

**ASPECTS OF THE REPRODUCTIVE ECOLOGY
OF BULL TROUT (*Salvelinus confluentus*)
IN THE CHOWADE RIVER, BRITISH COLUMBIA**

by

JAMES S. BAXTER

B.Sc., The University of British Columbia, 1992

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE
in

THE FACULTY OF GRADUATE STUDIES
(Department of Zoology)

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
March 1997

© James S. Baxter

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of Zoology

The University of British Columbia
Vancouver, Canada

Date March 27, 1997

ABSTRACT

In the Chowade River in northeastern British Columbia, bull trout (*Salvelinus confluentus*) males were observed to exhibit two reproductive strategies. The most common strategy was that of an individual being a dominant male, and controlling access (through direct aggression) of other males to a reproductive female. A less common strategy was that of an individual being a sneaker male, and not engaging in aggressive encounters with other males to gain access to a female. Dominant males and sneaker males differed significantly in size (length and mass), growth, reproductive pattern, morphology (mainly kype growth) and sexual colouration. Sneaker males were more similar in morphology and colouration to reproductive females, suggesting that female mimicry by sneaker males may be occurring. Dominant males were observed to be more aggressive to other large brightly coloured males than they were to smaller and duller coloured males. Experimental trials on dominant male aggression towards coloured models demonstrated that dominant males were more aggressive towards brightly coloured (male like) models than they were towards less coloured (female like) models. These results suggested that the reduced secondary sexual characteristics of sneaker males may enable them to get within close proximity to a spawning pair to allow sneak fertilizations. These studies demonstrate that variation in male reproductive strategies occur, and provide the possible mechanism by which smaller males may spawn successfully without actively courting or guarding a female. In terms of sexual selection the study suggests that as the spawning period progresses, there may be a shift in which type of strategy is at an advantage.

Microhabitat at bull trout redd sites was also measured, and found to be similar to data reported from other northern latitudes. Bull trout were highly specific in areas of the upper river where they spawned, and where a high degree of redd superimposition was observed. Bull trout females selected areas of groundwater discharge for spawning that may provide high quality incubation sites for eggs. An experiment designed to measure egg to alevin survival at selected and non-selected sites with similar habitat attributes other than groundwater infiltration, demonstrated that egg to alevin survival was significantly higher at selected sites than randomly available sites. The areas selected for spawning were areas of groundwater discharge and had

more stable and warmer incubation temperatures than non-selected sites. This study has conclusively demonstrated that bull trout do spawn in areas of groundwater upwelling, and that an individual female's reproductive success may be increased by site selection.

TABLE OF CONTENTS

ABSTRACT	ii
TABLE OF CONTENTS	iv
LIST OF TABLES	vii
LIST OF FIGURES	x
ACKNOWLEDGEMENTS	xii

CHAPTER 1 - INTRODUCTION

GENERAL INTRODUCTION	1
SUMMARY OF LIFE HISTORY INFORMATION ON THE SPAWNING COMPONENT OF THE CHOWADE RIVER BULL TROUT POPULATION	4
STUDY SITE	5

CHAPTER 2 - EVIDENCE OF ALTERNATIVE MALE REPRODUCTIVE STRATEGIES

INTRODUCTION	8
MATERIALS AND METHODS	15
I. DATA COLLECTION	15
A. Angling	15
<i>Size Data</i>	15
<i>Morphology and Colouration Data</i>	15
<i>Ageing Data</i>	17
<i>Fin rays</i>	17
<i>Scales</i>	17
B. Visual Observations	18
<i>Behavioural Observations</i>	18
<i>Experimental Tests on Dominant Male Aggression</i>	20

II. DATA ANALYSIS	23
A. Angling	23
<i>Size Data</i>	23
<i>Morphology and Colouration Data</i>	23
<i>Principal Component Analysis</i>	23
<i>Kype Depth/Fork Length Relationship</i>	24
<i>Colour Data</i>	25
Ageing Data	26
<i>Fin rays</i>	26
<i>Scales</i>	26
B. Visual Observations	26
<i>Behavioural Observations</i>	26
<i>Experimental Tests on Dominant Male Aggression</i>	27
RESULTS	28
A. Angling	28
<i>Size Data</i>	28
<i>Morphology and Colouration Data</i>	28
<i>Principal Component Analysis</i>	28
<i>Kype Depth/Fork Length Relationship</i>	38
<i>Colour Data</i>	38
Ageing Data	43
<i>Fin rays</i>	43
<i>Scales</i>	48
B. Visual Observations	48
<i>Behavioural Observations</i>	48
<i>Experimental Tests on Dominant Male Aggression</i>	51
DISCUSSION	57

CHAPTER 3 - MICROHABITAT AT BULL TROUT REDD SITES AND THE EFFECT OF REDD SITE SELECTION ON EGG TO ALEVIN SURVIVAL

INTRODUCTION	66
MATERIALS AND METHODS	68
I. DATA COLLECTION	68
Redd Surveys	68
Egg to Alevin Survival Studies	68
<i>Site Selection and Microhabitat Measurements</i>	71
<i>Spawning Procedure, Egg Capsule Placement, and Temperature Measurements</i>	71
<i>Capsule Retrieval</i>	72
<i>Alevin Length Measurements and Estimation of Fertilization Success</i>	72
<i>Groundwater Measurements</i>	72
II. DATA ANALYSIS	73
RESULTS	75
Redd Surveys	75
Egg to Alevin Survival Studies	75
DISCUSSION	81

CHAPTER 4 - CONCLUSIONS

SUMMARY AND AREAS FOR FUTURE RESEARCH	86
REFERENCES	88

LIST OF TABLES

Table 1.	Examples of alternative male mating strategies in various species (adapted from Gross 1996).....	9
Table 2.	Linear measurements taken for analysis of morphological variation of mature bull trout (<i>Salvelinus confluentus</i>) in the Chowade River.....	16
Table 3.	Description of criteria used to assess aggressive behaviour of dominant male bull trout (<i>Salvelinus confluentus</i>) towards other mature male bull trout in the Chowade River.....	21
Table 4.	Mean \pm SE (n) fork length, estimated total length, and mass for mature male and female bull trout (<i>Salvelinus confluentus</i>) in the Chowade River in 1995 and 1996, plus a summary of comparisons between years (*=statistical significance, $P \leq 0.05$).....	29
Table 5.	Mean \pm SE (n) fork length, estimated total length, and mass for mature male and female bull trout (<i>Salvelinus confluentus</i>) in the Chowade River for pooled 1995 and 1996 data, plus a summary of comparisons between the sexes (*=statistical significance, $P \leq 0.05$).....	29
Table 6.	Component coefficients for principal component analysis on all measured morphological traits of mature bull trout (<i>Salvelinus confluentus</i>) in the Chowade River.....	35
Table 7.	Component coefficients for principal component analysis on all measured morphological traits except eye diameter, kype depth and adipose fin base length of mature bull trout (<i>Salvelinus confluentus</i>) in the Chowade River.....	37
Table 8.	Percentage of each morphological characters variance accounted for by PC 1 in the principal component analysis on all traits for mature bull trout (<i>Salvelinus confluentus</i>) in the Chowade River.....	39
Table 9.	The relationship between fork length (FL) and kype depth (KD) for three classes of mature bull trout (<i>Salvelinus confluentus</i>) in the Chowade River (*=statistical significance, α levels adjusted using sequential Bonferroni corrections).....	42
Table 10.	Analysis of covariance results from comparisons of kype growth among mature male and female bull trout (<i>Salvelinus confluentus</i>) in the Chowade River (F-test, *=statistical significance, α levels adjusted using sequential Bonferroni corrections).....	42

Table 11.	Comparisons of colour variation in the belly, throat, fins, and back region among three classes of mature bull trout (<i>Salvelinus confluentus</i>) (all individuals). Data are mean (\pm SE) intensity of the grey wavelength of light tested with non-parametric one way analysis of variance on ranks (Kruskal-Wallis one way ANOVA, a posteriori pairwise comparisons made using a Newman-Keuls test, *=statistical significance, α levels adjusted using sequential Bonferroni corrections).....	44
Table 12.	Comparisons of colour variation in the belly, throat, fins, and back region among three classes of mature bull trout (<i>Salvelinus confluentus</i>) (outliers removed). Data are mean (\pm SE) intensity of the grey wavelength of light tested with non-parametric one way analysis of variance on ranks (Kruskal-Wallis one way ANOVA, a posteriori pairwise comparisons made using a Newman-Keuls test, *=statistical significance, α levels adjusted using sequential Bonferroni corrections).....	45
Table 13.	Comparisons of colour variation in the belly, throat, fins, and back region for the combined intensity of the red, green, and blue wavelengths of light among three classes of mature bull trout (<i>Salvelinus confluentus</i>), (*=statistical significance, α levels adjusted using sequential Bonferroni corrections) using multivariate analysis of variance (MANOVA). Pairwise comparisons were made using a F-test.....	46
Table 14.	Mean estimated back calculated lengths at age from scales for bull trout (<i>Salvelinus confluentus</i>) males classified as dominant and sneakers in the Chowade River (*=statistical significance between types).....	49
Table 15.	Mean (\pm SE) estimated total length of three classes of mature male bull trout (<i>Salvelinus confluentus</i>) at redd sites in the Chowade River for pooled 1995 and 1996 data, and a summary of comparisons between the mean estimated total length of individuals in these groups (t-test, *=statistical significance, α levels adjusted using sequential Bonferroni corrections).....	53
Table 16.	Cover types associated bull trout (<i>Salvelinus confluentus</i>) spawning redds in the Chowade River.....	70
Table 17.	Summary of microhabitat measurements at bull trout (<i>Salvelinus confluentus</i>) redd sites in the Chowade River in 1994.....	76
Table 18.	Summary of microhabitat measurements at bull trout (<i>Salvelinus confluentus</i>) redd sites in the Chowade River in 1995.....	76
Table 19.	Summary of mean (\pm SE) microhabitat characteristics at bull trout (<i>Salvelinus confluentus</i>) selected sites and non-selected sites used for the egg to alevin survival studies (*=statistical significance between sites, $P \leq 0.05$).....	77

Table 20.	Summary of mean alevin length at bull trout (<i>Salvelinus confluentus</i>) selected sites and non-selected sites (*=statistical significance between sites, $P \leq 0.05$).....	79
Table 21.	Summary of mean alevin survival at bull trout (<i>Salvelinus confluentus</i>) selected sites and non-selected sites (*=statistical significance between sites, $P \leq 0.05$).....	79
Table 22.	Summary of mean incubation temperature at bull trout (<i>Salvelinus confluentus</i>) selected sites and non-selected sites (*=statistical significance between sites, $P \leq 0.05$).....	79

LIST OF FIGURES

Figure 1.	The geographical distribution of bull trout (<i>Salvelinus confluentus</i>) and Dolly Varden (<i>S. malma</i>) in British Columbia, showing possible areas of overlap.....	2
Figure 2.	The Chowade River study area in northeastern British Columbia.....	6
Figure 3.	Photographs of male (top) and female (bottom) bull trout (<i>Salvelinus confluentus</i>) during non-spawning period indicating minimal secondary sexual characteristic differences (photos by Gordon Haas).....	11
Figure 4.	Photographs of male (top) and female (bottom) bull trout (<i>Salvelinus confluentus</i>) during spawning period showing secondary sexual characteristic differences...	12
Figure 5.	Photograph of a bull trout (<i>Salvelinus confluentus</i>) scale at 30 times magnification. Annulus is indicated by (a), spawning check is indicated by (b).....	19
Figure 6.	Photographs of the male model (top) and the female model (bottom) used to examine dominant male aggression.....	22
Figure 7.	Fork length frequency histogram of mature male (a) and female (b) bull trout (<i>Salvelinus confluentus</i>) from the Chowade River (pooled 1995 and 1996 samples).....	30
Figure 8.	Estimated total length frequency histogram of mature male (a) and female (b) bull trout (<i>Salvelinus confluentus</i>) from the Chowade River (pooled 1995 and 1996 samples).....	31
Figure 9.	Mass frequency histogram of mature male (a) and female (b) bull trout (<i>Salvelinus confluentus</i>) from the Chowade River (pooled 1995 and 1996 samples).....	32
Figure 10.	Scatter plots of the principal component analysis done on the complete character set (a) for principal component one vs. principal component two, and (b) for principal component one vs. principal component three (F = mature females, S = mature sneaker males, D = mature dominant males. Large letters are group centroids).....	33
Figure 11.	Scatter plots of the principal component analysis excluding eye diameter, kype depth, and adipose fin base length (a) for principal component one vs. principal component two, and (b) for principal component one vs. principal component three (F = mature females, S = mature sneaker males, D = mature dominant males. Large letters are group centroids).....	36

- Figure 12. Scatter plots of the principal component analysis done of eye diameter, kype depth and adipose fin base length (a) for principal component one vs. principal component two, and (b) for principal component one vs. principal component three (F = mature females, S = mature sneaker males, D = mature dominant males. Large letters are group centroids)..... 40
- Figure 13. Growth of the kype relative to fork length for three classes of mature bull trout (*Salvelinus confluentus*) in the Chowade River (D = Dominant male, S = Sneaker male, F = Female)..... 41
- Figure 14. The linear relationship of age (based on fin ray sections) and fork length of mature male bull trout (*Salvelinus confluentus*) age 2 to 4, and age 5 to 13 in the Chowade River..... 47
- Figure 15. The association between estimated total length of mature males and estimated total length of mature females for paired bull trout (*Salvelinus confluentus*) at redd sites in the Chowade River in 1995 and 1996 ($r_s=0.37$, $n=64$, $P=0.0018$)..... 50
- Figure 16. Relationship of the probability from logistic regression analysis of a mature male bull trout (*Salvelinus confluentus*) being paired with a reproductive female in the Chowade River based on its estimated total length from visual observations..... 52
- Figure 17. Barplots of the mean number of aggressive acts per ten minutes (\pm SE) exhibited by a dominant male bull trout (*Salvelinus confluentus*) at a redd site towards satellite and sneaker males..... 54
- Figure 18. Barplots of the mean number of aggressive acts per ten minutes (\pm SE) exhibited by a dominant male bull trout (*Salvelinus confluentus*) at a redd site towards male and female models..... 56
- Figure 19. Photographs showing bull trout (*Salvelinus confluentus*) redds from the air... 69
- Figure 20. Cumulative temperature unit profile at egg incubation sites (solid line is profile of bull trout selected sites, dashed line is profile of adjacent non-selected sites)..... 80

ACKNOWLEDGEMENTS

I am humbled to finally complete this work through the direct support of friends and family whose encouragement has enabled me to carry this thesis to a conclusion. Jason Ladell, Kerry Harvey, Jeff Burrows, Joe DeLaronde, Peter Mylchreest, Ian Kusabs, Peter Troffe, Brad and Dianne Culling, and Margo Treble all helped with aspects of field and lab work. Mike Chamberlain worked directly in the field with me for the past three summers, put up with all my bossing him around, and maintained the decency to not punch my lights out a couple of times. Gordon Haas helped with field work during 1996, and was also giving of his time with regards to data analysis, editing initial drafts, and discussion. Ernest Keeley also helped me greatly with data analysis, editing and discussion, and was always able to suggest another test I could carry out when I reached what I thought was the end. Dave O'Brien collected auxiliary data for me, provided help with scale ageing, edited various reports related to this work, and as usual was always good for some pertinent discussion. Ted Euchner of the Ministry of Environment, Lands and Parks (Fort St. John) was immensely important in enabling me to carry out my work through the indirect financial support of contracts that allowed me to get into the Chowade field site. He also provided help in the field, edited versions of this thesis, and showed the general Ted Euchner enthusiasm for all my studies. He has become a good friend. My immediate family supported me emotionally through some trying times during the past three years.

I am also appreciative for the advice I received from my committee members. In particular, my supervisor Dr. J.D. McPhail allowed me to pursue my own interests and provided direct financial support. Dr. Ted Down of the Ministry of Environment, Lands and Parks (Victoria) convinced me to work in the Chowade system. Dr. Carl Walters chided me for studying the genus "Slimelinus", but also didn't direct me away from carrying out my own work. Dr. Rick Taylor always provided his interesting insights, and has been immensely helpful in collaborations on other work.

Financial support for aspects of my work came from an NSERC operating grant to my supervisor (J.D. McPhail), and from the B.C. Ministry of Environment, Lands and Parks (Fisheries Research Section, U.B.C.) for which I am thankful. Field equipment was loaned to me by the B.C. Ministry of Environment, Lands and Parks (Fort St. John).

Finally to the most important person of all I offer my deepest love and affection. Robyn you have put up with all my bad moods and emotional baggage over the last three years. That is more than anyone could ask, and this work is dedicated to you.

CHAPTER 1 - INTRODUCTION

GENERAL INTRODUCTION

The bull trout (*Salvelinus confluentus*) is an endemic western North American char species (Cavender 1978; Haas and McPhail 1991; McPhail and Baxter 1996) that occurs throughout British Columbia, usually east of the Coast Mountains (Figure 1). Bull trout are morphologically similar to Dolly Varden (*S. malma*) and, for some time, the species were considered conspecific. Bull trout, however, possess some morphological distinctions (Cavender 1978; Haas and McPhail 1991), as well as showing genetic differences to Dolly Varden (Grewe et al. 1990; Phillips and Pleyte 1991). In some areas where the two species occur sympatrically, they differ in their ecologies and life-histories, and are good biological species (McPhail and Taylor 1995; Baxter et al. 1997). These recent data provide the strongest evidence for the species-level distinctiveness of bull trout and Dolly Varden.

Despite the fact that they are economically important in recreational sport fisheries in British Columbia (Cannings 1996; Jones and Michiel 1996; McPhail and Baxter 1996), and ecologically important as an indicator of watershed health (see Rieman and McIntyre 1993), very little is known about the biology of the bull trout. Generally, the species does not occur in high densities, a tendency that is partly due to the extreme environments in which they live (cold, unproductive waters), and partly related to the biology of the fish (Rieman and McIntyre 1995).

