ratios for the Big Fish River population by 25 mm fork length intervals. Bond (1989) determined that the majority of Babbage River char smoltify at three years of age. It was also determined from a small random sample of smolts taken during weir operations on both the Babbage and Big Fish Rivers in 1991 that the majority of char from these two systems smoltify at three years (Babbage River $n=11$, 9% at 2 years, 55% at 3 years, and 36% at 4 years, Sandstrom, Harwood and Reist, unpublished data; Big Fish River $n=15$, 7% at 2 years, 60% at 3 years, and 33% at 4 years, Harwood and Sandstrom, unpublished data). Thus, using 3 years of age and the smallest modal fork length to denote the smolt life history stage, almost 60% of female char from the Big Fish River population in the 375-399 mm size class (majority probably five-year-olds) and 100% of females in the 400-424 mm size class (majority probably six-year-olds) were spawning in a given year. In comparison, only 30% (in 1991) to 40% (in 1992) of the female char from the Babbage River in the 375-399 mm size class and 25% (in 1991) to 50% (in 1992) in the 400-424 mm size class were spawning in a given year. Thus, based on the maturity ratios of the 25 mm fork length classes and the presumed average age of the fork length classes, it would appear that the majority of Big Fish River females spawn in their fifth year and the remainder in their sixth year. In contrast, a smaller percent of Babbage River females

spawn in their fifth year, with the majority delaying spawning until their sixth year, if not later. Consistent with this, Bain (1974) also determined that over 50% of the anadromous females from the Babbage River were mature at age 6 and similarly concluded that this is the age at which most females spawn for the first time. Also, the relative absence of spawning females under 430 mm in size in the Babbage River (Figure 8 a, b and c), but not in the Big Fish River (Figure 9 a and b), is also suggestive of an older age at first maturation in the Babbage River. Consequently, by delaying maturity by one year, the initial size at which Babbage River females enter the spawning population will, on average, be larger than that for females in the Big Fish River, thus explaining the size discrepancy seen between the adult populations (Figure 14).

4.4.2 Smaller Size and Younger Age-of-First Maturation in Females from the Big Fish River

A smaller mean fork length and presumably younger age-at-first maturation of females from the Big Fish River population may be responsible for the smaller mean size of adult females observed in this population, in comparison to the Babbage River. However, it is unclear why females appear to mature one year earlier in the Big Fish River. It may be that the age at which a population spawns for the first time has a genetic component (Roff, 1991). A number of studies have shown that for Atlantic salmon, age-at-first maturity may be inherited rather than the result of environmental effects (in Schaffer and Elson, 1975; Naevdal et al., 1978). Alternatively, experimental releases of hatchery coho and chinook smolts of different sizes determined that larger smolts tended to mature at an earlier age (Bilton et al., 1982; Bilton, 1984). Peterman (1982) also found

a similar relationship between smolt size and age-at-first maturation in wild salmon populations. Thus, the larger returning smolt size observed in the Big Fish River population could allow a greater percentage of females to attain maturity at a smaller size and younger age in this system.

Love (1980) noted that fish in general tend to mature for the first time at a particular fork length rather than at a particular age. There appears to exist some minimal size at which the body of the fish is sufficiently large enough to accommodate the energy reserves required to reproduce. In both the Babbage and Big Fish Rivers the smallest females captured in the study were around 360 mm and thus this may represent the absolute minimum female body size required to spawn for north slope char. If the trigger for ultimate sexual maturation for the first time depends on the body length of the individual in the spring time period, then using an estimated post-smolt growth rate of 75 mm and a known returning modal smolt size of 300 mm, the majority of females from the Big Fish River can attain a fork length well in excess of this minimal threshold body size after just one post-smolt summer (i.e., two summers of estuarine and/or marine growth)(Figure 7 a and b). In comparison, the majority of females from the Babbage River either just attain or more likely fall short of this threshold size limit after one post-smolt summer of growth. Using the known returning modal smolt fork length of 270 mm and a similar post-smolt growth rate to that of females from the Big Fish River, female char from the Babbage River can only attain a mean fork length of around 350 mm after two summers of growth at sea (Figure 6 a and b). As a consequence, the following spring the majority of female post-smolts from the Babbage River will be of a size that is insufficient for spawning that

year. Thus, these fish will undertake an additional year of post-smolt growth. As suggested earlier, this additional year of post-smolt growth in females from the Babbage River allows them to surpass females from the Big Fish River in mean adult size.

Alternatively, life history theory predicts that populations faced with high mortality rates should mature at an earlier age (and thus smaller size) and put proportionately more energy into each reproductive attempt at all ages (Schaffer and Elson, 1975; Roff, 1991). Jensen (1985) showed that increases in mortality in lake whitefish were associated with an earlier age and smaller size-at-first maturation. The smaller size-at-first maturity and the lower growth rate following maturity resulted in a lower asymptotic size in lake whitefish populations faced with high mortality rates. Based on this, the smaller size and earlier age-of-first maturation observed in females from the Big Fish River population suggest this population may experience higher natural mortality rates than the Babbage River population. Some evidence to support this hypothesis comes from scarring-frequency data. These data suggest that Big Fish River anadromous adult and juvenile females may experience higher mortality rates than their Babbage River counterparts during the marine feeding stage of the life history due to a greater risk of being predated by seal, whale, bird, fish, and lamprey. Returning Big Fish River migrant char, examined during weir enumerations during the course of this research, were more likely to have fresh seal and lamprey scars, which may be indicative of a higher marine mortality rate for the Big Fish River stock (1991 Big Fish R.= 11%, 1990 Babbage R.= 2%, 1991 Babbage R.= 2%, 1992 Babbage R.= 3%; Sandstrom, Harwood and Reist, unpublished data). Sparling and Stewart (1986) also found, during domestic harvest monitoring at the mouth of the Big