Currently, bull trout are in decline throughout their range, and the species is listed as one of concern by the American Fisheries Society (Williams et al. 1987). The species is also currently the only fish listed as identified wildlife under the Forest Practices Code, and has been blue listed (as sensitive and vulnerable) by the British Columbia Ministry of Environment, Lands and Parks Conservation Data Centre (Cannings 1996). In the U.S. Pacific Northwest, bull trout were recently petitioned for status as an endangered species, however, the request was deferred (U.S. Federal Register June 10, 1994 vol. 59 (111): 30254-30255) because the information on population trends in Canada and Alaska was insufficient to warrant listing throughout the species entire range. Impacts of human activities, however, probably have had negative effects on bull

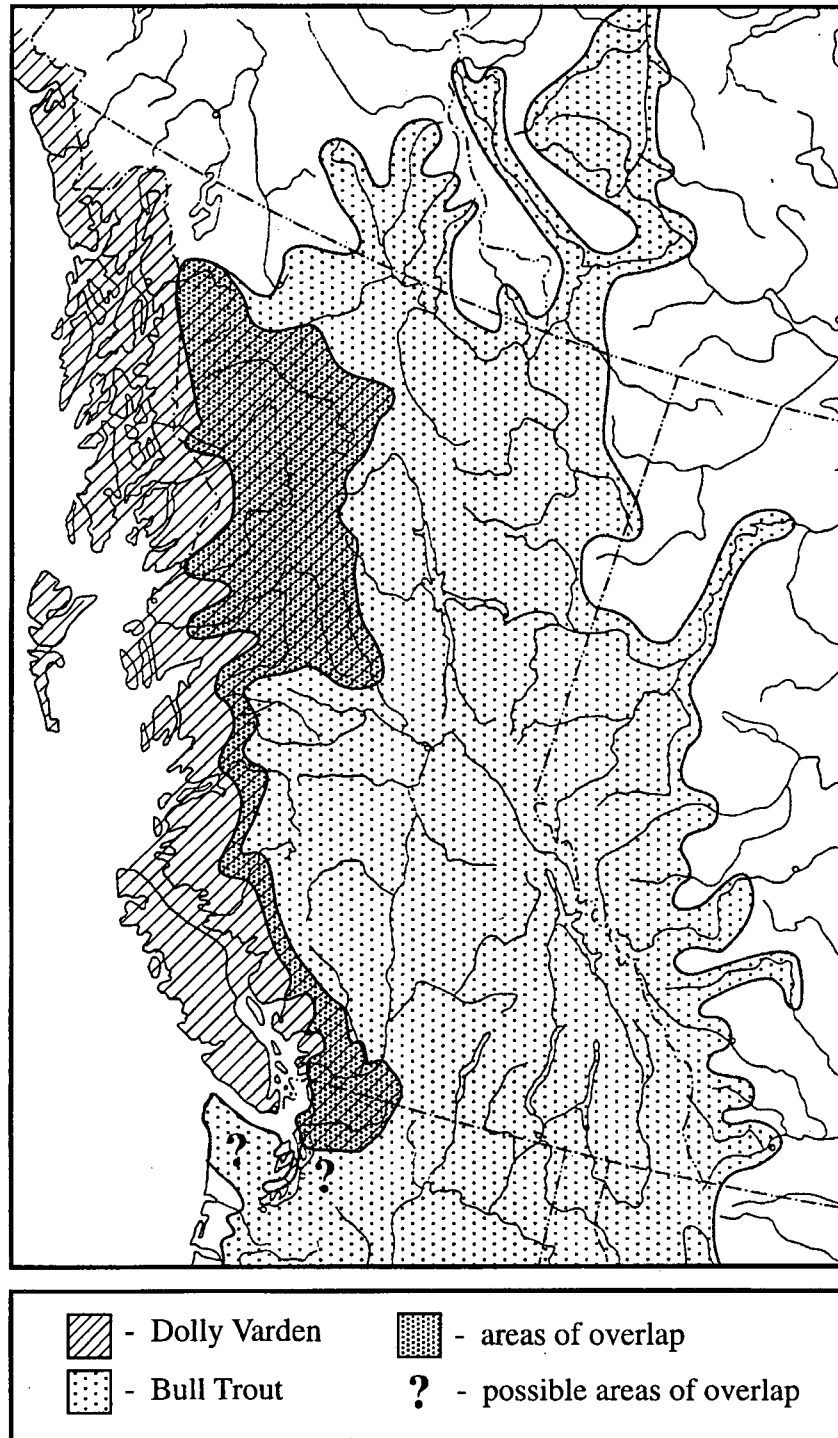


Figure 1. The geographical distribution of bull trout (*Salvelinus confluentus*) and Dolly Varden (*S. malma*) in British Columbia, showing possible areas of overlap.

trout populations (see Ratliff and Howell 1992), and proper management of the species is hindered by the current lack of biological and ecological information. In British Columbia, the reproductive biology of bull trout has also been affected by human activities that have depleted spawners through overharvest (Hagen 1993a, 1993b; Hagen and Baxter 1992; Al Stobbart, Department of Fisheries and Oceans, New Westminster, British Columbia, pers. comm.), and destroyed spawning habitat through direct physical impacts (McPhail and Baxter 1996). Many areas throughout B.C. where bull trout now occur in pristine watersheds (e.g., tributaries to the Peace, Liard, and Columbia river systems) are slated for resource development, and this may adversely affect currently healthy bull trout populations. Given the increase in resource extraction activity, there is a critical need for ecological information on the population dynamics, reproductive biology, and habitat use of bull trout. Such information is essential for the development of rational management and enhancement programs.

Understanding salmonid reproductive and mating systems also is important in the general fields of ecology and ethology. These animals provide excellent material for investigating how mating tactics of individuals within a population differ, and how these different tactics affect population dynamics and reproductive success (Gross 1984, 1985, 1991). The general habitat requirements and, especially male reproductive strategies of spawning bull trout, are poorly understood. It has been suggested that male bull trout of different sizes may have alternative reproductive strategies (Baxter 1994a; Kitano et al. 1994; Sexauer 1994; James and Sexauer 1997), and that spawning habitat use by the species may be highly specific (e.g., Fraley and Shepard 1989; Goetz 1989; Pratt 1992; Rieman and McIntyre 1993, 1995; Baxter 1995). By fully understanding how trade offs might be made with regards to spawning success through deciding where or when to spawn, population dynamics of the species are more completely understood.

Presently, over the species entire range, the bull trout bearing watersheds of northern British Columbia are the least impacted by human activities. Thus, they offer the opportunity to study bull trout in a relatively pristine environment. One such system is the Chowade River. This river is one of the premier bull trout systems in northern British Columbia in terms of the size and number of spawners that utilize the river (Baxter 1994a, 1994b, 1995; R.L. & L. Environmental

Services Ltd. 1994; Ted Euchner, Ministry of Environment, Lands and Parks, Fort St. John, British Columbia, pers. comm.), and I was fortunate enough to have the opportunity to study this relatively undisturbed population.

The main objective of this thesis was to investigate whether or not alternative male mating strategies exist in the Chowade River population. If such strategies exist, what those strategies are, and how males adopting different strategies interact with each other, were important components of my first objective. A second objective of this thesis was to examine microhabitat relationships of spawning bull trout in the Chowade River, and to determine what affect spawning site selection has on egg to alevin survival. How this might influence reproductive success was the main component of this objective. To set the stage for these studies, this first chapter includes a short summary of the relevant life history information on the spawning bull trout population in the system, and a description of the study area. Chapter two addresses questions regarding reproductive strategies of bull trout males, while chapter three discusses bull trout spawning site selection. The final chapter provides general conclusions and suggestions for further study.

SUMMARY OF LIFE HISTORY INFORMATION ON THE SPAWNING COMPONENT OF THE CHOWADE RIVER BULL TROUT POPULATION

The Peace River is a large tributary to the Mackenzie River system, and in British Columbia is blocked by the Peace Canyon Dam at the town of Hudsons Hope. This dam prevents the upstream movement of fish. Of the remaining tributaries to the Peace River in British Columbia below the Peace Canyon Dam, the Halfway River, and its main tributaries (Graham River, Cypress Creek, Chowade River), drain the east slope of the Rocky Mountain Foothills. The mature bull trout that use the Chowade River for reproduction are fluvial migrants. Adults make migrations between large rivers where they overwinter and grow to maturity (Peace and Halfway rivers) into smaller order streams (Chowade River) where they spawn and feed, and where the juveniles rear. Some individuals that return to the Chowade system migrate from up to 300 km (i.e., from Alberta) down the mainstem Halfway and Peace rivers (unpublished data from tag returns and preliminary radiotracking). After the spring freshet, as water levels recede in July, spawners begin their upstream migration into the Chowade River. Most of the fish that will spawn in the fall reach the upper river spawning areas by mid to late August (Baxter 1994a, 1995,

1997a). Males enter the system first, and immediately concentrate in deeper, slower areas where there is an abundance of cover (e.g., log jams, large pools) (Baxter 1995).

Data, collected over the past three years, on the total number of mature males and females using the Chowade River indicate that the sex ratio is approximately 1:1 (R.L. & L. Environmental Services Ltd. 1994; Baxter 1995). Spawning begins as early as the fourth week of August, and is completed by the end of September with peak spawning activity occurring during the second week of September (Baxter 1995). Females select spawning sites and dig a series of nests (redd) where male and female gametes are deposited. Despite the apparent abundance of suitable spawning habitat throughout the system, spawning is primarily concentrated in a short (~500 meter) section of stream. Redd superimposition is common. Males pair with females, and aggressively defend the territory surrounding a redd site from other males (Baxter 1995). Spawning activity occurs throughout the day, and is usually concentrated in areas with an abundance of small cobble substrate. After reproduction, emigration from spawning areas is rapid. Once a female is spent she will leave the system quickly, whereas males remain close to spawning areas throughout the entire spawning period (R.L. & L. Environmental Services Ltd. 1994). Some large males spawn with more than one female over the course of the breeding season (personal observations).

Bull trout are iteroparous (i.e., they do not necessarily die after spawning). In 1995, I found that approximately 25 % of the population were repeat spawners from the previous year (Baxter 1995). With the onset of winter, and subsequent freezing in the Peace region, bull trout move into deep water areas in the Halfway River and the Peace River. Here they overwinter, and presumably feed, in areas where prey species, such as mountain whitefish (*Prosopium williamsoni*) accumulate.

STUDY SITE

The Chowade River is located in the northeastern corner of the province (Figure 2), approximately 200 km northwest of Ft. St. John (56°41'N, 122°32'W). It is a major tributary to the

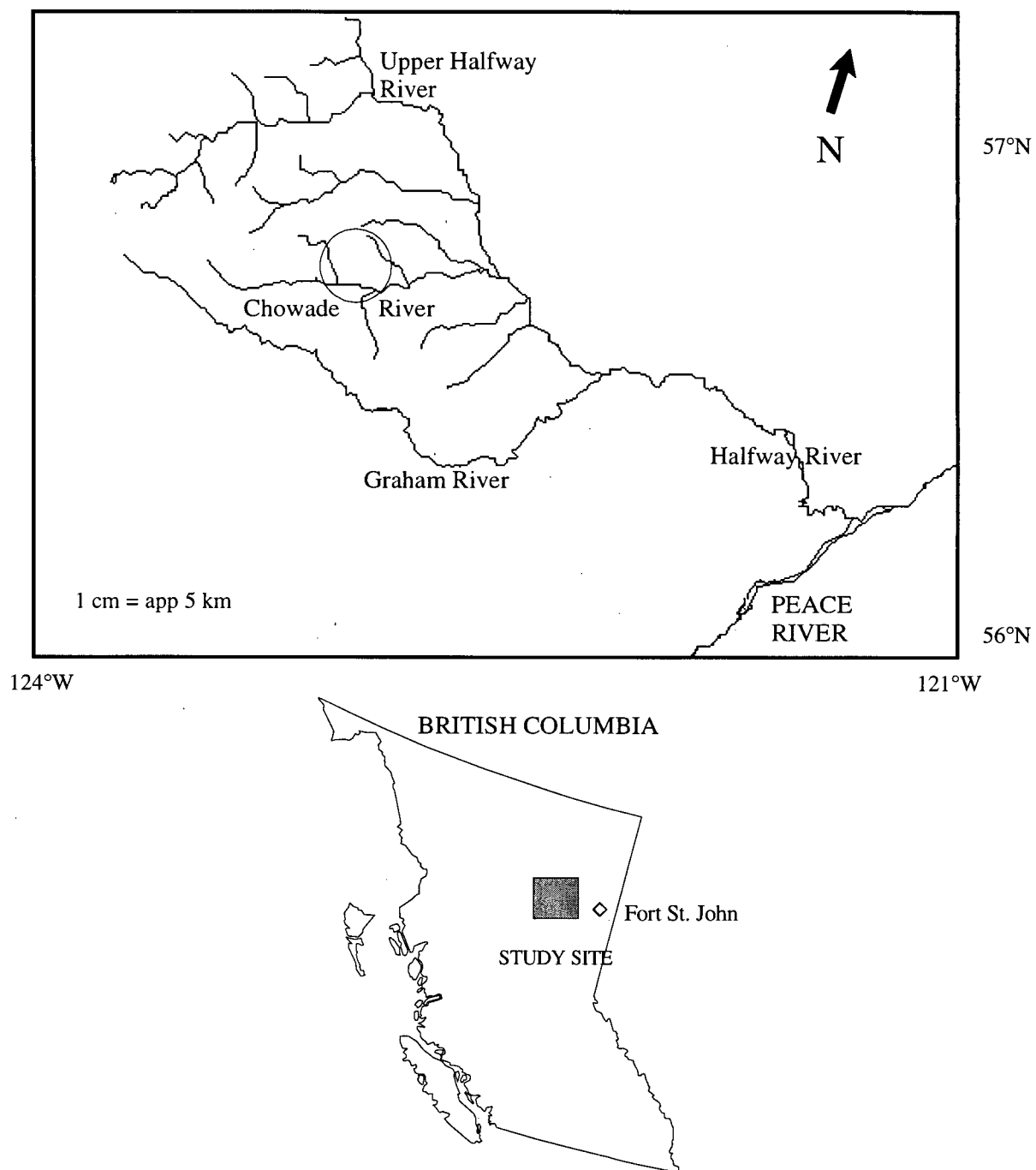


Figure 2. The Chowade River study area in northeastern British Columbia.

Halfway River, which is part of the Peace River drainage, and is located in the Engelmann Spruce-Subalpine Fir Biogeoclimatic zone (Meidinger and Pojar 1991). Based on the classification system of Strahler (1952, 1964), at the study sites, the Chowade River is a second order stream. The river's headwaters originate from snowmelt and underground upwelling in the Rocky Mountain Foothills at an elevation of approximately 1400 m. It has five major tributaries, of which three are known to contain juvenile bull trout (Baxter 1994b). From its source, the river flows in a easterly direction for 70 km until its confluence with the Halfway River. It is a low to medium gradient system that has no impassable barriers to fish.

Other fish species that occupy the river include rainbow trout (*Oncorhynchus mykiss*), Arctic grayling (*Thymallus arcticus*), mountain whitefish, slimy sculpin (*Cottus cognatus*), longnose dace (*Rhinichthys cataractae*), and longnose suckers (*Catostomus catostomus*). Although adult rainbow trout, Arctic grayling and mountain whitefish are found in the upper river, apparently only bull trout spawn in this area. This conclusion is based on the absence of juvenile fish in the upper river except bull trout and slimy sculpins (Baxter 1994a, 1994b, 1995).

All of my work was conducted in the upper section of the Chowade River (56°40'N, 122°57'W to 56°42'N, 123°15'W), where spawning was concentrated and water visibility allowed excellent viewing opportunities. The characteristics of this section of the system were low gradient, an abundance of side channels, a high percentage of gravel and cobble for spawning, and adequate cover for pre-spawning adults. The only habitat impacts in this area are small amounts of tree cutting for seismic line work carried out by the petroleum industry. Access to the system is by helicopter, or motorized All Terrain Vehicle using a trail along the river. My study sites were located approximately 54 km upstream of the confluence of the Chowade River with the Halfway River.

CHAPTER 2 - EVIDENCE OF ALTERNATIVE MALE REPRODUCTIVE STRATEGIES

INTRODUCTION

In reference to the reproductive strategies of fishes, Wootton (1984) suggested that the theory of evolution through natural selection involves some form of conflict. Consequently, the use of the term *strategies* with respect to reproduction implies that living organisms are involved in some form of conflict, and to reproduce, individuals must adopt tactics that allow them to compete successfully with conspecifics for mates or mating sites. A reproductive strategy is therefore the overall pattern of reproduction typically shown by individuals in a species (Wootton 1984; Turner 1993), and, in the case of populations, it makes intuitive sense that individuals (e.g., males) within that population should have one reproductive strategy that would maximize an individual's reproductive success (Gross 1984). Many species (see Table 1 and Gross 1996), however, have alternative male mating strategies, probably because males are the individuals that are primarily in conflict over access to reproductive females.

Energetically, reproduction is a costly component of an individual's life history, and it has associated costs that are imposed by physiological, ecological, and genetic constraints (Hutchings 1994). Reproduction also involves direct competition for resources, usually for mates, but also for mating sites. Obviously, male reproductive success requires access to females (Davies 1991) and, thus, it is males that fight for mates. In most species where fighting for access to females occurs, it is through direct aggressive competition; however, in situations where an individual is not large enough to successfully compete, he may adopt an alternative mating strategy or tactic. In these cases sexual selection may act on males to cause a divergence in reproductive strategies (Turner 1993).

The act of reproduction is a particularly sensitive life history stage for bull trout populations which generally consist of small numbers of long-lived individuals that inhabit relatively unstable and unproductive stream environments. In such populations, success depends on mature fish adopting favorable reproductive strategies. Generally, bull trout spawning is similar to that of other salmonids (Leggett 1969, 1980; Sexauer 1994). Intrasexual competition

Table 1. Examples of alternative male mating strategies in various species (adapted from Gross 1996).

Species	Alternative male strategies	Reference
<i>Oncorhynchus kisutch</i> (coho salmon)	-Dominant (fight) -Sneaker	Gross 1985
<i>Salmo salar</i> (Atlantic salmon)	-Dominant (fight) -Sneaker	Jones 1959
<i>Uta stansburiana</i> (side-blotched lizard)	-Dominant (fight) -Sneaker (female mimic)	Sinervo and Lively 1996
<i>Ficedula hypoleuca</i> (pied flycatcher)	-Territorial -Non territorial (female mimics)	Slagsvold and Saetre 1991
<i>Salvelinus malma miyabei</i> (miyabe char)	-Dominant (fight) -Sneaker	Maekawa and Onozato 1986
<i>Onthophagus binodis</i> (dung beetle)	-Dominant -Sneak	Cook 1990
<i>Leistotrophus versicolour</i> (rove beetle)	-Dominant -Female mimics	Forsyth and Alcock 1990
<i>Lepomis macrochirus</i> (bluegill sunfish)	-Dominant (nest builders) -Cukolder (sneakers, female mimics)	Gross 1991
<i>Cervus elaphus</i> (red deer)	-Dominant -Sneaker	Clutton-Brock et al. 1982

among males is focused before males and females pair. Once paired, the female excavates a redd in the stream substrate into which gametes are released. After spawning, the female covers the eggs with gravel, and the fertilized eggs remain in the gravel where they incubate over the winter.

Like most salmonids, bull trout are sexually dimorphic in morphology and colouration during their reproductive phase. They differ from most teleosts in that males are usually larger than females (McPhail and Murray 1979; Carl et al. 1989; Kitano et al. 1994; Baxter 1995). This suggests that size is important in male-male encounters. Aside from size, another sexually dimorphic character is kype development (the large hooked lower jaw). Again, it is a trait that is thought to be advantageous in male-male aggressive encounters. Females show only a minimal kype development, apparently reflecting the non-aggressive nature of female-female interactions (James and Sexauer 1997). Perhaps, the most obvious difference between the sexes at spawning time is colour, especially colour on the head, belly, and ventral fins. Outside of the spawning season it is virtually impossible to sex these fish on external characteristics (David O'Brien, Department of Zoology, University of British Columbia, Vancouver, British Columbia, pers. comm.), and there are no obvious colour differences between the sexes (Figure 3). At the onset of spawning, however, males develop a greenish back, the lower jaw and opercula become black, the lower sides of the belly develop an orange to red colour, and the ventral fins develop a tricolour pattern with white leading edges and black backs (Figure 4). Females also undergo colour changes at spawning time, but these changes are less pronounced, and the female is almost entirely bronze-green with a slight contrast to the ventral fins. The belly colour in females remains white (Figure 4).

Discussions of alternative reproductive strategies in male salmonids (see Gross 1985), emphasize anadromous Pacific salmon, especially the coho (*Oncorhynchus kisutch*) and the sockeye (*O. nerka*). These fish are semelparous, and die after spawning. Two "types" of males are commonly found in these species: dominant males and sneaker/jack males. Dominant males usually are the largest males at a spawning site, and are elaborately coloured with large kypes. Once paired with a female at a redd site they are highly aggressive to other males. Among these large males there may also be "satellite" males. Satellite males are also large males and have the

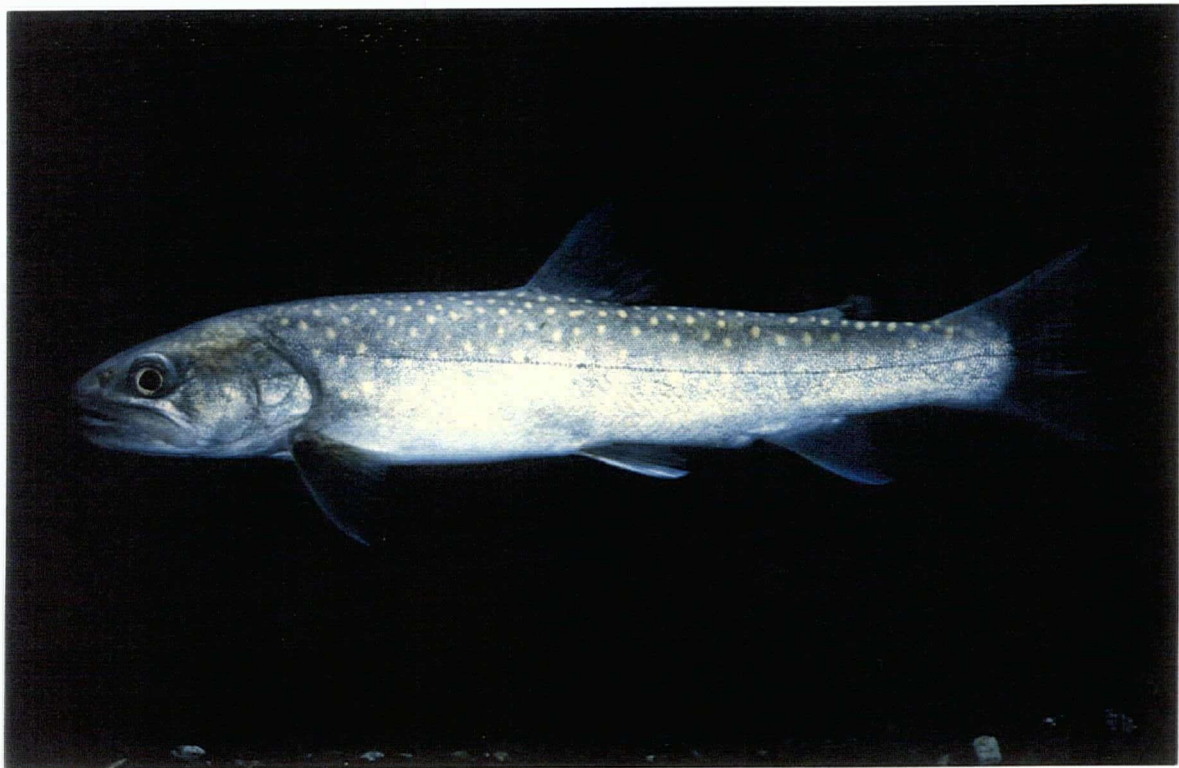


Figure 3. Photographs of male (top) and female (bottom) bull trout (*Salvelinus confluentus*) during non-spawning period indicating no secondary sexual characteristic differences (photos by Gordon Haas).



Figure 4. Photographs of male (top) and female (bottom) bull trout (*Salvelinus confluentus*) during spawning period showing secondary sexual characteristic differences.

secondary sexual characteristics of dominant males. In some situations they can be dominant males, but usually they lose fights with other males and, so, take up positions downstream from the redd site. In contrast to dominant males, sneakers are smaller and usually younger males that are too small to win aggressive encounters with dominants and satellites. They adopt a "lie and wait" strategy to gain fertilizations (Gross 1985; Hutchings and Myers 1988), by sneaking in under a spawning pair, and releasing gametes. Sometimes these smaller males are typically less coloured than bigger males, and have a minimal development of secondary sexual characteristics.

Like other salmonids, bull trout spawning behaviour is complex, and detailed observations in the wild suggest the possibility of alternative male reproductive strategies in this species (Kitano et al. 1994; Sexauer 1994; James and Sexauer 1997). If the largest males win most of the fight, and if females prefer to mate with larger males, then small males must adopt some strategy other than direct competition in order to gain fertilizations.

Based on suggestions of alternative male reproductive strategies in bull trout in other systems, and previous observations of a 1:1 sex ratio among bull trout in the Chowade River (Baxter 1995), I decided to investigate male reproduction in the Chowade River population. With a 1:1 sex ratio, I hypothesized that every male should have the opportunity to reproduce with a female, and, thus, only one "type" of reproductive male may exist in this system. The specific objectives of this component of my thesis were to test the hypothesis that within the bull trout population of the Chowade River there were alternative male types that differed in colouration and morphology.

If two types of males were found, I wanted to examine what advantages variation in male secondary sexual colouration might give to small sneaker males. To test the hypothesis of whether reduced secondary sexual colouration benefited small males in some way, I conducted behavioural observations of aggression of the dominant male at a redd site towards males of different size and colour, and towards fish models of the same size but different colour. The specific prediction was that males with reduced coloration would experience less aggression towards them from the dominant male than their brightly coloured conspecifics, and thus would be able to move into close proximity to redd sites. Most studies on alternative male reproductive

behaviour focus on the relative fitness of alternative types, and not on interactions among types. I wanted to determine if small sneaking males minimize their secondary sexual characteristics, and have an advantage that allows them to increase their proximity to the female for potential mating. I hypothesized that this reduced colouration, or possible mimicking of females, causes the dominant males to ignore sneaker males as a sexual competitor, and therefore results in a reduction in the amount of aggression sneaker males would receive from dominant males.

MATERIALS AND METHODS

I. DATA COLLECTION

This investigation was done in the upper Chowade River during the months of August and September in 1994, 1995, and 1996. These months coincide with the spawning period of bull trout in this system. Data for this work were collected primarily through two techniques; angling, and visual observation from the stream bank.

A. Angling

Size Data

Individual bull trout were sampled by angling with artificial spoons and baited hooks. All bull trout captured were measured for fork length (mm), mass (g), and sex. I used sexual dimorphism in colouration and morphology to determine sex. Whenever possible, I also used slight pressure on the belly to look for the release of gametes.

Morphology and Colouration Data

In 1996, morphology and colour variation data were gathered from individuals that I collected by angling. Individual fish were anesthetized in a 20 L pail, containing 1 ml of clove oil diluted with 10 L of water to a concentration of 100 PPM (Soto and Burhanuddin 1995; Anderson et al. 1997). Fish reached stage V of anesthesia (loss of equilibrium, operculum movement slow and irregular, no response to external stimuli) after a period of 3 to 4 minutes, and then were placed on a water soaked small mesh net. Fourteen linear measurements were taken with a tape measure to the nearest 1 mm (Table 2). Colour on four body areas (belly, throat, back, ventral fins) was also assessed using two methods. The first was subjective, and involved the classification of colour (e.g., black, red, white, grey) in the areas by the observer. In the second method a standardized colour slide of each fish was taken. These standardized conditions were:

- 1) Kodachrome 64 slide film exposed at 80 a.s.a., shot with an Olympus OM-2 camera equipped with a light polarizer to reduce glare.

Table 2. Linear measurements taken for analysis of morphological variation of mature bull trout (*Salvelinus confluentus*) in the Chowade River.

Measurement	Definition
Fork Length	Length from tip of snout to fork in caudal fin
Post Orbital Hypural Length	Length from posterior margin of eye orbit to hypural plate
Body Depth	Depth of the body from dorsal to ventral at dorsal fin base origin
Head Length	Length from tip of snout to posterior end of operculum
Head Depth	Depth of the head from dorsal to ventral at posterior end of operculum
Post Orbital Head Length	Length from posterior margin of eye orbit to posterior end of operculum
Eye Diameter	Length of eye ball from anterior to posterior
Snout Length	Length from tip of snout to anterior margin of eye orbit
Upper Jaw Length	Length from tip of snout to posterior end of maxillary
Lower Jaw Length	Length from tip of lower jaw to posterior end of maxillary
Kype Depth	Length of the kype from top to base of kype on lower jaw
Pectoral Fin Length	Length from origin of pectoral fin to tip of first pectoral fin ray
Adipose Fin Base Length	Length of adipose fin from origin to insertion
Adipose Fin Height	Greatest height of adipose fin from dorsal to ventral

- 2) Exposure of film at 1/60th of a second under natural light conditions, against a standardized green background.

Colour variation among individuals was then analyzed using a Macintosh 9500 Power PC, and Adobe Photoshop. Slides were converted to computer image files by scanning the 35 mm slides using a Kodak SC 2500 slide scanner. All slides were scanned at a resolution of 1600 d.p.i., and a contrast increase of plus five. Once slides were converted to image files that the program could use, each file was accessed, and colour measured in the four areas on the body. Difference in colour between individuals was assessed by using standardized landmarks within each body area of individual fish, and calculating the mean intensity (a range from 1 to 255) of the grey, red, green, and blue wavelengths reflected from each body area. Background colour was not assessed as a control for different light conditions, as I had to use natural light levels to take pictures in the field.

Ageing Data

Fin rays

The first three rays and bases of the left pelvic fin were removed from each individual sampled in 1994, 1995, and 1996. These were collected by myself and other biological consultants working in the Chowade River. The ageing of these structures was done by North South Biological Consultants (Winnipeg, Manitoba). Fin rays were mounted in epoxy, microtomed, and aged to the year. The purpose was to assess the ages of mature males, and the possible association of age with size.

Scales

To assess the age of individuals and identify spawning frequency, scales were collected from the males sampled in 1996. Scales were removed from the fish's side directly behind the dorsal fin, and five rows up from the lateral line (MacLellan 1987). These were placed between two glass slides and labelled. In the laboratory the scales were cleaned by soaking them for 24 hours in distilled water. The cleaned scales were then placed between two glass slides and viewed

in a microfiche reader at 30 times magnification. A picture was taken of each projected image using a 100 mm macro lens at an exposure of $1/15^{\text{th}}$ of a second and 400 a.s.a. film.

The pictures of each scale were used to identify annuli (periods of reduced growth), and spawning checks that result from scale re-absorption during reproduction. For each scale, annuli were marked where there was a definite reduction in scale growth (i.e., where circuli became closely packed) (Figure 5). Scale checking was defined as where there was definite re-absorption of the scale through circuli (Figure 5). For each scale, the total age of the fish, and age at different spawnings, were estimated.

B. Visual Observations

Behavioural Observations

Visual observation from the stream bank was a useful technique for collecting data on the bull trout population in the Chowade River. Total length of individual fish (to the nearest 50 mm) was estimated visually. When estimated and actual lengths were compared they were all within ± 50 mm ($n=10$).

Data collected by visual observations at specific redd sites were the total length of all bull trout at the redd site (site where a female was digging), sex of all bull trout at the redd site, the number of satellite and sneaker males at the redd site, and the aggressive behaviour of the dominant male at the redd site towards satellite and sneaker males. Non-dominant males at a redd site were classified as either satellites or sneakers. The two categories were separated on the basis of the size of the male, colouration of the male, proximity of the male to the redd site, and general behaviour of the fish. Satellite males had secondary sexual characteristics similar to dominant males, but were repeatedly chased from the redd site by the dominant male when they actively tried to court the female. All satellite males were larger than 500 mm and were brightly coloured. In contrast, sneakers were small (averaging around 300 mm, but ranging from 300 to 500 mm) and displayed no male sexual colouration. Sneakers were attacked infrequently by the dominant male, even though they were in close proximity to the redd site. These fish would not try to actively court the female.

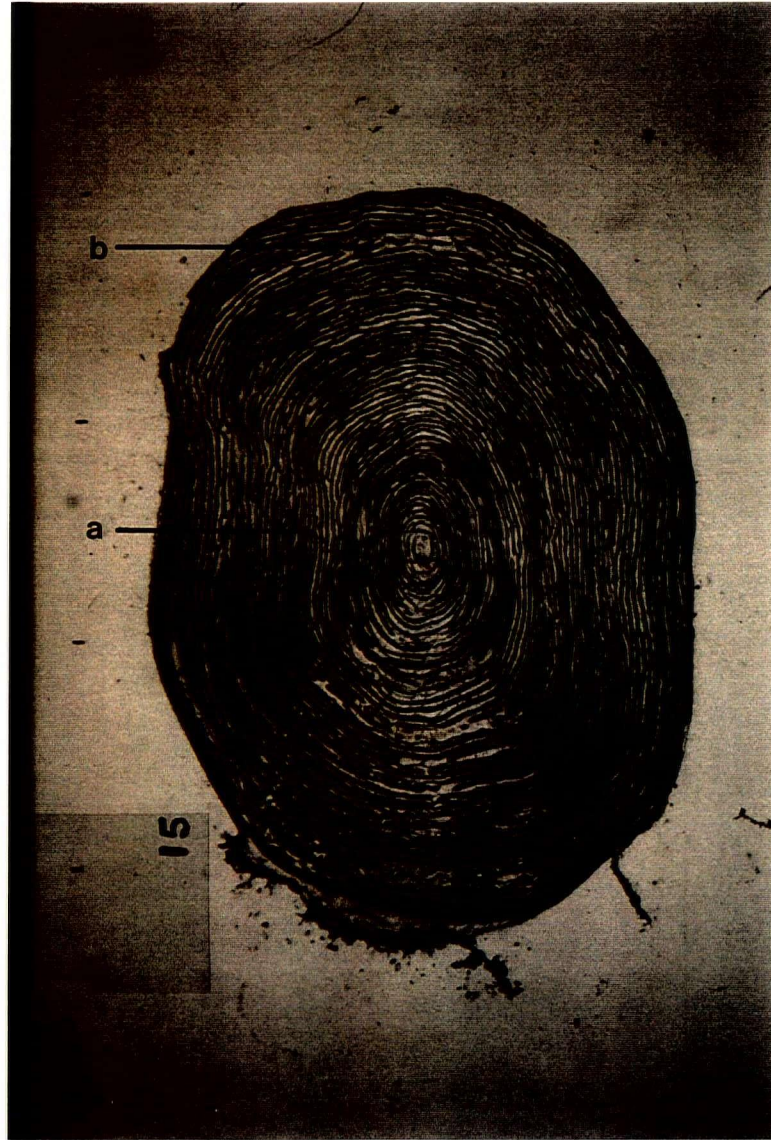


Figure 5. Photograph of a bull trout (*Salvelinus confluentus*) scale at 30 times magnification. Annulus is indicated by (a), spawning check is indicated by (b).

The aggressive behaviour of the dominant male bull trout at a redd site towards other males in proximity to that redd site was measured at a number of redd sites. Each trial consisted of an observer standing quietly in a position close to a redd site, estimating the total length and sex of all individuals at the redd site, and recording behaviour of the dominant male towards other males. The observation period was ten minutes, and the behaviours recorded are listed in Table 3.

Experimental Tests on Dominant Male Aggression

To determine the role male sexual colouration, independent of size, played in eliciting aggressive behaviour by the dominant male towards other males, experimental trials with models were undertaken. Dominant males are heavily coloured, primarily with red in the belly region, black on the lower opercula and throat, and black on the ventral fins. The affect of these colours on male aggression was measured by observing the response of the dominant male towards different coloured models. These two dimensional models were 280 mm in fork length (typical of the size of sneaking males), and made out of plywood. The different models were exact replicates, except for differences in the colouration of the belly area, the ventral fins, and the throat region. Models were either male coloured (i.e., with red belly, black ventral fins, and black throat), or female coloured (i.e., with a bronze belly, and no black colouration on the fins or the throat) (Figure 6).

Each trial consisted of the observer disturbing a redd site on which a female and dominant male were paired, and placing one of each of the models (on stands) facing upstream into the current at the head and tail of each redd site. The models were placed one meter to the left of the redd site (looking upstream). The aggressive responses of the dominant male (listed in Table 3) towards the different coloured models were then recorded during a 10 minute trial. Recording was by either direct visual observation in 1995, and by videotaping the trial and later transcribing data in 1996. To determine if model position influenced aggressive behaviour by the dominant male, in separate trials the different coloured models were alternated at either the head or tail of the redd.

Table 3. Description of criteria used to assess aggressive behaviour of dominant male bull trout (*Salvelinus confluentus*) towards other mature male bull trout in the Chowade River.