Fish River in 1986, that a high percentage (13.3%) of the anadromous char had fresh scars. MacDonell (1987) found that only 3.9% of Big Fish River anadromous char examined during a weir enumeration in 1987 had fresh scars, however, most of the fish examined in that study were under 400 mm and may have been less likely to escape predators. The higher risk of predation, and therefore mortality, for fish from the Big Fish River may be due to the proximity of this river to the Mackenzie Delta where there is perhaps a greater abundance of predators. Alternatively, the anadromous component of this population may spend a longer period at sea feeding (discussed in section 4.4.6) during the summer, which would result in a longer exposure to the risk of predation.

It is also possible that greater current and past exploitation of the fish from the Big Fish River, compared to the Babbage River, may compound an already high anadromous adult and juvenile natural mortality rate and thus contribute to an earlier age of first maturation in this population. The population in the Big Fish River has faced considerable exploitation in the past (prior to 1986) at the mouth of the river in August and again at the spawning and overwintering site in November. Although the Big Fish River itself has been closed to fishing since 1986, the population is still presently being fished (more distantly and to a lesser extent) during the summer at Shingle Point on the Beaufort Sea coast. Tag recaptures from the subsistence harvest at Shingle Point have shown that the catch is made up of fish from the Babbage, Rat and Big Fish River populations (Harwood, unpublished data). Char from the Rat and Big Fish Rivers probably comprise a greater percentage of the catch, than char from the Babbage River, simply due to the closer proximity of these systems to Shingle Point. Only rough estimates are available as to the number of char

taken each year by this fishery but the catch probably numbers between 200 and 500 char annually (Harwood, personal communication). In contrast, the Babbage River population has faced little in the way of exploitation, other than those individuals taken each summer along the coast. It is unlikely that exploitation is solely responsible for the hypothesized higher mortality rate for the anadromous fish of the Big Fish River, because it has been operating as a selective force (evolutionarily speaking) for a very short time (since 1970) and the level of exploitation and the life history stage targeted by the fishery have been variable during this time. It is, however, highly probable that exploitation has contributed to the higher mortality rate in the Big Fish River and therefore to the younger age-of-first maturation.

Furthermore, Stearns (1976) noted that general life history theory predicts that in a stable population where reproductive success depends on size, age and social status, the age of maturation should be delayed. However, in growing populations, such as one recovering from exploitation, selection should push the age-of-first maturation to the physiological minimum. He used the analogy of compound interest in banking to explain the rationale behind this: that is, it is best to get your money into the bank as soon as possible so that the compounding interest rate will get to work more rapidly. More specifically, the sooner the individual reproduces, the sooner their offspring (carrying their genes) will reproduce and thus, ultimately the greater the contribution will be of that individual to future genotypes. Based on this, it is possible that the earlier age at maturation seen in females from the Big Fish River is due to the population still being in a recovery phase (i.e., not stable) from past exploitation. Thus, from this prediction it would

be expected that once reaching stability some time in the future, the mean age-of-first maturation would increase to some new optimal age. However, this prediction may not apply to char populations like that of the Big Fish River population in which the progeny of younger, smaller individuals is speculated to suffer disproportionately greater mortality rates than the progeny of larger individuals (discussed in section 4.4.4). Stearn's hypothesis also may not apply to char in the Big Fish River as the ratio of anadromous spawning females to anadromous spawning males is significantly higher in this population in comparison to the Babbage River (4.5 females to each male in the Big Fish (Harwood and Sandstrom, unpublished results); 1.5 females to each male in the Babbage River (Sandstrom, Harwood, and Reist, unpublished data)). The reason for the highly skewed sex ratio in the Big Fish River is unknown. In general, access to the spawning males (if limited in abundance) tends to be size dependent, with larger females getting preferential access (Roff, 1992). As a result, an earlier maturing smaller female may be less likely to gain access to a spawning male and thus successfully spawn in the Big Fish River population. These two observations would consequently, decrease the advantage of the life history strategy suggested by Stearns and thus the expression of it for these reasons alone. Furthermore, observations and analysis of the population conducted in this research occurred between five and eight years after the population was closed to large-scale fishing effort and thus some degree of recovery possibly occurred during this time. The fact that there was not a significant change in the mean fork length of the female population observed over the three years of this study suggests that the population has recovered somewhat since the closure of the fishery and is nearing stability in its size

composition. Thus, it is unlikely that instability of the population in the Big Fish River is solely responsible for the earlier age-of-first maturation, however, it should not be discounted as a possible factor. Some resolution of this prediction would be possible with the continued monitoring of the population, in the absence of fishing, over the next three to five years to see if the mean age-of-first maturation increases.

In conclusion, the smaller size and younger age-of-first maturation in the Big Fish River char population is probably the factor responsible for the difference in mean size of the adult female populations. The underlying cause for the earlier maturation in females from the Big Fish River is unclear but probably due more to a larger smolt size and/or a higher mortality rate (natural or man-made) in this population, than to the possibility that this population is still recovering from past exploitation with natural selection acting to minimize the age-of-first maturation. Insight into whether the earlier maturation of females from the Big Fish River results from their ability (i.e., larger smolt size) or the necessity for this (i.e., increased anadromous mortality rates) becomes more apparent from comparison of the relative egg diameter data within the Big Fish River population in the next two sections.