Aggressive Behaviour	Description
Flanking	Dominant male approaches other male with body tense, mouth open, and fins extended
Backing Down	Dominant male backs down on other male with fins extended, forcing the other male away from the redd site
Bite	Dominant male bites other male
Charge	Dominant male rushes at another stationary male
Chase	Dominant male rushes at a another male moving within a close proximity of the redd site

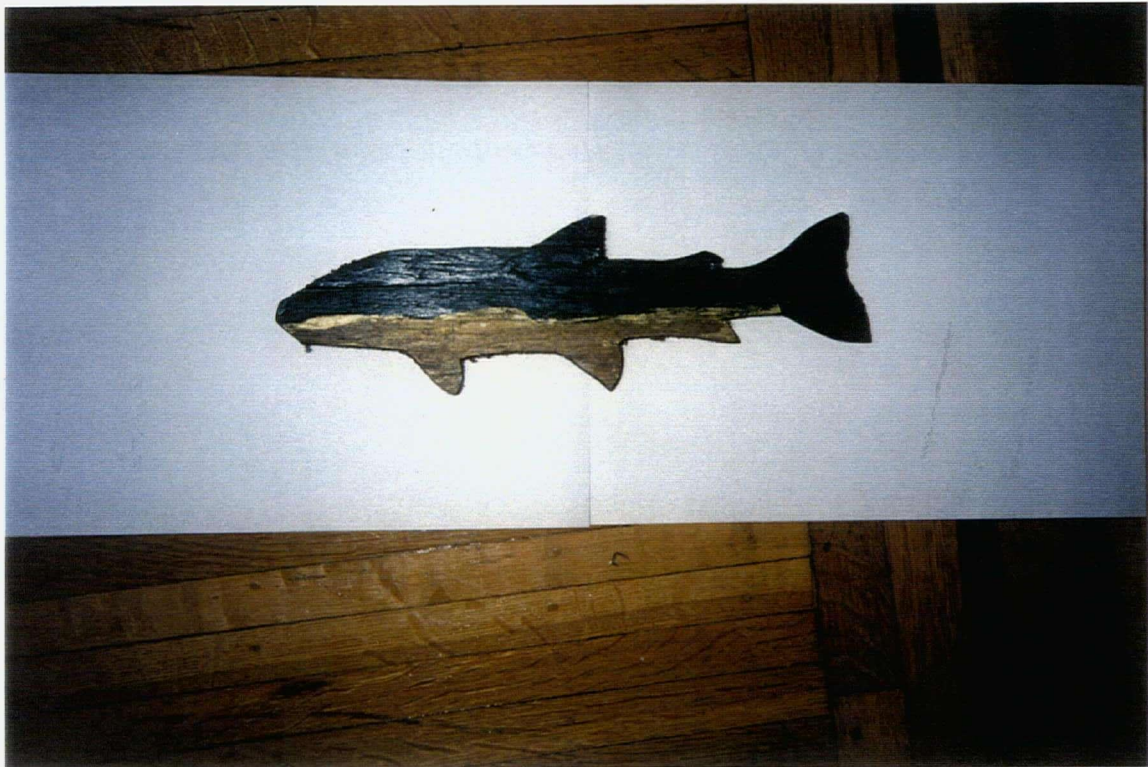
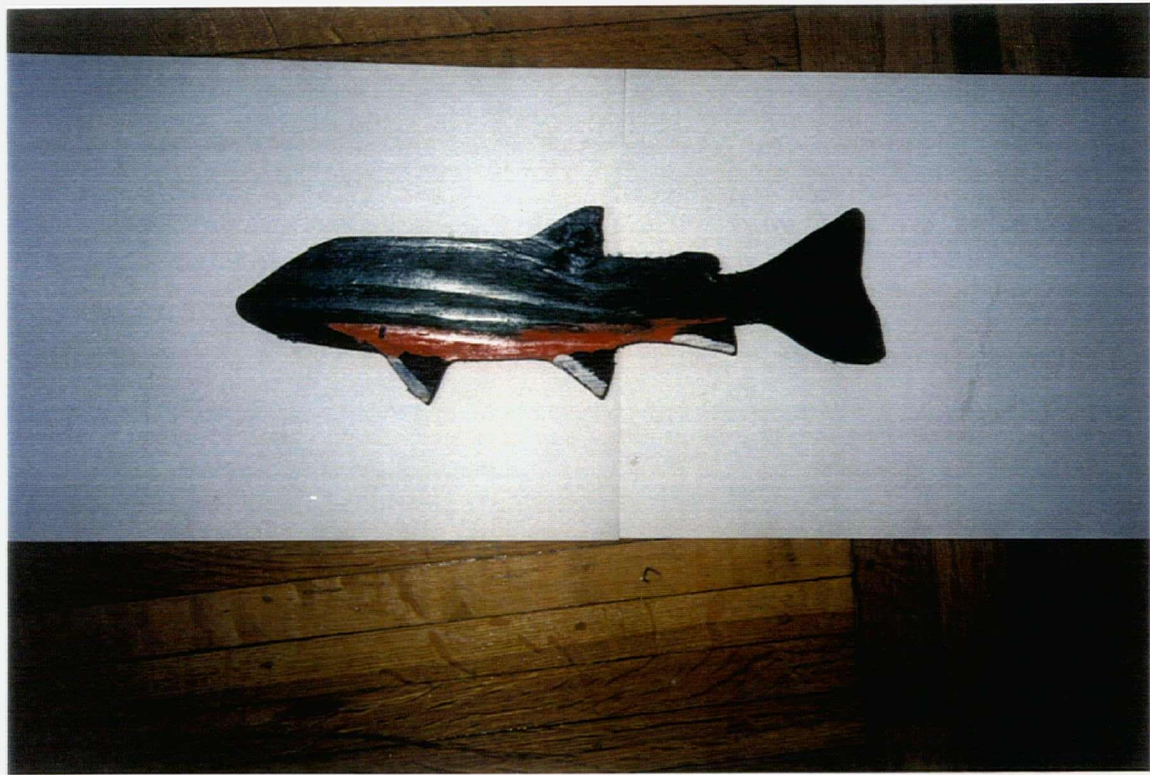


Figure 6. Photographs of the male model (top) and the female model (bottom) used to examine dominant male aggression.

II. DATA ANALYSIS

A. Angling

Size Data

Fork length, mass, and estimated total length data were compared between years (1995 and 1996) using a two sample t-test with statistical significance assessed at $\alpha=0.05$. If there were no between year differences, the data were pooled. Frequency histograms of fork length, mass, and estimated total fork length for males and females were constructed, and comparisons between the sexes made using a two sample t-test with statistical significance assessed at $\alpha=0.05$.

Morphology and Colouration Data

Principal Component Analysis

Principal component analysis (PCA) is a procedure used to examine large multivariate data sets, and which analyzes all morphological traits to produce new independent size and shape variables for each of the characters. The major benefit is pattern recognition (Pimental 1979; Haas 1988). Principal component analysis reduces multiple measurements of traits of an individual into a single score which aids in data analysis, resulting in a new data matrix that explains the maximum possible variation along each new matrix axis while remaining uncorrelated to each other (Pimental 1979; Haas 1988). The new axis for each character variable is called an eigenvector, with each eigenvector consisting of a number of values corresponding to the number of characters measured and included in the analysis. Each value in an eigenvector is termed a loading, and refers to the significance a variable has in that eigenvector. A high character loading suggests that the specific character contributed significantly to most of the observed variation in that eigenvector.

In PCA, the first eigenvector is usually a size vector, and accounts for most of the observed variance. Most loadings in the first eigenvector for each character variable have the same sign (polarity, and approximate value), and indicate the relation of changes among character variables with respect to size differences. As the first eigenvector usually accounts for most of the observed variation, the second eigenvector accounts for most of the remaining variation, and is

the shape vector. The second eigenvector usually points out pattern differences in the shape of individuals irrespective of size (Pimental 1979).

Because of allometric growth relationships among body parts (Pimental 1979), and the fact that measures of body size tend to be log-normally distributed (Harvey 1982), I used \log_{10} transformed variables for the PCA which was conducted on the covariance matrices. Significant eigenvectors and principal components were identified using the graphical Scree test (Cattell 1966; Somers 1986; Haas 1988), and Kaisers criteria (S-Plus 1995). The Scree test visually plots the eigenvalues against their indices, with the break in the downward slope indicating the important principal components. Kaisers criteria involves calculating the mean of all eigenvalues and excluding those components with eigenvalues less than the mean.

One way analysis of variance (ANOVA) was used to determine if there were differences in mean PC scores among the different groups examined. Statistical analysis was assessed at $\alpha=0.05$. If a significant difference was found using the ANOVA, multiple pairwise comparisons were carried out using a Bonferroni t-test to determine the differences between the groups. Significance levels for these comparisons were adjusted using the sequential Bonferroni technique (Holm 1979; Rice 1989) to account for inflating α levels from multiple tests due to group comparisons.

Kype Depth/Fork Length Relationship

The growth of the kype relative to body growth was compared among groups by \log_{10} transforming kype depth and fork length for mature males and females, and regressing the transformed fork length vs. transformed kype depth. Comparisons of the slope of this relationship for females, dominant and satellite males (males greater than 500 mm), and sneaker males (males less than 500 mm) were made using an analysis of covariance. Because group comparisons were carried out, significance levels were adjusted using the sequential Bonferroni technique (Holm 1979; Rice 1989).

Colour Data

Two data sets resulted from the colour analysis. The first set was a relative measure of the darkness (grey scale) of each body area sampled, and simply quantified how white or black an area was. Differences among mature females, dominant and satellite males (greater than 500 mm), and sneaker males (less than 500 mm) in the designated body areas were compared with a non-parametric Kruskal-Wallis one way ANOVA. This was necessary since the data are not normally distributed, and variances are unequal among the three groups. A posteriori pairwise comparisons between the groups were made using Newman-Keuls comparisons where significance was found using the Kruskal-Wallis ANOVA. Two analyses were made, one included all data, while a second excluded obvious outliers (points well outside the 95% confidence limits). Again, since multiple comparisons were carried out, significance levels for these comparisons were adjusted using the sequential Bonferroni technique (Holm 1979; Rice 1989).

The second, and more relevant, analysis was on the ratios of the intensity of the red, green, and blue wavelengths reflected from each body area. Colour is determined as the ratio of these three primary colours. In most vertebrates the visible spectrum of light ranges from wavelength values of 400 nm (blue) to 700 nm (red) (Endler 1990). What appears as white is the maximum value of the red, green and blue spectral ranges (Adobe photoshop levels of intensity of 255 of each), and what appears as black is the minimum value of red, green, and blue spectral ranges (Adobe photoshop levels of intensity of 0 of each). Differences among mature females, dominant males and sneaker males were analyzed using a multivariate ANOVA for the three colour variables measured for each individual in each body area. A posteriori pairwise comparisons were made using an F-test to contrast the groups. Again, because multiple comparisons were carried out, significance levels were adjusted using the sequential Bonferroni technique (Holm 1979; Rice 1989).

Ageing Data

Fin rays

An initial plot of age based on fin rays vs. \log_{10} fork length suggested a striking increase in growth between ages four and five. Based on this observation, separate linear relationships for age vs. fork length were calculated for male bull trout between ages 2 and 4, and from ages 5 and over. Differences in the mean age of the two size classes (less than 500 mm, greater than 500 mm) of mature male bull trout were compared using a two sample t-test on data collected in 1994 and 1995.

Scales

For each fish, length at age was back calculated using the Fraser-Lee method (Devries and Frie 1996), by measuring the length of the fish at capture, the radius of the scale at capture, and the radius of the scale to the outer edge of each annulus. For individuals identified as either dominant or sneaker males, the mean back calculated length at each age, the mean total age, the mean fork length, the mean total number of spawnings, the mean back calculated length at first spawning, and the mean age at first spawning were compared between the two groups with a t-test.

B. Visual Observations

Behavioural Observations

Data on the estimated size of paired females and males during spawning were \log_{10} transformed, and a Spearman's rank correlation was conducted to determine if size assortative mating occurs. Spearman's rank correlation was used as error variances of estimated size were not normally distributed. Differences between estimated total lengths of paired males and females during spawning were compared using a two sample t-test.

Logistic regression was used to predict the probability of a mature male being paired with a female based on a males estimated total length. Differences in the mean estimated total length

of males adopting different mating strategies, and positions at redd sites, were compared using a two sample t-test.

Relationships between the number of satellite males and sneaker males per redd, and the size of the dominant male and female at the redd site were examined through Spearman's rank correlation analysis. Spearman's rank correlation was used as error variances of estimated sized were not normally distributed.

To detect for any influence of male density on the aggressive behaviour of the dominant male at a redd site, the relationship of the number of attacks directed at subdominant males (satellites and sneakers) and male density was examined. Differences between the mean number of attacks on satellite and sneaker males were tested with a two sample t-test.

Experimental Tests on Dominant Male Aggression

During the experimental tests, the two model types were manipulated in terms of their placement along side the redd site. To test for any affects of placement on the aggressive behaviour by the dominant male, two sample t-tests were carried out on the mean number of attacks on the different models at the different positions. Differences in the mean number of aggressive behaviours of the dominant male at a redd site observed towards male coloured and female coloured models were compared using a two sample t-test.

RESULTS

A. Angling

Size Data

There were no differences between years in mean male fork length, mass, and estimated total length (Table 4) so the data from both years was pooled. Similarly, there were no differences in mean female fork length and estimated total length between years; however, there were differences between years in mean female mass (Table 4). This difference in mass between years may be due to either the smaller sample size in 1996, or to the fact that males were the focal sex in 1996. In any event, the data were combined between years to get an overall distribution of female mass.

There were no significant differences between fork length or estimated total length when mature male and female bull trout were compared over the two year study period, but there were significant differences in mass between males and females: males were significantly ($P=0.0071$) heavier than females (Table 5). Fork length, estimated total length and mass frequency histograms for mature male and female bull trout suggested that all variables are bimodally distributed in males (Figures 7a, 8a, 9a), and unimodally distributed in females (Figures 7b, 8b, 9b), particularly for mass (Figure 9).

Morphology and Colouration Data

Principal Component Analysis

Three principal component analyses (PCA) are relevant to this study: 1) the complete data set of all morphometric variables; 2) all the variables but with eye diameter, kype depth, and adipose fin base length removed and; 3) an analysis of only eye diameter, kype depth, and adipose fin base length. The PCA on the complete data set of measured variables revealed that the first three eigenvectors and principal components (PCs) 1, 2, and 3 were significant (Scree test, Kaisers Criteria), with PC 1 accounting for 83.4 % of the variation, PC 2 accounting for 12.0% of the variation, and PC 3 accounting for 2.3 % of the variation (Figure 10). Plots of PC 1 vs. PC 2

Table 4. Mean \pm SE (n) fork length, estimated total length, and mass for mature male and female bull trout (*Salvelinus confluentus*) in the Chowade River in 1995 and 1996, plus a summary of comparisons between years (*=statistical significance, $P \leq 0.05$).

Sex	Body Size	Year		t	df	P
		1995	1996			
Male	Fork length (mm)	636.02 \pm 139.14 (44)	620.93 \pm 174.46 (29)	0.41	71	0.68
	Estimated TL (mm)	626 \pm 159 (146)	637 \pm 141 (95)	-0.54	239	0.59
	Mass (g)	3440.54 \pm 1777.13 (37)	2928.52 \pm 2040.90 (27)	1.07	62	0.29
Female	Fork length (mm)	621.02 \pm 74.42 (44)	589.92 \pm 84.05 (25)	1.59	67	0.12
	Estimated TL (mm)	642 \pm 65 (91)	645 \pm 79 (49)	-0.20	138	0.84
	Mass (g)	2745.41 \pm 869.53 (35)	2087.50 \pm 896.52 (24)	2.82	57	0.01*

Table 5. Mean \pm SE (n) fork length, estimated total length, and mass for mature male and female bull trout (*Salvelinus confluentus*) in the Chowade River for pooled 1995 and 1996 data, plus a summary of comparisons between the sexes (*=statistical significance, $P \leq 0.05$).

Variable	Sex		t	df	P
	Male	Female			
Fork Length (mm)	630.03 \pm 17.92 (73)	609.75 \pm 9.50 (69)	0.98	140	0.33
Estimated TL (mm)	630 \pm 10 (241)	643 \pm 6 (140)	-0.95	379	0.34
Mass (g)	3224.53 \pm 236.80 (64)	2477.97 \pm 121.31 (59)	2.74	121	0.01*

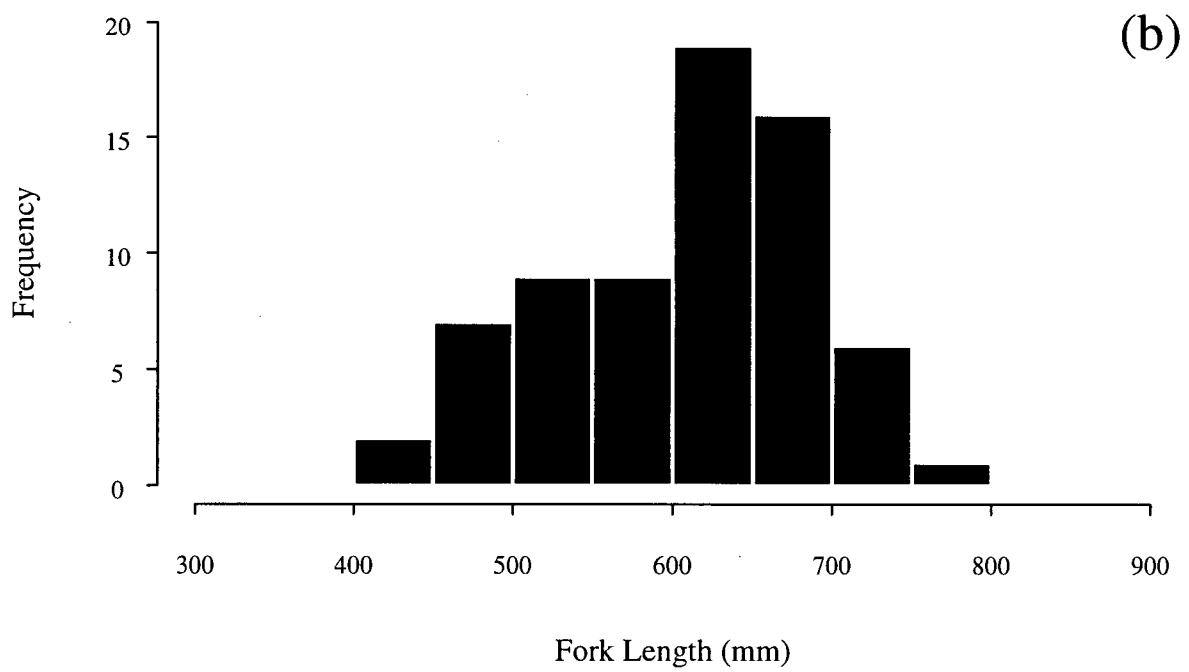
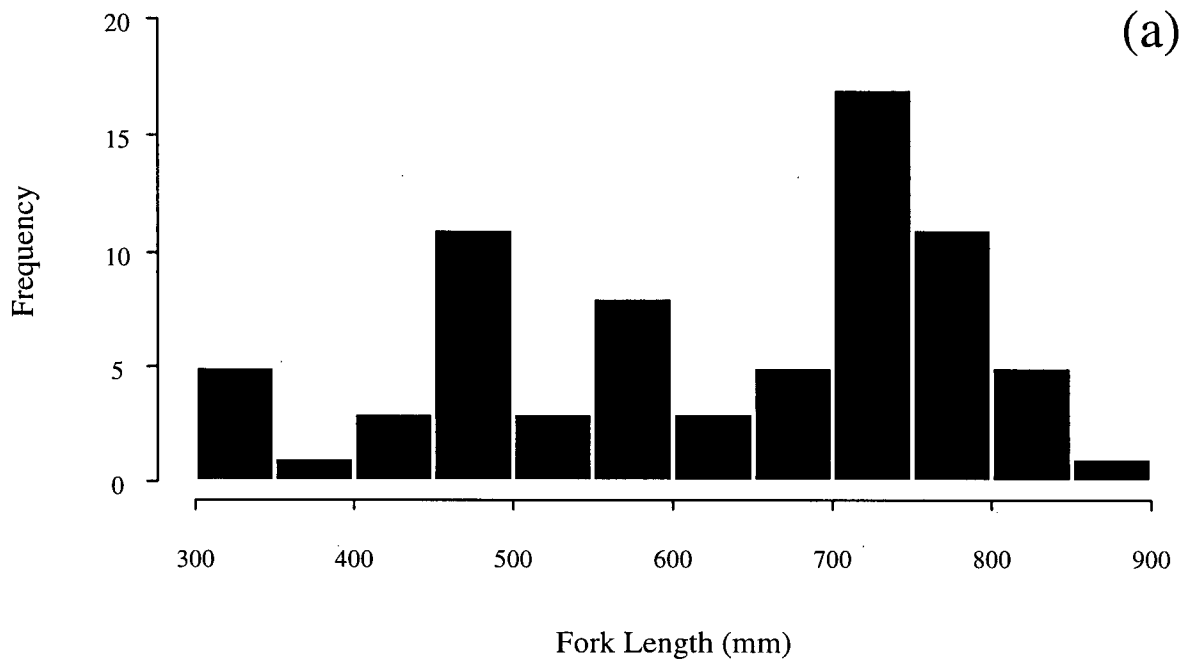


Figure 7. Fork length frequency histogram of mature male (a) and female (b) bull trout (*Salvelinus confluentus*) from the Chowade River (pooled 1995 and 1996 samples).