4.4.3 Larger Relative Egg Diameters in Females from the Big Fish River

Life history theory predicts that the fitness return from the amount invested per offspring, and not the total number of offspring produced by the female, is usually optimized by natural selection (Stearns, 1976; Roff, 1992). Thus, the clutch size of the female will reflect an optimal investment per offspring, and because this optimum is higher

for some populations, the number of offspring produced by these populations will decrease accordingly. Fleming and Gross (1990) found that although egg number varied significantly between years in Atlantic salmon, the annual variation in egg diameter was slight. However, in the present study the relative mean egg diameter adjusted for fork length in females from the Big Fish and Babbage Rivers was shown to vary significantly between 1992 and 1993. In both populations the mean egg diameter was significantly higher in 1993 by approximately 0.3 mm. This is contrary to the hypothesis that predicts egg diameter should remain constant, whereas fecundity should fluctuate with changes in energy allocated to reproduction. The reason for the observed inter-year differences in relative egg diameter in females from these two populations is unknown. It may have been due to small sample sizes compounded by large variation in egg diameter at a given fork length or perhaps to an age effect that went unnoticed because of the difficulty in consistently aging adult fish from these populations. Future work should investigate this, by comparing a larger sample of ripe females from each system, and determine whether egg diameter fluctuates annually, as found in this research, or whether it is relatively constant over time, as life-history theory predicts.

In general, larger eggs produce larger fry (Bagenal, 1969; Beacham and Murray, 1990; Kazakov, 1981; Wallace and Aasjord, 1984; Beacham *et. al.*, 1984; Roff 1992). However, because fish are poikilotherms, development rates and hatching size of the embryo are affected by water temperatures during incubation (Braum in Gerking, 1978; Heggberget, 1988; Duarte and Alcaraz, 1989). Heming (1982) showed that increasing incubation temperature not only decreases the incubation time, but it also decreases the

efficiency with which yolk is converted to body tissue for chinook salmon (*Oncorhynchus tshawytscha*)(Walbaum) eggs. Furthermore, Beacham and Murray (1985) found that chum salmon (*Oncorhynchus keta*)(Walbaum) eggs incubated at 4° C produced longer alevins than similar-sized eggs incubated at either 8° C or 12° C. Thus, larger eggs laid by females from the Big Fish River may not produce alevins that are significantly longer than alevins from smaller eggs in the Babbage River. This results from the higher incubation temperature and thus greater overwintering maintenance costs associated with the spawning site on the Big Fish River. Thus, although the two populations differ significantly with regard to egg diameter they may not differ significantly with respect to the size of the alevin. This expectation/hypothesis should be tested by appropriate research.

Shortly before the yolk sac is exhausted, the alevin will make its way to the surface of the gravel and emerge as a free swimming fry. The size of the fry upon emergence from the gravel will ultimately depend on the initial size of the alevin. It is likely that emergent fry size is optimized in the local environment to maximize survival of the fry. Thus, the mean egg diameter exhibited may be a result of environmentally induced selection for an optimal emergent fry size. Females must then produce eggs of sufficient size, with the final size being dependent on the particular site-specific incubation temperatures, to insure that the resulting emerging fry will be of optimal size to maximize survival.

The factor(s) determining the optimal emergent fry size for these populations is unknown and beyond the scope of this research, although a number of possible explanations can be put forward. First, fry must be at least a certain minimal size to

successfully emerge from the substrate in the spring. Second, because the swimming ability of the fry increases with body size (Braum in Gerking, 1978), fry must be of a certain size to maintain station and establish feeding territories in the river once they emerge from the gravel, particularly during the spring freshet. Third, because the size of the mouth gape generally increases with body size (Braum in Gerking, 1978), the fry must be a certain size at emergence in order to eat the food resource that is available in these systems in the spring. Finally, because the yolk sac is proportionately bigger in larger fry, these fry should have increased resistance to starvation and, therefore, increased probability of encountering a favourable environment (Wallace and Aasjord, 1984; Duarte and Alcaraz, 1989). This increased resistance to starvation may be of particular importance to fry in the Big Fish River because elevated temperatures are known to shorten the incubation time of eggs (Brannon, 1987; Duarte and Alcaraz, 1989; Beacham and Murray, 1990).

Beacham and Murray (1987) found for chum salmon and Wallace and Heggberget (1988) for Atlantic salmon that there was no genetic influence controlling development rate in embryos of different populations. This suggests that the duration of incubation and thus subsequent hatching date will depend on the specific thermal regime of the particular river used by the stock. Thus, time at hatch will depend on time of spawning. Brannon (1987) found spawning time among the sockeye salmon (*Oncorhynchus nerka*)(Walbaum) sub-populations returning to the Fraser River covered a period of five months. However, each stock spawned at a certain time, with all members of a particular sub-population spawning, on average, within ten days of each other. The temporal

regularity in spawning times was demonstrated to be directly related to the temperature regime of the particular stream used for egg incubation. Late-spawning stocks were found in streams with high mean temperatures and early-spawning stocks found in streams with low mean temperatures. Since the length of the incubation period shortens with increasing temperature but the optimal time for emergence of the fry is similar for all the sockeye populations, populations utilizing the warmer habitat with the shortened incubation period spawned later. This insured that larval emergence of all sub-populations occurred at a specific and optimal time for survival of the fry. A similar observation between the time of spawning and mean temperature during incubation was made for Atlantic Salmon stocks in Norway (Heggberget, 1988).