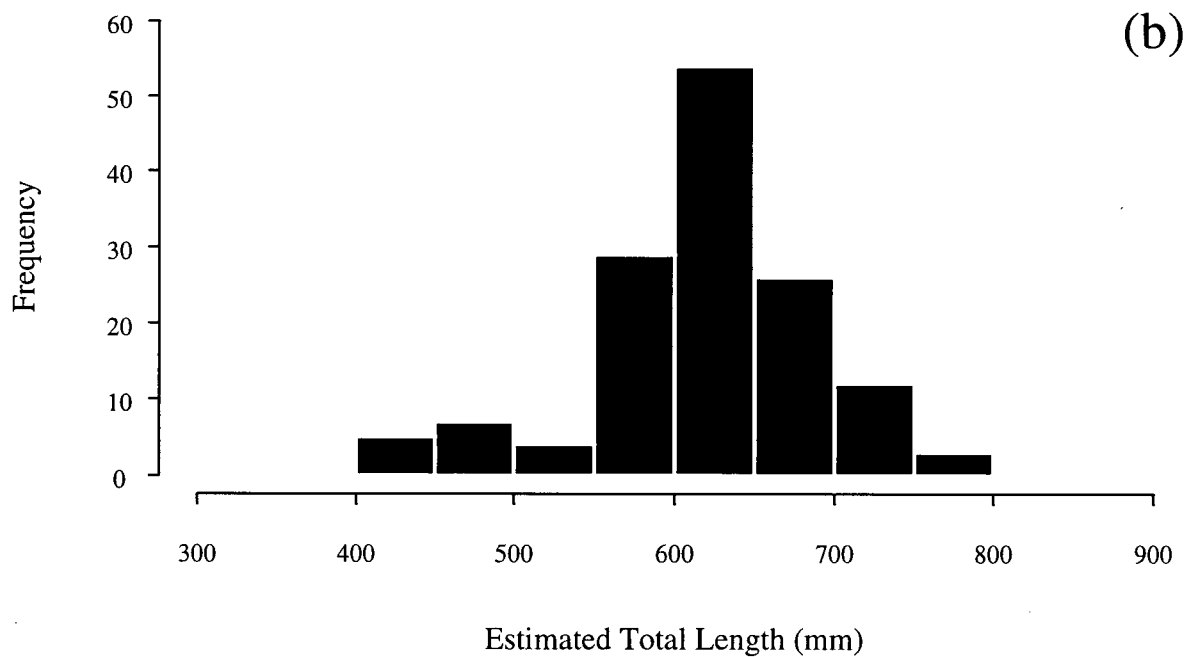
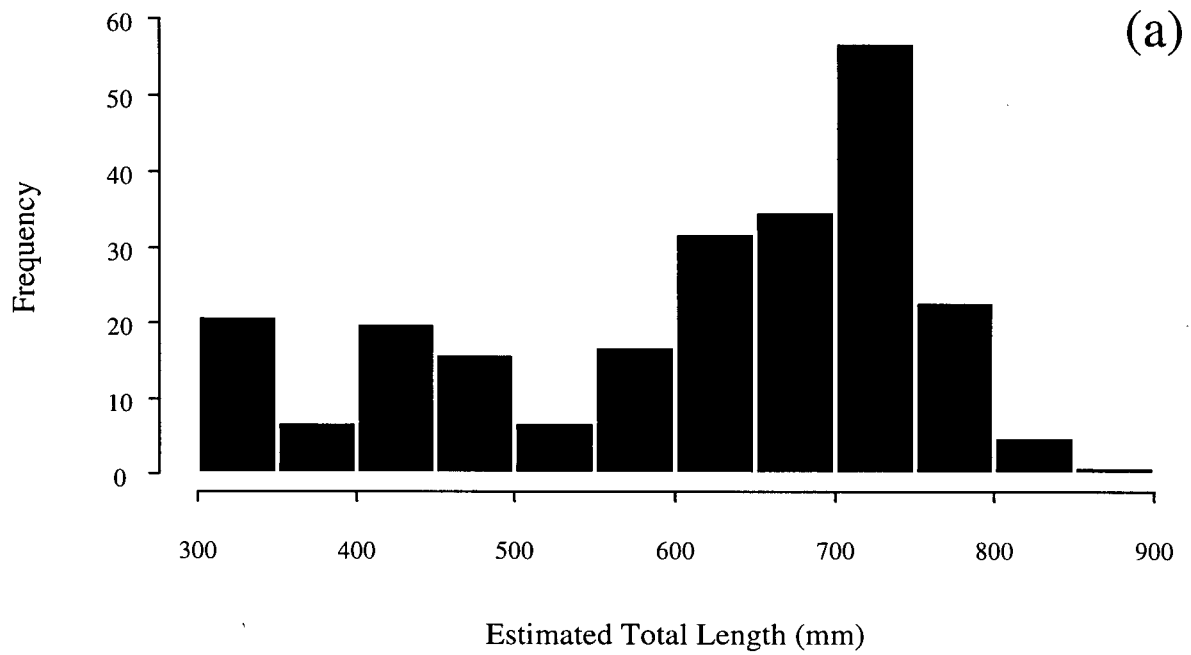


Figure 8. Estimated total length frequency histogram of mature male (a) and female (b) bull trout (*Salvelinus confluentus*) from the Chowade River (pooled 1995 and 1996 samples).

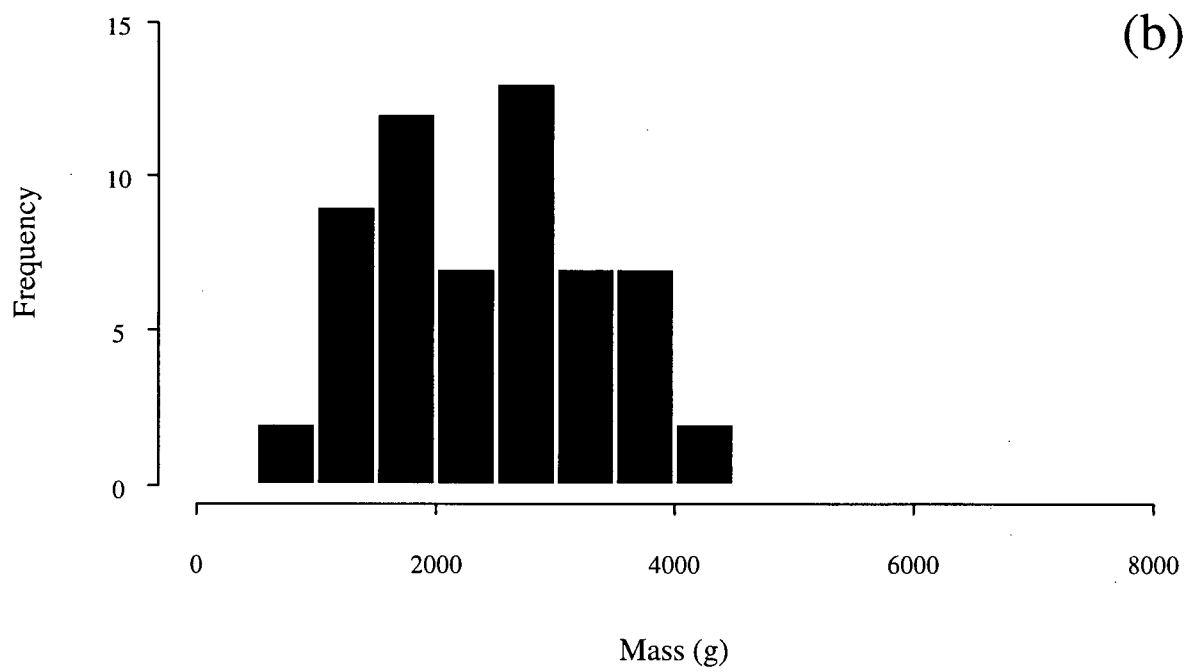
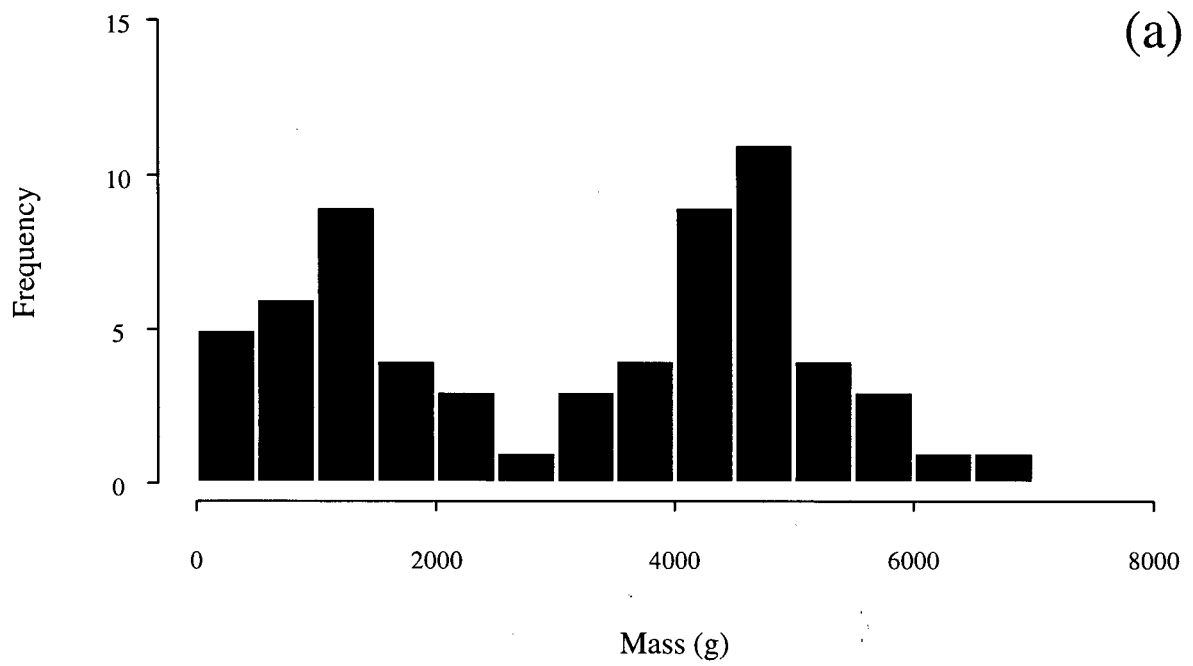


Figure 9. Mass frequency histogram of mature male (a) and female (b) bull trout (*Salvelinus confluentus*) from the Chowade River (pooled 1995 and 1996 samples).

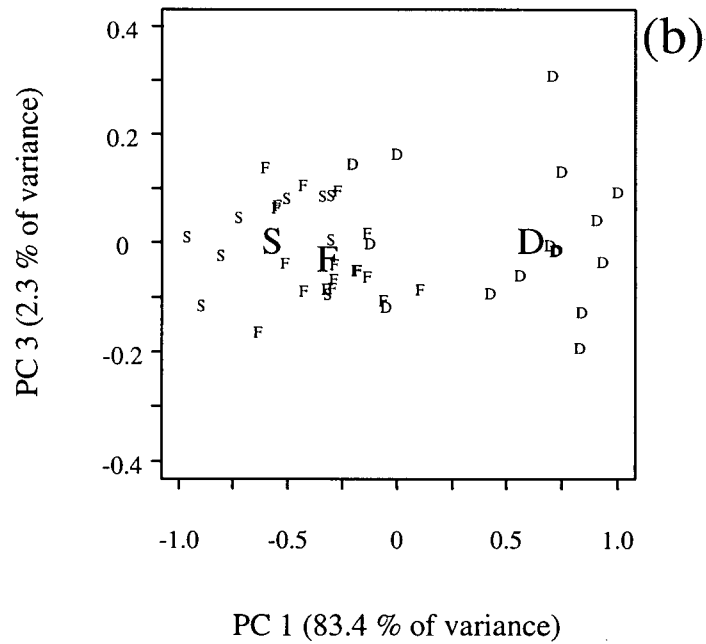
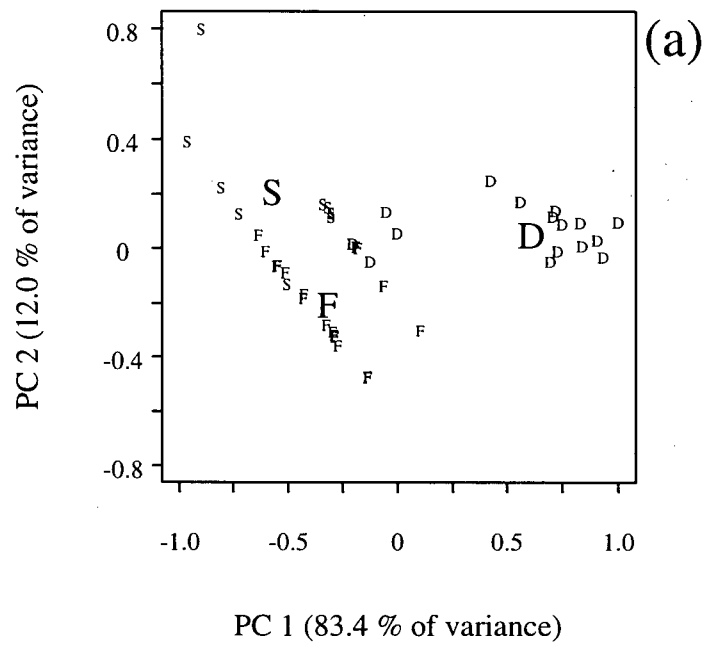


Figure 10. Scatter plots of the principal component analysis done on the complete character set (a) for principal component one vs. principal component two, and (b) for principal component one vs. principal component three (F = mature females, S = mature sneaker males, D = mature dominant males. Large letters are group centroids).

(Figure 10a) and PC 1 vs. PC 3 (Figure 10b) reveal two clear groups: a group containing females and sneakers, and a group containing dominant males. When the centroids (large letters) for females, sneakers, and dominant males are plotted, however, there is evidence of three groups (Figures 10a and 10b): one for dominant males, one for females, and one for sneaker males. Interestingly, although females and small males grouped more closely together for PC 1 separation on the PC 1 axis was not completely due to size since females were much larger on average than sneaker males. Still, they grouped out with small males rather than with larger males. This was despite the fact that dominant males and females sampled for this analysis were within the same size range. In this analysis PC 1 was affected by both size and shape due to the low total variance accounted for, and the fact that kype depth had a significant character loading (Table 6). In terms of mean PC 1 scores, females were also significantly different from dominant males (ANOVA, $P < 0.05$), but not different from sneaker males (ANOVA, $P > 0.05$). Analysis of variance on mean PC 2 scores identified that dominant males and sneaker males were not significantly different ($P > 0.05$), but females were significantly different from sneaker males and dominant males ($P < 0.05$). The groups were not significantly different in their mean PC 3 score (ANOVA, $P = 0.56$).

Consequently, the variables of eye diameter, kype depth and adipose fin base length were removed, and the analysis repeated. This new analysis revealed that the first three eigenvectors and PCs 1, 2, and 3 were significant (Scree test, Kaisers Criteria), with PC 1 accounting for 96.2 % of the variation, PC 2 accounting for 1.5 % of the variation, and PC 3 accounting for 1.0 % of the variation (Figure 11). The only pattern of variation suggested was a difference between the sexes, with females differing from sneaker males and dominant males on both the PC 2 (Figure 11a) and PC 3 (Figure 11b) axes. Separation on the PC 1 axis was due to size (large total variance accounted for, low variation in all trait character loadings, Table 7), and separation on the PC 2 and PC 3 axis was due to shape. Analysis of variance on mean PC 1 scores indicated that all groups were significantly different (ANOVA, $P < 0.05$) which would be expected due to size differences. The three groups were not significantly different in their mean PC 2 score (ANOVA, $P = 0.61$), although sneaker males and dominant males had more similar mean PC 2 scores. Males and females were separated on their mean PC 3 scores (ANOVA, $P < 0.05$).