McCart (1980) suggested that the char population at the Big Fish River may spawn considerably later (i.e., December) than other north slope char populations due to the high incubation temperatures documented at this site. However, in the present study spent females were collected from both char populations in the Babbage and Big Fish Rivers at the end of September. Thus, spawning appears to occur at approximately the same time (mid-September to early October) in both the Babbage and Big Fish Rivers. Spawning of the char stock in the Big Fish River may have to occur at this time because access to more thermally optimal areas of the overwintering site, nearer the *aufeis* field, would not be possible much later than October. This is because riffle areas separating the upper warmer spawning site and the lower cooler overwintering site freeze over towards the end of October and beginning of November, cutting off the access for spent spawning char to the lower site. Being trapped in the upper warmer spawning site would result in energy

reserves becoming too depleted for the individual char to survive the winter, because of the greater metabolic rate. Because of the higher incubation temperatures and the earlier spawning date, it can be speculated that all other factors being equal, the hatch of eggs in the Big Fish River may occur somewhat earlier than those from the Babbage River. Bain (1974) reported that the emergence of fry from the gravel at the Babbage River occurred between the middle to the end of May which corresponds with spring break-up. This is the time, presumably, when conditions are most optimal for the survival of the emergent fry. Alevins and fry still remaining in the gravel at the time of spring break-up would probably not survive the scouring of the gravel by ice and water during the freshet. If hatch and emergence does occur earlier in the Big Fish River, the increased ability of large fry to resist starvation due to the proportionately larger yolk sac, may allow them to survive until spring break-up when more food resources become available. Alternatively, whatever the reason, selection for a particular size of emergent fry, and the site-specific incubation temperature regime of the spawning site may determine the optimal egg diameter for each of these populations. Fleming and Gross (1990) came to a similar conclusion to explain the significant positive relationship between latitude and egg number in coho salmon. They found that northern coho populations produced more eggs than southern coho populations because egg size was observed to decrease with increasing latitude. Because average incubation temperature generally decreases with increasing latitude, the optimal egg diameter need not be as large in the northern populations and metabolic efficiency improves with the cooler incubation temperatures (Fleming and Gross, 1990). Variation in egg size among populations of similar latitude was attributed

to site-specific temperature differences.

Blair et al. (1993) found, in a study of sub-populations of sockeye salmon, that females from populations that spawned along beaches in the lake had, on average, lower fecundity but greater gonad mass and larger egg diameters than females spawning in adjoining rivers. They concluded that fecundity differences were again due to differences in egg diameter and that observed variation in egg diameter was, in part, an adaptation to spawning and incubation conditions of the particular sites. Although not suggested by these authors, the mean water temperature of the lake environment over the winter would likely be higher than that found in the river. Thus, a larger mean egg diameter may be necessary to insure adequate survival of the egg and/or resulting alevin in the warmer lake environment.

As mentioned above, the hatching of eggs and the emergence of fry from the gravel ("swim-up") should occur when conditions are optimal for the survival of the fry. Because the swim-up stage represents the point at which the fry switches from endogenous to exogenous food sources, the optimal time for hatching and emergence should also coincide with the time food resources for the fry are most abundant (Brannon, 1987; Roff, 1992). For the north slope char populations this time appears to be during and shortly after spring break-up in May. Because embryos developing in larger eggs generally take more time to complete yolk absorption than do embryos in smaller eggs (Kamler and Kato, 1983; Brannon, 1987), it is feasible that egg diameter may be a mechanism by which fish can influence the incubation duration of the egg and thus the time at which fry will emerge from the substrate. In the case of the population in the Big Fish River, where

increased incubation temperatures would presumably result in a quicker development rate of the eggs, the larger mean egg diameter in the population may also be a method of prolonging the incubation of the eggs to ensure that the hatch occurs closer to spring break-up. However, Beacham and Murray (1985) incubated eggs and alevins of five chum salmon families in each of three female size classes at three different water temperatures and found no correlation between egg size, hatch time of the alevins and temperature. Brannon (1987) found in comparing egg diameter and hatch date for ten sockeye salmon populations from the Fraser River that egg size apparently did not influence incubation time. Kazakov (1981) found no difference in the rate of embryonic development of different-sized eggs of Atlantic salmon, with the hatch of different-sized eggs occurring synchronously. Finally, Roff (1992) found, on review of the literature, that there was little evidence to suggest that egg diameter and hatch date are related in naturally occurring fish populations. Based on this, it appears that variation in relative egg diameter between the Babbage and Big Fish Rivers probably relates more to an optimal emergent fry size rather than to incubation timing.

Hamor and Garside (1977) showed that Atlantic salmon eggs incubated under low levels of dissolved oxygen had prolonged incubations and produced smaller embryos than eggs incubated at high levels of dissolved oxygen. Garside (1966) produced similar findings for brook trout (*Salvelinus fontinalis*)(Mitchill). Mutch and McCart (1974) found that the spring water from the major orifice at the spawning and overwintering site on the Big Fish River had significantly higher salinity and significantly lower dissolved oxygen levels than water from the major spring at the Babbage River site. Thus, it is