Table 6. Component coefficients for principal component analysis on all measured morphological traits of mature bull trout (*Salvelinus confluentus*) in the Chowade River.

Trait	PC 1	PC 2	PC 3
Fork Length	0.159	-0.220	0.022
Post Orbital Hypural Length	0.158	-0.236	-0.002
Body Depth	0.206	-0.206	0.025
Head Length	0.181	-0.199	0.091
Head Depth	0.202	-0.206	0.105
Post Orbital Head Length	0.174	-0.201	0.062
Eye Diameter	0.145	-0.284	0.082
Snout Length	0.202	-0.181	0.156
Upper Jaw Length	0.205	-0.193	0.126
Lower Jaw Length	0.234	-0.173	0.108
Kype Depth	0.724	0.675	0.063
Pectoral Fin Length	0.166	-0.187	0.039
Adipose Fin Base Length	0.203	-0.117	-0.954
Adipose Fin Height	0.226	-0.217	-0.043

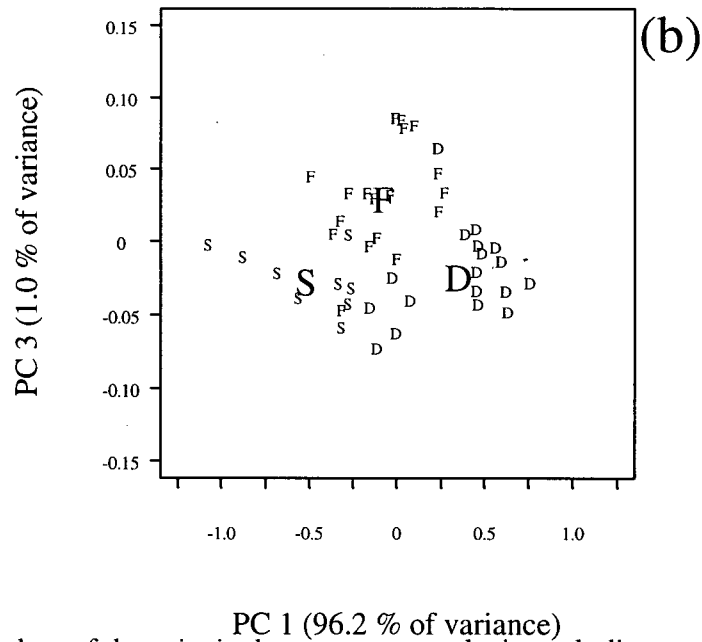
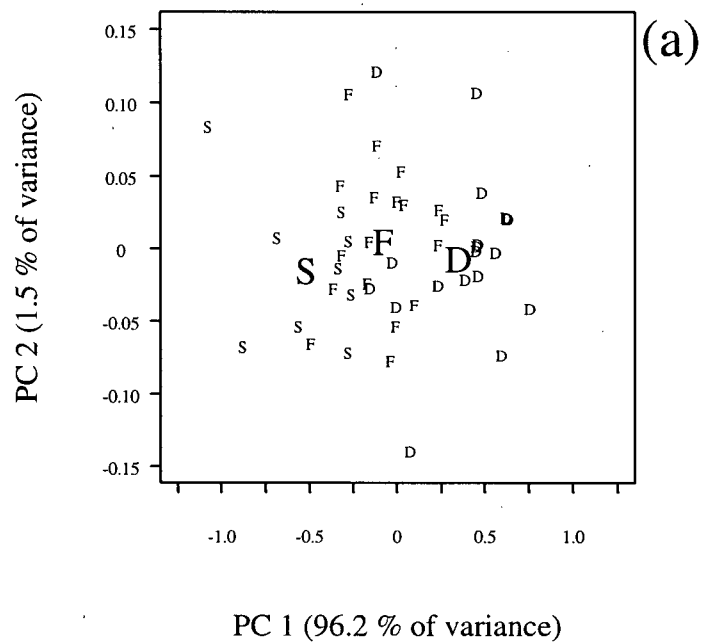


Figure 11. Scatter plots of the principal component analysis excluding eye diameter, kype depth, and adipose fin base length (a) for principal component one vs. principal component two, and (b) for principal component one vs. principal component three (F = mature females, S = mature sneaker males, D = mature dominant males. Large letters are group centroids).

Table 7. Component coefficients for principal component analysis on all measured morphological traits except eye diameter, kype depth and adipose fin base length of mature bull trout (*Salvelinus confluentus*) in the Chowade River.

Trait	PC 1	PC 2	PC 3
Fork Length	0.259	0.202	0.333
Post Orbital Hypural Length	0.260	0.185	0.542
Body Depth	0.319	0.061	0.335
Head Length	0.285	0.143	-0.027
Head Depth	0.315	0.149	-0.033
Post Orbital Head Length	0.276	0.114	0.047
Snout Length	0.310	0.018	-0.520
Upper Jaw Length	0.315	0.133	-0.286
Lower Jaw Length	0.351	0.127	-0.341
Pectoral Fin Length	0.260	-0.063	0.029
Adipose Fin Height	0.346	-0.909	0.101

A third PCA compared variation in the characters of eye diameter, kype depth, and adipose fin base length. This analysis was carried out on the three traits that did not follow typical patterns of growth as indicated by the percent of each variable variance accounted for by PC 1 in the initial analysis of all characters (Table 8). This analysis revealed that the first three eigenvectors and PCs 1, 2, and 3 were significant (Scree test, Kaisers Criteria), with PC 1 accounting for 90.4 % of the variation, PC 2 accounting for 6.6 % of the variation, and PC 3 accounting for 3.0 % of the variation. In this analysis, plots of PC 1 vs. PC 2 (Figure 12a) and PC 1 vs. PC 3 (Figure 12b) for individual fish, and the centroid plots for dominant males, sneakers, and females revealed that three distinct patterns existed: one for dominant males, one for females, and one for sneaker males. Females and small males grouped together on the PC 1 and PC 3 axes, but all three groups were separated on the PC 2 axis. Analysis of variance of mean PC 1 scores indicated that females were significantly different than dominant males ($P<0.05$), but not from sneaker males ($P>0.05$). Mean PC 2 scores were significantly different between females and males ($P<0.05$), but not between different male types ($P>0.05$). There was no difference between groups in their mean PC 3 scores (ANOVA, $P=0.93$).

Kype Depth/Fork Length Relationship

Growth of the kype, relative to fork length, differed significantly among the three groups (Figure 13). There was a significant increase in kype depth with increasing fork length for dominant males, but not for females or sneaker males (Table 9). Analysis of covariance indicated that the rate of kype growth (slope of the regression line) differed significantly between dominant males and sneaker males, and between dominant males and females (Table 10). There was, however, no difference between females and sneaker males (Table 10).

Colour Data

Non-parametric one way analysis of variance (Kruskal-Wallis) comparisons for variation in the grey scale intensity among dominant males, females, and sneaker males indicated that there were two differences in colour in the four body areas among the groups. For the complete data set there were significant differences between sneaker males and dominant males in the belly,

Table 8. Percentage of each morphological characters variance accounted for by PC 1 in the principal component analysis on all traits for mature bull trout (*Salvelinus confluentus*) in the Chowade River.

Trait	PC 1
Fork Length	99.83
Post Orbital Hypural Length	98.74
Body Depth	95.35
Head Length	97.00
Head Depth	93.04
Post Orbital Head Length	97.20
Eye Diameter	63.79
Snout Length	89.11
Upper Jaw Length	93.49
Lower Jaw Length	91.93
Kype Depth	59.65
Pectoral Fin Length	93.42
Adipose Fin Base Length	56.86
Adipose Fin Height	82.46

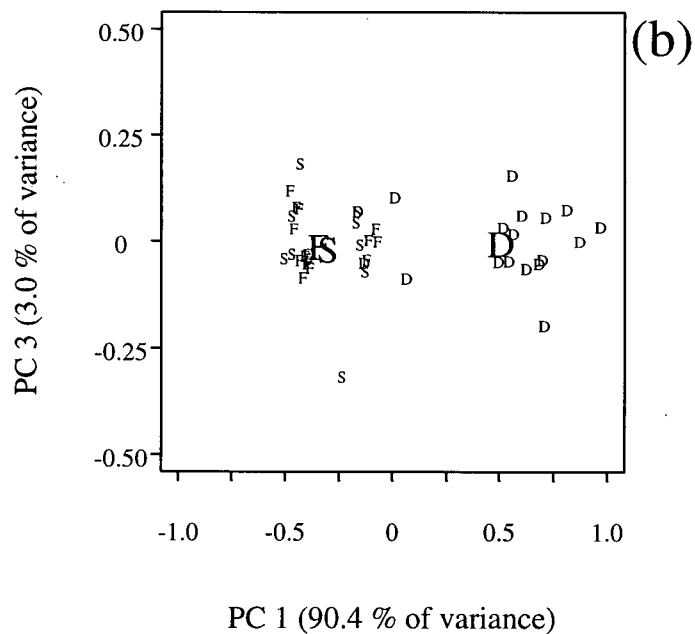
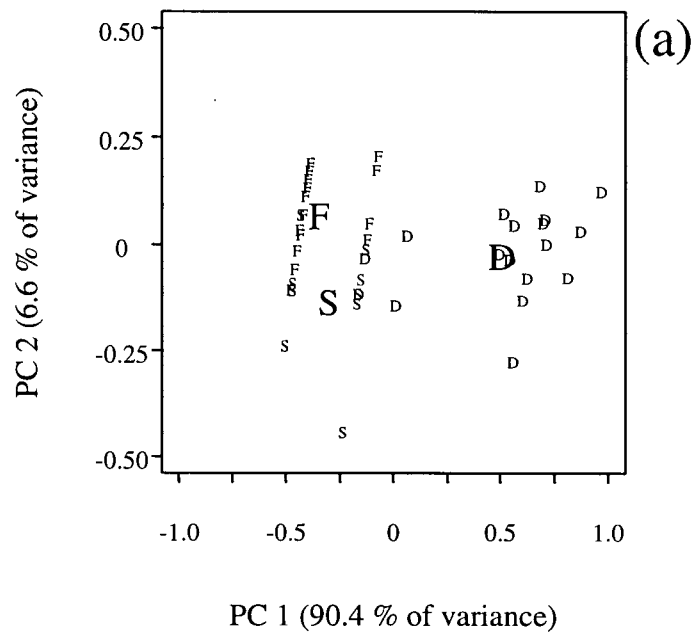


Figure 12. Scatter plots of the principal component analysis of eye diameter, kype depth and adipose fin base length (a) for principal component one vs. principal component two, and (b) for principal component one vs. principal component three (F = mature females, S = mature sneaker males, D = mature dominant males. Large letters are group centroids).

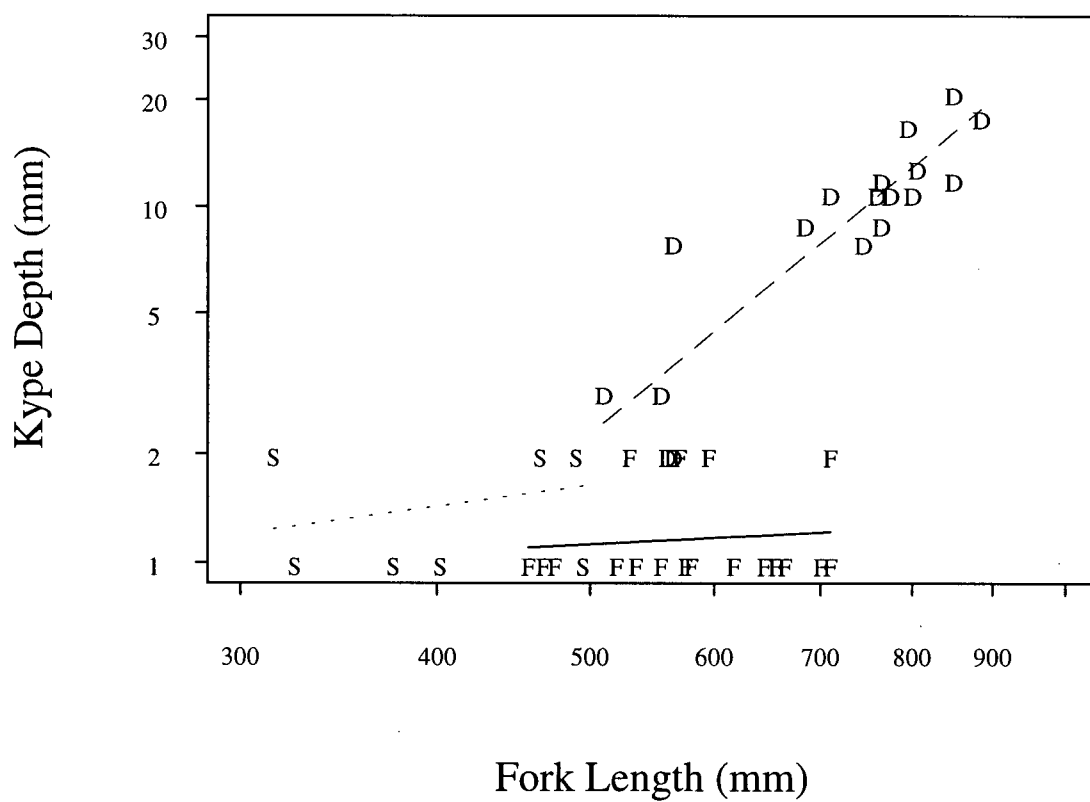


Figure 13. Growth of the kype relative to fork length for three classes of mature bull trout (*Salvelinus confluentus*) in the Chowade River (D = Dominant male, S = Sneaker male, F = Female).

Table 9. The relationship between fork length (FL) and kype depth (KD) for three classes of mature bull trout (*Salvelinus confluentus*) in the Chowade River (*=statistical significance, α levels adjusted using sequential Bonferroni corrections).

Class	Regression Equation	r^2	P
Female	$\log_{10} \text{KD} = -0.56 + 0.23 \log_{10} \text{FL}$	0.01	0.66
Sneaker male	$\log_{10} \text{KD} = -1.43 + 0.61 \log_{10} \text{FL}$	0.09	0.45
Dominant male	$\log_{10} \text{KD} = -9.66 + 3.71 \log_{10} \text{FL}$	0.79	<0.001*

Table 10. Analysis of covariance comparisons of kype growth among mature male and female bull trout (*Salvelinus confluentus*) in the Chowade River (F-test, *=statistical significance, α levels adjusted using sequential Bonferroni corrections).

Class Comparison	Variable	F	df	P
Dominant male vs. Female	\log_{10} fork length	30.60	33	<0.0001*
	group	20.82	33	<0.0001*
Dominant male vs. Sneaker male	\log_{10} fork length	25.29	24	<0.0001*
	group	12.62	24	<0.001*
Female vs. Sneaker male	\log_{10} fork length	0.93	25	0.34
	group	0.14	25	0.71

throat, and fin region (Table 11), and likewise in comparisons with outliers removed from the analysis (Table 12). Dominant males had darker bellies, throats, and fins than sneaker males. In the complete data set, comparisons between females and dominant males identified significant differences only in the throat (Table 11), but with outliers removed there were differences in the belly and throat region (Table 12). Dominant males had darker bellies and throats than females. There were no significant differences between sneaker males and females in colouration in the belly, throat, fin, and back regions in comparisons of data from all individuals (Table 11) and in comparisons with outliers removed from the analysis (Table 12). This suggested that females and small males were similarly coloured.

Multivariate analysis of variance among the three classes of mature bull trout for the intensity of the combined red, green, and blue scale wavelengths of light indicated that there were differences among the classes for all body regions where colours were measured (Table 13). Sneaker males differed from dominant males in all regions, while females differed from dominant males in the colouration of the belly, throat, and back areas. Females and sneaker males did not differ significantly in their colouration in any area. Again, these results suggest that females and sneaker males are similar in their sexual colouration, whereas females and sneakers differ from dominant males.

Ageing Data

Fin rays

The linear relationships of fin ray age and \log_{10} fork length for age class 2 to 4 ($\log_{10} \text{FL} = 2.310 + 0.057 \times \text{Age}$, $r^2=0.43$, $P<0.0003$), and age class 5 and above ($\log_{10} \text{FL} = 2.705 + 0.014 \times \text{Age}$, $r^2=0.09$, $P=0.008$) were both significant and indicated a substantial growth increase between age 4 and 5 (Figure 14). Also, there was a significant difference ($t=-9.801$, $df=110$, $P<0.0001$) in the mean age of males smaller than 500 mm (mean \pm SE = 3.81 ± 0.23 years), and males larger than 500 mm (mean \pm SE = 7.08 ± 0.20 years).

Table 11. Comparisons of colour variation in the belly, throat, fins, and back region among three classes of mature bull trout (*Salvelinus confluentus*) (all individuals). Data are mean (\pm SE) intensity of the grey wavelength of light tested with non-parametric one way analysis of variance on ranks (Kruskal-Wallis one way ANOVA, a posteriori pairwise comparisons made using a Newman-Keuls test, *=statistical significance, ∞ levels adjusted using sequential Bonferroni corrections).

Body Region	Class	Mean Intensity of the Grey Wavelength of Light	P (ANOVA)	Pairwise Comparison
Belly	Female (F)	223.5 (3.40)	0.0003*	F vs. S
	Sneaker male (S)	231.2 (2.29)		F vs. D
	Dominant male (D)	215.3 (4.13)		S vs. D*
Throat	Female (F)	93.6 (10.93)	<0.0001*	F vs. S
	Sneaker male (S)	131.3 (16.47)		F vs. D*
	Dominant male (D)	35.0 (5.98)		S vs. D*
Fins	Female (F)	52.7 (5.44)	0.02*	F vs. S
	Sneaker male (S)	66.5 (5.80)		F vs. D
	Dominant male (D)	43.2 (4.14)		S vs. D*
Back	Female (F)	94.0 (6.59)	0.111	F vs. S
	Sneaker male (S)	116.2 (15.85)		F vs. D
	Dominant male (D)	117.3 (6.78)		S vs. D

Table 12. Comparisons of colour variation in the belly, throat, fins, and back region among three classes of mature bull trout (*Salvelinus confluentus*) (outliers removed). Data are mean (\pm SE) intensity of the grey wavelength of light tested with non-parametric one way analysis of variance on ranks (Kruskal-Wallis one way ANOVA, a posteriori pairwise comparisons made using a Newman-Keuls test, *=statistical significance, α levels adjusted using sequential Bonferroni corrections).

Body Region	Class	Mean Intensity of the Grey Wavelength of Light	P (ANOVA)	Pairwise Comparison
Belly	Female (F)	226.6 (1.42)	0.0003*	F vs. S
	Sneaker male (S)	231.2 (2.29)		F vs. D*
	Dominant male (D)	213.5 (3.98)		S vs. D*
Throat	Female (F)	98.8 (10.26)	<0.0001*	F vs. S
	Sneaker male (S)	131.3 (16.47)		F vs. D*
	Dominant male (D)	30.6 (4.36)		S vs. D*
Fins	Female (F)	54.3 (5.54)	0.0132*	F vs. S
	Sneaker male (S)	66.5 (5.80)		F vs. D
	Dominant male (D)	42.1 (4.23)		S vs. D*
Back	Female (F)	96.7 (6.79)	0.2129	F vs. S
	Sneaker male (S)	116.2 (15.85)		F vs. D
	Dominant male (D)	116.4 (7.13)		S vs. D

Table 13. Comparisons of colour variation in the belly, throat, fins, and back region for the combined intensity of the red, green, and blue wavelengths of light among three classes of mature bull trout (*Salvelinus confluentus*), (*=statistical significance, ∞ levels adjusted using sequential Bonferroni corrections) using multivariate analysis of variance (MANOVA). Pairwise comparisons were made using a F-test.

Body Region	Class	Between-group variation (Wilks' Lambda)	P (ANOVA)	Pairwise Comparison
Belly	Female (F)	5.6394 (df=6)	<0.0001*	F vs. S
	Sneaker male (S)			F vs. D*
	Dominant male (D)			S vs. D*
Throat	Female (F)	6.6065 (df=6)	<0.0001*	F vs. S
	Sneaker male (S)			F vs. D*
	Dominant male (D)			S vs. D*
Fins	Female (F)	2.2315 (df=6)	0.0486*	F vs. S
	Sneaker male (S)			F vs. D
	Dominant male (D)			S vs. D*
Back	Female (F)	4.3107 (df=6)	0.0008*	F vs. S
	Sneaker male (S)			F vs. D*
	Dominant male (D)			S vs. D*

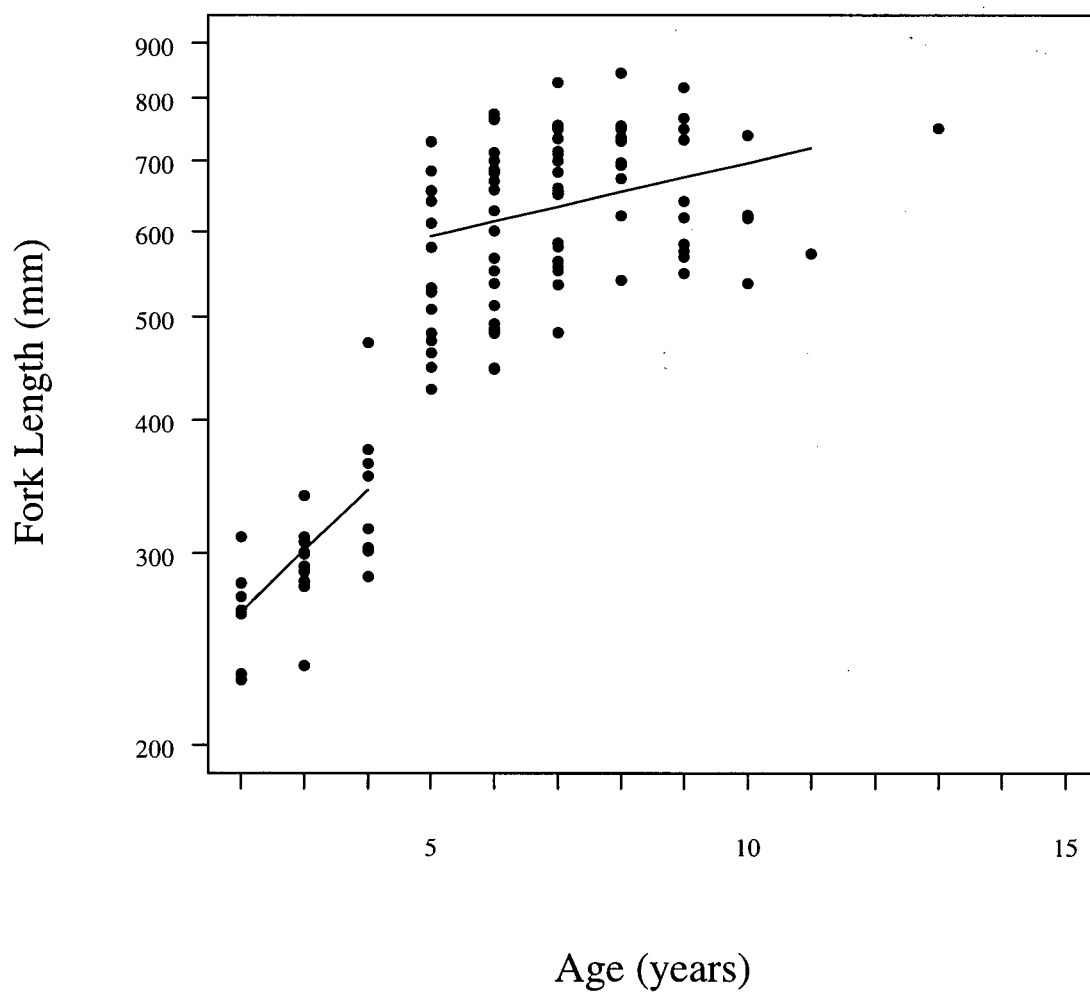


Figure 14. The linear relationship of age (based on fin ray sections) and fork length of mature male bull trout (*Salvelinus confluentus*) age 2 to 4, and age 5 to 13 in the Chowade River.

Scales

At ages 1, 2, and 3 (before the first spawning) there were significant differences between the mean back calculated length at age for dominant and sneaker male bull trout. Individuals that had characteristics of dominant males were larger in the first three years of life (Table 14). Although dominant males were still larger than sneakers at age 4 and 5, these differences were not significant. There were no significant differences in the mean length at first maturity ($t=-1.83$, $df=22$, $P=0.08$), and age (5) at first maturity ($t=-1.06$, $df=22$, $P=0.30$) between dominant and sneaker males; however individuals that were identified as dominant males grew significantly larger than individuals identified as sneakers after their first spawning (Table 14). On average dominant males sampled in 1996 were older (mean \pm SE = 10.6 ± 0.3 years) than sneaker males (mean \pm SE = 8.3 ± 0.3 years) ($t=-5.19$, $df=22$, $P<0.0001$), larger (mean \pm SE = 718.7 ± 30.6 mm) than sneaker males (mean \pm SE = 421.9 ± 23.3 mm) ($t=-6.80$, $df=22$, $P<0.0001$), and had spawned more times (mean \pm SE = 3.93 ± 0.8 times) than sneaker males (mean \pm SE = 2.89 ± 0.4 times) ($t=-2.61$, $df=22$, $P=0.02$). The average time to second spawning was different between male types. Sneaker males on average spawn repeatedly in successive years (mean \pm SE = 1.22 ± 0.15 years) but dominant males spawn on average in alternate years (mean \pm SE = 2.00 ± 0.18 years) after their first spawning. This difference was statistically significant ($t=2.89$, $df=23$, $P<0.005$).

B. Visual Observations

Behavioural Observations

Although there were significant differences between the mean size of males (mean \pm SE = 734.62 ± 10.04 mm, $n=65$) and females (mean \pm SE = 650.76 ± 8.40 mm, $n=65$) paired at a redd site ($t=-6.4142$, $df=129$, $P<0.00001$), Spearman's rank correlation analysis on \log_{10} transformed size data of female/male pairings suggested ($r_s=0.37$, $n=64$, $P=0.0018$) size assortative mating (Figure 15).

Table 14. Mean estimated back calculated lengths at age from scales for bull trout (*Salvelinus confluentus*) males classified as dominant and sneakers in the Chowade River (*=statistical significance between types).

Male type	Length (mm) at age										
	1*	2*	3*	4	5	6	7*	8*	9	10	11
Dominant	47.8	90.0	139.0	196.8	261.3	336.8	431.2	526.1	594.7	666.3	750.2
Sneaker	31.4	67.0	112.2	170.3	236.5	293.2	351.3	403.8	440.0		

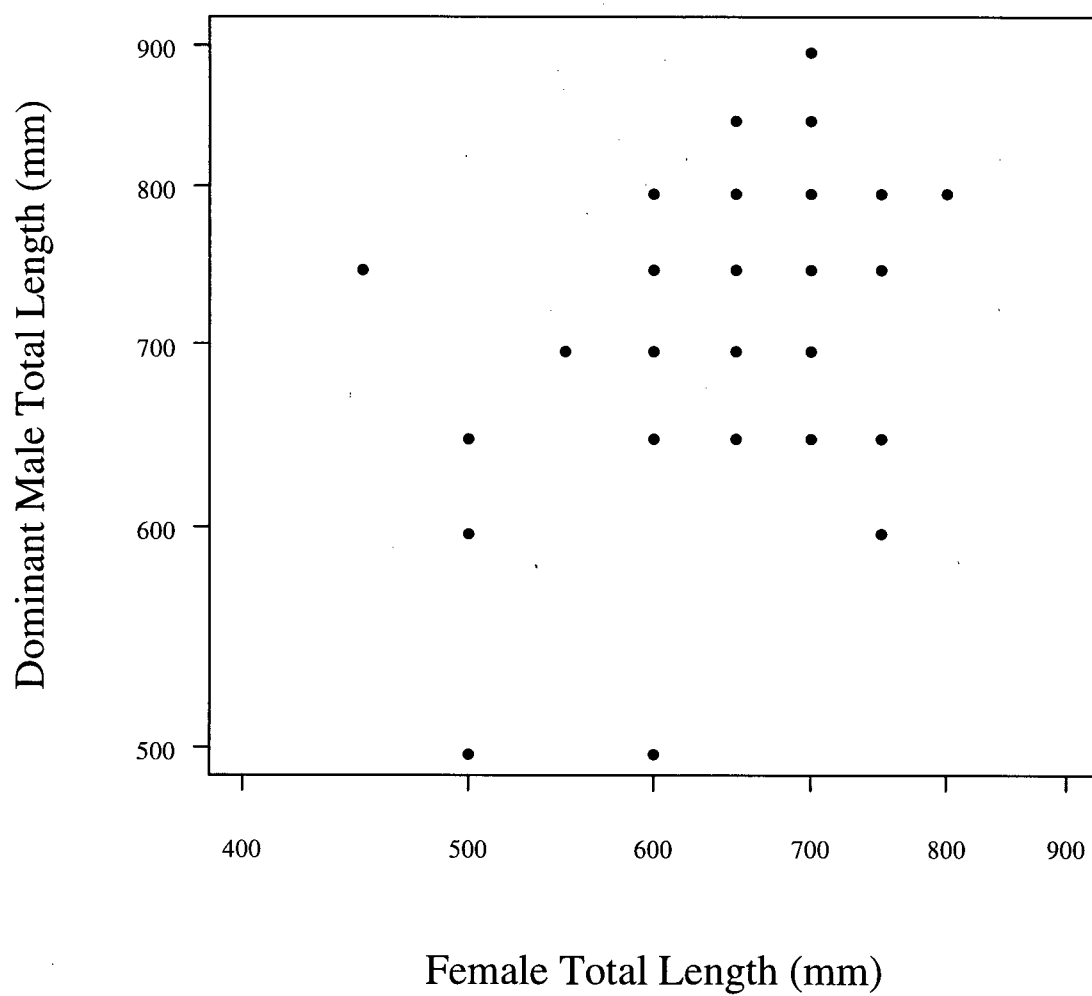


Figure 15. The association between estimated total length of mature males and estimated total length of mature females for paired bull trout (*Salvelinus confluentus*) at redd sites in the Chowade River in 1995 and 1996 ($r_s=0.37$, $n=64$, $P=0.0018$).

Logistic regression indicated that the probability of a mature male being paired with a female was dependent on the male's size (Probability of being paired = $-51.25 + 18.21 \times \log_{10}$ Estimated Total Length, $r^2 = 0.73$, $P < 0.0001$) (Figure 16). Estimated total length of males adopting different strategies at a redd site differed significantly, with dominant males larger, on average, than both satellite males and sneaker males, and with satellite males, on average, larger than sneaker males (Table 15).

Overall, the number of subdominant (satellites and sneakers) males at a redd site increased significantly with an increase in the size of the dominant male ($r_s = 0.33$, $n = 64$, $P = 0.004$), but not with an increase in the size of the female attending the redd site ($r_s = 0.09$, $n = 64$, $P = 0.24$). Specifically, the number of satellite males at a redd site was positively associated both with dominant male size ($r_s = 0.44$, $n = 64$, $P = 0.0002$) and female size ($r_s = 0.28$, $n = 64$, $P = 0.0133$). The number of sneaker males at a redd site, however, was not associated with either dominant male size ($r_s = -0.015$, $n = 64$, $P = 0.5464$), or female size ($r_s = -0.21$, $n = 64$, $P = 0.9504$).

The number of aggressive acts of the dominant male bull trout at a redd site partially (although not significantly) increased with increasing density of satellite males ($r^2 = 0.2503$, $n = 15$, $P = 0.057$), but did not increase with an increase in density of sneaker males ($r^2 = 0.1267$, $n = 14$, $P = 0.1929$). Although data from observations at redd sites suggested that dominant males were two times more likely to attack satellite males than sneaker males (Figure 17), differences in the mean aggressive behaviour by the dominant male at a redd site towards satellite males (mean \pm SE = 7.14 ± 1.59 encounters per ten minutes, $n = 15$) and sneaker males (mean \pm SE = 3.67 ± 0.87 encounters per ten minutes, $n = 14$) fell just short of statistical significance ($t = -1.95$, $df = 27$, $P = 0.0612$).

Experimental Tests on Dominant Male Aggression

There were no significant differences in the mean aggressive behaviour of the dominant male at a redd site towards the male coloured model ($t = 0.1502$, $df = 12$, $P = 0.8828$) either in the front (mean \pm SE = 4.17 ± 1.17 per ten minutes, $n = 6$) or rear (mean \pm SE = 4.37 ± 0.82 per ten minutes, $n = 8$) positions during the experimental trials, or towards the female coloured model

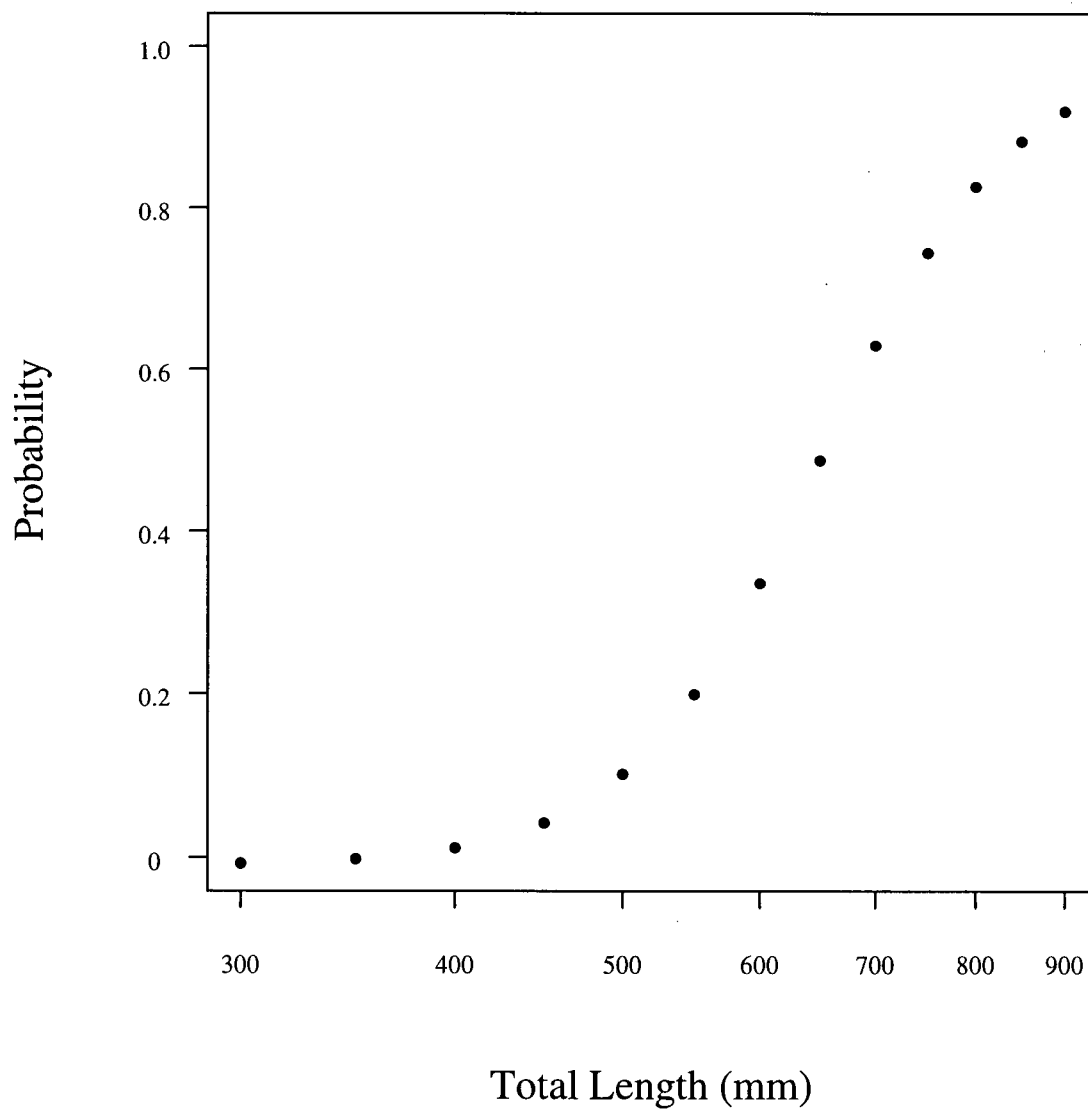


Figure 16. Relationship of the probability from logistic regression analysis of a mature male bull trout (*Salvelinus confluentus*) being paired with a reproductive female in the Chowade River based on its estimated total length from visual observations.

Table 15. Mean (\pm SE) estimated total length of three classes of mature male bull trout (*Salvelinus confluentus*) at redd sites in the Chowade River for pooled 1995 and 1996 data, and a summary of comparisons between the mean estimated total length of individuals in these groups (t-test, *=statistical significance, ∞ levels adjusted using sequential Bonferroni corrections).