possible that one or both of these abiotic factors, in conjunction with the higher water temperature, might also select for a larger relative egg diameter in females from the Big Fish River. McCart and Bain (1974), however, presented data on dissolved oxygen levels at the spawning and overwintering site at the Big Fish River, which showed the levels experienced by incubating eggs in this system would not be all that much different than those levels experienced by Babbage River eggs (Table 15). The dissolved oxygen concentrations recorded by Mutch and McCart at the Babbage River site (76% of saturation) are probably representative of those encountered by the incubating egg because spawning for this population takes place at or near the spring orifice where the water samples were taken. However, in the Big Fish River the major orifice is located several hundred meters upstream of the spawning grounds above a series of waterfalls. As water flows over these falls it experiences oxygenation and, thus, although dissolved oxygen concentrations recorded at the orifice are extremely low (20% of saturation), those at or near the spawning grounds are significantly higher (82% of saturation) and similar to those found at the Babbage River. As a consequence, dissolved oxygen concentrations at the Big Fish River overwintering site are probably not responsible for the differences in egg diameter between this stock and that of the Babbage River. However, it is not known what effect the difference in salinity has on the hatch success of different-sized eggs of this species and thus, the extent this factor contributes to the observed larger mean egg diameters in the population of the Big Fish River. This point deserves closer investigation in the future and would probably have to be accomplished through hatchery and lab studies.

Table 15. Changes in water temperature and oxygen concentration downstream of the major spring orifice at the Cache Creek (Big Fish River, N.W.T.) charr overwintering site, May 10, 1973. Data was obtained at midstream. The sample at 650 m is approximately 250 m downstream of the impassable falls and approximately at the upstream limit at which spawning of anadromous charr were observed (McCart and Bain, 1974).

Approx. distance downstream of major orifice (m)	Water temp (°C)	Oxygen Concn (ppm)	% Saturation
0	16	0.2	2
7	15	1.2	12
15	15	1.2	12
24	15	2.1	21
40	15	2.2	22
75	15	3.6	37
150	15	4.4	45
300	14	6.8	67
650	11	8.8	82

4.4.4 Correlation of Egg Diameter with Fork Length in Females from the Big Fish River

In this study, females from the Big Fish River showed a significant positive correlation of egg diameter with fish body length, whereas females from the Babbage River showed little or no such correlation. Bain (1974) also found no correlation between egg diameter and fork length in spawning females from the Babbage River population. Furthermore, he also found a similar mean terminal egg diameter (1974; 4.4 ± 0.2 , $n = 10$) in ripe females from the Babbage River to that found in the present study for (1993; 4.4 ± 0.2 , $n = 18$). If the larger relative egg diameter of females in the Big Fish River compensate for the higher incubation temperatures and lower yolk-to-tissue conversion efficiencies (thus ensuring a certain emergent fry size), then it is reasonable to assume that offspring of smaller females of the Big Fish River will experience a greater level of post-emergent mortality associated with their smaller egg diameters and resulting sub-optimal emergent fry sizes. It is unclear why the smaller females in the Big Fish River appear to produce eggs with smaller, apparently less optimal, diameters. It may be that only large females can successfully produce, accommodate, and extrude large diameter eggs. Thus, large egg size simply may be constrained by body size and perhaps age, and is not an adaptive trait. Fleming and Gross (1990) postulated that the variation of egg diameter with fork length in salmon was a result of intra-specific competition for breeding sites. Larger diameter eggs survive less well than smaller eggs in substrate of poorer quality, but larger females acquire the breeding sites with the best quality substrate. Therefore smaller females, by producing smaller eggs, increase the survival of their eggs in the poorer quality nesting sites they are

forced to use. Although comparison of spawning substrate used by large and small spawning female char both within and between sites was not undertaken in this study, it is unlikely that this factor would account for the correlation between egg diameter with fork length in the population from Big Fish River. This is because no correlation between egg diameter and fork length was found in the population from the Babbage River, although differences in substrate quality and the competition for the optimal areas at the spawning site in the Babbage River almost certainly do exist. The reason for the positive relationship between egg diameter and fork length in the Big Fish but not the Babbage River female population deserves closer investigation in the future.

The correlation of egg diameter and fork length in the females from the Big Fish River may provide some insight into whether earlier maturation of females in this population is more likely due to the larger smolt size or to a higher anadromous mortality rate in this population. Life history theory predicts that the age-of-first maturity for a population should reflect a balance between age-specific reproductive potential and risks of mortality (Blair et al., 1993). The majority of females from the Big Fish River appear to sacrifice an additional year of post-smolt growth in order to spawn a year earlier at a smaller body size, even though in this population a smaller body size means producing smaller eggs with presumably lower survivorship. Larger body size in the Big Fish River imparts an extra degree of reproductive fitness, beyond just being able to produce more eggs and being more successful in mating. Knowing this, life history theory would predict that if small eggs have sub-optimal survivorship and egg size is dependent on fork length, females in the Big Fish River should delay maturity to attain a body size capable of producing eggs

with more suitable (i.e., larger) diameters. This would occur not only at the time-of-first maturation, but also because growth rate is constant thereafter, at all subsequent spawning attempts as well. This statement holds true if anadromous adult and juvenile females face relatively low levels of mortality and the chances of a future reproductive attempt are good, even if the fish utilize an additional year for growth prior to maturing. However, if the anadromous adult and juvenile mortality rates are high, then life history theory predicts that females should attempt to spawn at the earliest possible age and size, because the longer they delay maturation the more likely they will die without getting a chance to spawn (Schaffer and Elson, 1975). Evidence from scarring frequency data suggests that mortality rates may be higher in the population from the Big Fish River than those from the Babbage River. Thus, the fact that females in the Big Fish River spawn earlier than females in the Babbage River even when it does not seem to be of obvious advantage, suggests that a greater anadromous mortality rate and not larger smolt size may be the major driving force behind the earlier age-of-first maturation.

4.4.5 Evidence of Sequential Spawning in Females from the Big Fish River

The maturity frequency (number of spawners vs. non-spawners) of adult female char (>425 mm) from the Babbage River varied notably between 1991 and 1992. In almost all size classes, spawning females made up a greater percentage of each size class in 1992 compared to 1991. The reason for the smaller percentage of non-spawning adult females in 1992 (27%) compared to 1991 (46%) is unknown, but could be the consequence of a better feeding season in 1991, perhaps due to an earlier than average (2 weeks early)

break-up of the river that spring (Moe Hanson, Inland Waters, Inuvik N.W.T., personal communication). As a result of possible increased feeding opportunity for the char stock from the Babbage River, a greater percentage of resting and virgin adult char may have been able to accumulate sufficient reserves during the summer of 1991 thus allowing them to spawn in the fall of 1992.

The maturity frequency of female char was also observed to vary considerably between the two populations in 1991. Whereas considerable numbers of non-spawning female char were captured over the entire size range (350 mm to 600 mm) of all char caught in the Babbage River, non-spawning females in the Big Fish River population were limited primarily to the 325-399 mm size classes, but were also observed to make up a very small percentage (5%) of the 425-474 mm size classes. Because no non-spawning females were captured in the 400-424 mm size class in 1991, the non-spawning females between 425-474 mm in the population in the Big Fish River probably represent a small number of resting first- or second-time spawning adult females. The remainder of the non-spawning females, those below 400 mm, are probably non-spawning post-smolt juveniles. The relative absence of non-spawning females greater than 400 mm in fork length in the Big Fish River suggests that females from this system, after maturing for the first time between 375 to 425 mm, spawn every year thereafter. Because a large percentage of the female char from the Babbage River, in all size classes over 425 mm, are non-spawners a certain percentage of adult females in this system are probably not able to spawn every year and thus alternate between spawning and 'resting' years. Furthermore, female char in the Babbage River appear to spawn for the first time around six years of age, but rarely live

to be more than ten years of age. Thus, females in the Babbage River most likely, on average, spawn two or perhaps three times and experience two resting (non-productive) years over their life span. In contrast, females from the Big Fish River appear to sequentially spawn upon reaching maturity around five years of age. However, evidence suggest that their life span may not be as long as that for females from the Babbage River. Assuming an average terminal age of eight years for females from the Big Fish River, these individuals may be able to spawn as many as three or four times over their lifespan.

4.4.6 Evidence of Greater Annual Net Accumulation of Energy in Females from the Big Fish River

Females from the Big Fish River were not only observed to have the ability to spawn sequentially but also to allocate similar energy to growth in fork length, and apparently more energy to muscle and gonad production than females from the Babbage River. In combination, these four factors suggest that females from the Big Fish River are capable of accumulating a greater amount of energy feeding along the coast during the summer than females from the Babbage River. This could be accomplished due to the proximity of the Big Fish River to the Mackenzie River drainage, affording these char earlier access to coastal food resources in the spring and, thus, a longer feeding opportunity than char from the Babbage River.

Jonsson and L'Abée-Lund (1993) concluded that the reason for the tendency of brown trout (*Salmo trutta*)(Linnaeus) in Europe to spawn repeatedly in consecutive years in southern rivers, rather than in alternate years as in northern rivers, was that the feeding period available to southern stocks was longer. Dutil (1986) concluded that the high rates

of energy accumulation in non-spawning Arctic char in the summer indicated that marine resources were not limiting in terms of quantity or quality, but rather limited in terms of the short period during which they can be utilized. Furthermore, DeCicco (1991) noted that the timing of the spring seaward migration of the northern form of Dolly Varden char in north-western Alaska depended on sea ice conditions. If sea ice was pushed onshore by winds, the out-migration of anadromous char could be delayed for up to two weeks. He found that if char encountered ice at the mouth of the river they would turn around and re-enter the lagoon, holding there until the ice moved offshore and permitted entry into the sea. In the case of the Canadian Dolly Varden stocks, due to the immense discharge of the Mackenzie River (mean flow ranges from 500 to 11,000 $\text{m}^3 \cdot \text{s}^{-1}$, but can reach highs of 22,000 $\text{m}^3 \cdot \text{s}^{-1}$; Bodaly et al., 1989) and the fact that it drains land far to the south, it breaks up earlier than the north slope rivers. As a result, coastal areas nearer the delta are free of ice sooner than coastal areas further to the west. This earlier break-up may allow char from the neighbouring Big Fish River to enter the coastal environment as much as a week or two earlier than char from the more distant Babbage River. The longer feeding period and greater associated energy gain for the char population in the Big Fish River would result in these char being able to allocate more energy to their reproductive effort (larger gonad) and to producing muscle (heavier dressed weight) than the stock in the Babbage River. The increased feeding period of the char population in the Big Fish River would also allow a greater percentage of post-spawned females from this system the opportunity not only to replenish depleted energy reserves from the previous fall spawning act but to build up sufficient reserves to spawn the following fall, all in the course of one

summer. The majority of post-spawned females from the Babbage River may have only enough time feeding to accumulate sufficient energy to "pay-off" energy debts accrued from the past spawning act and subsequent overwintering demands. Such fish would then require an additional summer to accumulate energy for spawning and as a result could not spawn in consecutive years.

5. SUMMARY

Higher overwintering site temperatures in the Big Fish River, as measured at the spring orifice, do not appear to require females from this population to allocate significantly more somatic energy reserves in the form of lipids for overwintering in comparison to females from the Babbage River. The most probable reason why adult females from the Big Fish River are not directly affected by the higher water temperatures is they are able to locate themselves in areas of the overwintering site with similar thermal characteristics to those areas used by females in the Babbage River for overwintering. These areas in the Big Fish River are probably the stretch of river nearest the top of the *aufeis* field or perhaps in tunnels within the *aufeis* field itself (which may be unique to this system) where water temperatures are near zero degrees Celsius. Alternatively, higher salinity concentrations at the overwintering site on the Big Fish River may decrease the overwintering osmotic demands of this population and balance, if any, the higher metabolic demands due to temperature. Thus, because energy allocation to overwintering metabolism appears to be similar between females from the two populations neither growth nor reproductive effort are compromised in the Big Fish River due to the higher

water temperatures. In fact, reproductive effort may be even higher in females from the Big Fish River, compared to females from the Babbage River.

This higher reproductive effort (i.e., greater relative energy allocation to gonadal tissue) in females from the Big Fish River combined with the higher dressed weight (i.e., muscle mass) and the fact that females from this stock appear to spawn annually, compared to biannual spawning in females from the Babbage River, suggests females from the Big Fish River have greater amounts of energy to allocate after fixed demands (i.e., migration, foraging, etc.) are met. The greater amount of energy available to females from the Big Fish River does not appear to be due to differences in migration demands because the combination of physical attributes (river length and elevation) of the two systems are similar. The greater energy available to female char from the Big Fish River is hypothesized to be the result of char from this system gaining earlier access to coastal food reserves due to the proximity of this system to the Mackenzie River Delta. This earlier access to coastal waters equates to a longer feeding window and thus a greater net energy accumulation for char from this stock.

The smaller fork length relative to age in females from the Big Fish River in comparison to those from the Babbage River may be the result of an earlier age and smaller size at first maturation in the former stock. This difference in size between the adult populations is then maintained over the life of the fish by similar adult growth rates. The earlier maturation in females from the Big Fish River is hypothesized to be due to either a larger smolt size in this population enabling females to mature at an earlier age, and/or an increased adult mortality rate. According to life history theory, these traits will

select for an earlier age-of-first maturation. Scarring frequency data suggests that char from the Big Fish River may experience greater mortality while feeding along the coast than do char from the Babbage River. It is also suggested that past and present exploitation of the char stock from the Big Fish River may also be acting as a selective force for earlier maturation in this stock.

The overwintering adult female char from the Big Fish River appear to be able to escape, to some extent, the higher water temperatures at this site by locating themselves in more thermally optimal areas. However, because the eggs are laid at or near the spring orifice they will be directly exposed to higher temperatures. Because the yolk-to-tissue conversion efficiency decreases with increasing incubation temperature, it is hypothesized that a larger egg diameter is required in the warmer incubation environment in order to provide an alevin of similar size as that of a smaller egg in a cooler incubation environment. Thus, larger relative egg diameters observed in females from the Big Fish River may be necessary to compensate for the higher incubation temperature in this system. By producing larger diameter eggs, females from the Big Fish River may be able to produce alevins of a certain 'optimal size' which maximizes their survival. It is also apparent from this research that not all females in the Big Fish River population are capable of producing these larger diameter eggs. Unlike females from the Babbage River, females in the Big Fish River showed a moderately strong positive correlation between egg diameter and fork length. The reason why smaller females in the Big Fish River do not produce large diameter eggs may be that egg diameter is dependent on fork length and perhaps age, with small females being less able to physically produce, accommodate,

and extrude large diameter eggs.

6. RELEVANCE OF FINDINGS TO MANAGEMENT

Higher water temperatures at the overwintering site in the Big Fish River may have three possible effects on the female component of the population that are of importance to the future management of this population. First, larger and older (8 to 9 yr olds, >475 mm) females appear to have a lower current reproductive potential (the number of offspring produced by a female during a specific spawning episode that survive to maturity) because they have significantly lower fecundities than similar-sized females in other populations like the Babbage River. This is because larger and older females in the Big Fish River produced eggs with larger diameters, presumably to compensate for the higher incubation temperatures in this system. Second, small female char in the Big Fish River may have reduced current reproductive potentials, because these individuals maybe less able to produce large diameter eggs. As a result, their small eggs could have lower survivorship in this system. Finally, the mean size of females from the Big Fish River is smaller at a given age than females in the Babbage River, even though the adult female growth rate in this population is similar to that seen for adult females in the Babbage River. The smaller mean size in the Big Fish River appears to be due to an earlier age and smaller size-of-first maturation in females of this stock.. These three factors together would compound to produce a population with an overall low productivity, not only in the number of fish surviving to fishery size but also the individual size of the fish.. Thus, if the population and its associated fishery is to be maintained over the long term, harvest levels

of char from this population may have to be proportionately lower than those for other north slope char populations, such as the Babbage River. Also, because only large females appear capable of producing large (>5.0 mm), presumably more optimal-sized eggs, the fishery should not target these individuals. However, the majority of the present fisheries for char from the Big Fish River are gillnet fisheries operating either along the coast during the summer or at the mouth of the river in late summer and early fall. In the past, gill and seine net fisheries also targeted the adults in the spawning and overwintering areas. Because, in general, the catch of gillnet fisheries tends to be skewed towards the larger and older fish, this component of the population is selectively removed. Thus, the long-term maintenance and recovery of larger, older and more fecund fish will be difficult unless steps are taken to reduce the selectivity for the larger fish.

Evidence of this size-selective fishing mortality for the Big Fish River population is visible from past data. In 1988, two years after the close of the fisheries at the mouth of the river and spawning and overwintering site, the mean size of the female population was approximately 419 mm (Fehr and Archie, 1988). At present (1993), after approximately eight years of relatively low harvest levels, the mean fork length of the female population in the Big Fish River has increased and appears to be stabilizing around 459 mm. Thus, in 1988 the majority of the spawning female component in the Big Fish River comprised small first- and second-time spawning females. These fish would produce not only small (sub-optimal) eggs with a presumed low survivorship, but also considerably fewer of them (<1500 compared to >2500 in a large female) due to their small body size. The reliance of the fishery in the 1980s on small females with relatively low current

reproductive potentials may have resulted in an overall decline in the population abundance in addition to that resulting from exploitation. This may explain why the population has been slow in recovering from past exploitation. Now that there is a greater proportion of large female spawners producing larger, more optimal, sized eggs in the population the overall abundance of the population may increase and be restored to levels previously thought to exist. Thus, in the case of the previously over-exploited char population in the Big Fish River, size-structure of critical components of the population may have to be restored first before overall abundance of the population can be restored. In comparison, if the population in the Babbage River was to be over-exploited it could be predicted that recovery would generally be quicker in this population, with abundance and composition being more or less restored simultaneously.

The majority of females in the Big Fish River appear to be able to spawn every year, whereas, a large percentage of females from the Babbage River probably spawn in alternate years. This ability to spawn each year for females from the Big Fish River does not appear to be due to differences in the overwintering habitat, but possibly to differences in the amount of energy accumulated each summer. Whatever the reason, it suggests that the lifetime reproductive potential of females from the Big Fish River may be higher than that of females from the Babbage River. However, results suggest that females from the Big Fish River suffer greater adult mortality rates than do females from the Babbage River. In fact, it is speculated in this research that an increased adult mortality rate in the Big Fish River char stock may be a major selective force causing the earlier age-of-first maturation seen in females from this population. Thus, although females from the Big

Fish River appear to spawn every fall they may not live as long and as a result the total number of lifetime spawning episodes may not be different from females from the Babbage River. However, if females from the Big Fish River do exhibit an extra spawning attempt over their reproductive life span, compared to females from the Babbage River, because fecundity is significantly higher in females in the Babbage River the total number of eggs produced by a female from either system over her life time is probably similar. This point would require further research to confirm.

7. RECOMMENDATIONS FOR FUTURE MANAGEMENT ACTIONS BASED ON THIS RESEARCH

1. Research should be undertaken to determine whether the offspring (embryo, alevin, and fry) from small diameter eggs (<4.5 mm) suffer disproportionately greater mortality than offspring from large diameter eggs (>5.0 mm) in the Big Fish River.
2. If the hypothesis given in recommendation number one is confirmed then steps should be taken to protect large (>475 mm) females from exploitation, not only during the fishery at the mouth of the Big Fish River but also during the fishery along the coast. This would primarily have to be accomplished by using smaller mesh sizes for the subsistence harvest.
3. The monitoring of the population in the Big Fish River by way of fall seining surveys at the overwintering site should be continued on an annual basis. This would be particularly beneficial if the moratorium is continued until such time as it can be determined that the mean fork length and the size composition of the adult female

population has stabilized. It may also be possible, if the moratorium is continued, to determine whether the age at first maturation in the char population in the Big Fish River will increase after the natural composition of the population has been restored. Once important factors such as these have been determined for the population, future monitoring of the composition of the female population could be used as an index as to the degree of recovery and/or exploitation.

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Appendix I

Method of extraction and determination of the percent lipid in freeze-dried muscle and gut samples

REAGENTS:

Chloroform - distilled in glass

Methanol - distilled in glass

Concentrated sulphuric acid

EXTRACTION:

Place weighed sample into large screw-cap tube (25 mm x 150 mm). Use an approximately 0.5 - 1.0 gram sample of tissue that has been previously freeze-dried to a constant weight and finely ground in a coffee mill.

Add 5.0 ml chloroform
 10.0 ml methanol
 4.0 ml distilled water

Homogenize 20 seconds

Add 5.0 ml chloroform
 5.0 ml distilled water

Homogenize 10 seconds

Rinse homogenizer between samples with chloroform:methanol (1:1) and discard rinse.

Filter homogenate through a Stefi sintered glass funnel using Whatman No. 1 filter paper (42.5 mm) into a medium screw-cap tube (20 x 150 mm). Rinse funnel between samples with chloroform:methanol (1:1) and discard rinse.

Allow layers to separate overnight in refrigerator. Many samples can be processed to this step until ready to proceed with the lipid determination. The upper layer will protect the lower layer from any chance of evaporation. When ready to conduct the lipid determination, aspirate off and discard upper methanol-water layer.

LIPID DETERMINATION:

Transfer an aliquot of the lower chloroform layer (i.e., 4 - 5 mls) to a pre-weighed and labelled aluminum weighing dish (60 mm). Use clean pipette for each sample. Place dishes on heating block in fume hood and allow stand for 30 minutes to evaporate solvent. Re-weigh dish containing lipid residue. Subtract original weight of dish to determine weight of lipid residue.

Appendix I (Continued)**CALCULATIONS:**

$$\% \text{ Lipid} = \left(\frac{100}{\text{Weight of Sample}} \right) \times \left(\frac{10}{\text{Volume of Aliquot}} \right) \times \text{Lipid Weight}$$

Where : Weight of sample is in grams (to four decimal places)
Volume of aliquot is in milliliters (to one decimal place)
Weight of lipid is in grams (to four decimal places)