Class	Mean estimated total length (mm)	Comparison	t	df	P
Dominant male (D)	734.62 (10.04)	D vs. Sa	2.78	94	0.006*
Satellite male (Sa)	687.10 (12.69)	Sa vs. S	15.71	72	<0.001*
Sneaker male (S)	411.63 (11.75)	S vs. D	20.69	106	<0.001*

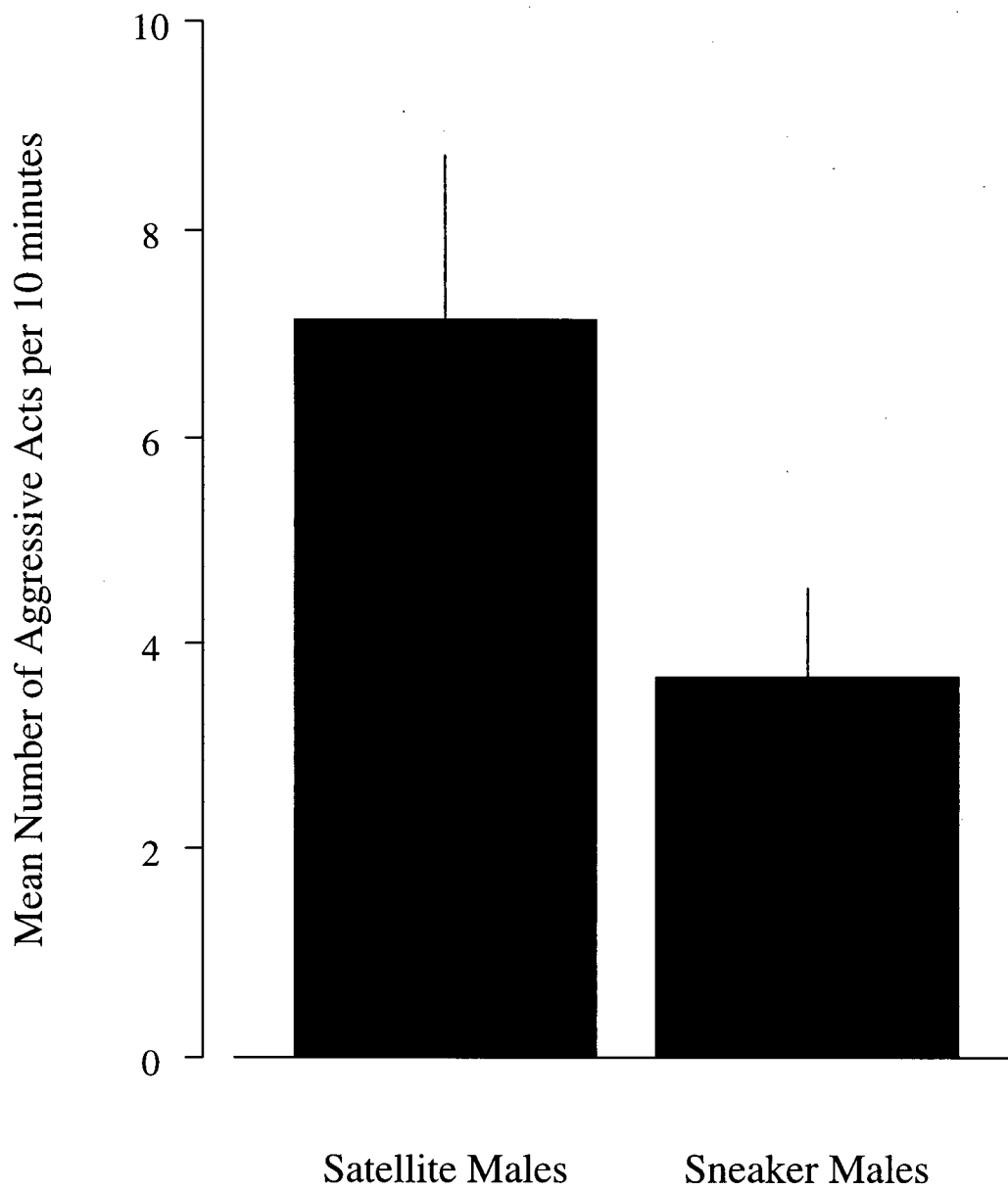


Figure 17. Barplots of the mean number of aggressive acts per ten minutes (\pm SE) exhibited by a dominant male bull trout (*Salvelinus confluentus*) at a redd site towards satellite and sneaker males.

($t=0.812$, $df=12$, $P=0.433$) in the front (mean \pm SE = 0.38 ± 0.18 per ten minutes, $n=8$) or rear (mean \pm SE = 0.17 ± 0.17 per ten minutes, $n=6$) positions. These results suggest that behaviour towards the different coloured models was independent of the position at the redd during individual trials. As a result, differences between aggressive behaviours towards the model were compared irrespective of model position.

A significant difference in the mean number of aggressive interactions directed by the dominant male towards the male coloured model (mean \pm SE = 4.29 ± 2.46 interactions per ten minutes, $n=14$) and the female coloured model (mean \pm SE = 0.29 ± 0.47 interactions per ten minutes, $n=14$) was observed (Figure 18) during the experimental trials ($t=5.97$, $df=26$, $P<0.0001$).

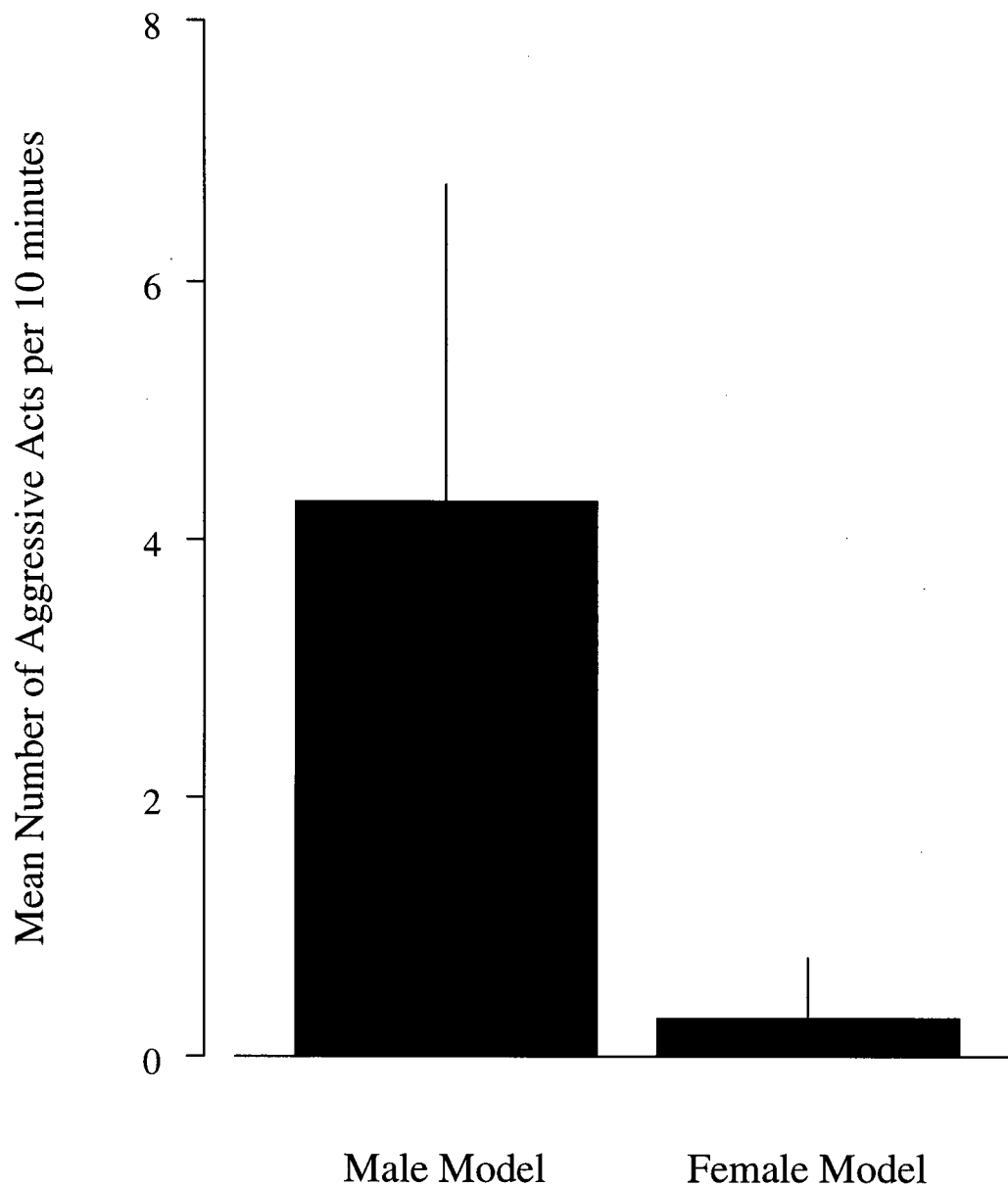


Figure 18. Barplots of the mean number of aggressive acts per ten minutes (\pm SE) exhibited by a dominant male bull trout (*Salvelinus confluentus*) at a redd site towards male and female models.

DISCUSSION

Because females tend to be limited in the number of gametes they produce, male-male competition is often for female gametes (Davies 1991). This is especially true in salmonids where females produce a relatively small number of large eggs. Thus, often in many salmonid species, a dominant male at a redd site controls access to a reproductive female by chasing off other males (Maekawa and Onozato 1986; Keenleyside and Dupuis 1988; Foote 1990; Quinn and Foote 1994), and it is assumed that such dominant males fertilize a high percentage of the eggs laid by that female (Schroder 1982; Chebanov et al. 1983; Maekawa and Onozato 1986; Hutchings and Myers 1988). If this is the general case in salmonids, then large males should have a reproductive advantage over smaller males and, thus, males should be selected for large body size.

My data for bull trout males in the Chowade River indicate that the largest males are both the most aggressive and the dominant males at redd sites in this breeding system. At a redd site, dominant males were on average larger (in estimated total length) than either satellite or sneaker (subdominant) males. These subdominant males maintained positions on the periphery of the redd site. Larger males were also more likely to be paired with a spawning female than subdominant males. If dominant bull trout males have a large reproductive advantage then, perhaps, it would be beneficial for individual males to delay maturity until they are large enough to be dominants. This would increase their probability of pairing with a female, and of winning male-male aggressive encounters. Presumably, this would improve their chances of achieving successful fertilizations, and increase their reproductive success. Also, if females choose males that contribute the best resources (i.e., "good genes") to their offspring (Sargent et al. 1986), then females should choose the largest males, and a consequence of female choice should be positive size assortative pairing. My data from observations of pairings on redds suggest that females do select large males. This is also the case in other salmonids (Foote 1988, 1989; Foote and Larkin 1988).

There are, however, trade offs to delayed maturity that must be balanced in terms of reproductive success. A male that delays maturity runs the risk of dying before having a chance to spawn. Thus, it might also benefit a male to return as a younger smaller male and obtain some

fertilizations by adopting sneaking as an alternative reproductive strategy. If, the smallest sneaker males are the most successful sneakers, and this outweighs reproduction costs in terms of lost growth opportunities, then sneakers may forfeit any possibility of growing to a dominant size. Under this situation, there should be two size classes of males: large dominant males, and small sneaker males. In the Chowade, there are two distinct size classes of mature male bull trout in the spawning areas. Similar observations of different types of males in other bull trout populations have been reported (McPhail and Murray 1979; Kitano et al. 1994; Sexauer 1994; James and Sexauer 1997), although these studies did not investigate whether the variation found among males reflects different reproductive strategies, or is simply an ontogenetic shift that continues throughout a male's life (i.e., small males eventually grow into large males).

Both types of males immigrate into the upper Chowade River to spawn. This suggests that the smaller males are not simply stream resident fish that remain in the Chowade River, and consequently do not grow as large as migrating individuals. Evidence from snorkel surveys in 1994 (Baxter 1994a) and radio telemetry in 1996 show that all mature bull trout leave the Chowade River when water temperatures drop to about 0°C, and move into the Halfway and Peace rivers. The Chowade River is a major rearing stream for juvenile bull trout with fish from age 1 to 4 found in the stream throughout the year (Baxter 1994b, 1995). My scale analysis data from males categorized as dominant or sneakers in 1996 showed no major differences in growth patterns that might point to a habitat difference in the two types. However, the scale data suggest that, as juveniles, dominant males grew significantly faster than sneaker males during their tributary stream rearing years and thus, were larger (dominant males: mean \pm SE = 261.3 \pm 13.1 mm, sneaker males: mean \pm SE = 236.5 \pm 11.1 mm) than sneaker males at first maturity. Although the mean length at first maturity was not significantly different between types, it is still indicative that dominant males grow larger during their juvenile years.

These data are opposite to what has been found in semelparous Pacific salmon, where mature jacks are the fish that tend to grow largest in their juvenile years due to environmental cues (Bilton et al. 1984). These apparent differences might suggest that environmental cues to maturity may not play as large a role in terms of early reproduction in northern environments.

There was no significant difference in the age at first maturity between dominant and sneaker males, and typically the pattern of growth in the early years is similar between the two types. The growth pattern, however, after first maturity is strikingly different: sneakers slow their growth, whereas dominants continue to grow. This suggests that sneaker males never grow into dominants and thus the two different types of males found on the spawning grounds are a direct result of males adopting two different reproductive strategies.

Interestingly, dominant males reach first maturity at a size (about 260 mm) where they would have a low probability of spawning as a pair. Consequently, they would have to sneak their first reproductions. After first maturity, however, the spawning pattern of the two types of males appears to differ. On average, sneaker males spawn repeatedly in successive years (repeat year spawning), whereas on average, dominant males spawn on alternate years after their first spawning. This alternate year spawning pattern facilitates greater growth by dominant males between spawnings, and causes the two types of males to diverge in size. Hence, dominant males grow larger after their first maturity (age 5) than sneaker males.

My data also indicates that mature males less than 500 mm essentially are excluded from pairing with females during spawning. This is suggested by a number of observations. First, size assortative mating occurs in the Chowade River, and the smallest female observed spawning during 1995 and 1996 was 450 mm. Since females usually pair with a male larger than themselves, it would be rare for a male of 500 mm, or less, to be paired with a female and actively defending a redd site against intrusions by other males. Even if a small male pairs with a female, there is evidence from other species that in such cases females might delay reproduction until larger males arrive at the spawning sites (Foote 1989; van den Berghe et al. 1989). This relationship was substantiated by the results of the logistic regression that calculated the probability of a male of given length being paired with a female. Males of 500 mm or less had only a 10 % probability of being paired with a female (Figure 16).

There must, however, be some advantage accruing to males adopting a sneaking strategy when they have a very low chance of pairing with female. One possible explanation is that even though small males may have a low reproductive success in any given year, by adopting a

sneaking strategy and spawning every year they may, over their lifetime, “catch” up to the spawning success of a dominant male that spawns only once every two to three years. Sneakers may also be able to spawn with more females by not having to defend a territory around a reproductive female. Studies on the other fish species have also determined that in some cases sneakers may fertilize the majority of eggs in some spawnings (e.g., Morán et al. 1996). Also it may be that in environments that are subject to the flash floods, extreme habitat alterations, and chaotic events that characterize bull trout spawning streams (see Rieman and McIntyre 1993, 1995), individuals (e.g., sneaker male) lose less if they don’t put “all their eggs into one basket” by reproducing once every two or three years (dominant male). For instance, if a sudden flash flood were to destroy all the eggs for a given years recruitment, then an individual that spawns every year could “catch up” the next year, and would have an increased reproductive success compared to an individual that puts all his energy into spawning every two years (i.e., dominants).

Another possibility that may favour a strategy other than being dominants is in situations where the operational sex ratio changes during spawning. There is evidence from data on bull trout immigration into the Chowade River spawning areas through a collection fence (R.L. & L. Environmental Services Ltd. 1994), and from data collected through angling (Baxter 1995), that the approximate ratio of males to females is 1:1. In situations where a male or a female could spawn only once in a season, one would expect that alternative male reproductive strategies would not exist because every male could access a female. Once a pair had spawned, the sex ratio in the reproductive population would remain at 1:1, and late arriving individuals to the spawning area could still mate. There is evidence, however, in the Chowade system that the operational sex ratio of bull trout changes through the spawning period.

Males arrive at the spawning area before females (Baxter 1995). Once spawning starts, dominant males may be at an advantage in aggressive contests with other males or, possibly, not having to fight at all for access to a female if a potential competitor moves on to the next available female rather than fight. My observations at redd sites when pairing and spawning first starts tend to support this contention: most sites contain only pairs (one male and one female). There are no sneakers or peripheral males present at redd sites during this period. After a female bull trout has spawned all her gametes, there is no benefit to her remaining in the spawning areas as females

don't show post-spawning parental care. Again, there is evidence that females emigrate from the upper river spawning areas well before males emigrate (R.L. & L. Environmental Services Ltd. 1994). Thus, as this occurs, the operational sex ratio becomes skewed towards males as the spawning period advances. As the ratio of males to females increases in the upper river, large males might lose some of their advantages. At this time the number of males at redd sites increase, and the amount of energy dominant males must expend to control access to a female is probably greater than it was early in the spawning period. With more males in attendance at a redd site, a dominant male trying to control access to a female also spends more time chasing other large males off, and this might allow sneaker males more time to get within close proximity to a female. This extra cost of late season spawning to dominants may give sneakers an equal reproductive success to dominants over the spawning period. Such situations are thought to occur in sockeye salmon (*Oncorhynchus nerka*) breeding systems (Quinn and Foote 1994).

There is evidence in pink salmon, *Oncorhynchus gorbuscha*, (Keenleyside and Dupuis 1988) and dark chub, *Zacco temminckii*, (Katano 1990) that once the number of males at a redd site increases to a point where dominant males are fully occupied chasing away competitors, at the time of gamete release the dominant male may not be closest to the female. In these situations all males around a redd site will rush towards the pair and release sperm in the nest site, in some cases with the sneakers having a high fertilization success (Morán et al. 1996). Assuming that sperm from all males has an equal chance of fertilizing an egg, under this situation a dominant male may not benefit and, in fact, may be at a disadvantage in that energy expenditures during spawning (e.g., fighting) may be high enough to decrease disease resistance or increase the chance of mortality. In this case, it may be that an alternative reproductive strategy has evolved through negative frequency-dependent sexual selection (Gross and Charnov 1980; Maynard Smith 1982). In an increasing operational sex ratio situation where the ratio of males at a redd site increases, individuals using the sneaker strategy are rarer and may have a greater success (Gross 1991).

Although, I classified male bull trout in the Chowade River as one of two types, I observed a high degree of phenotypic variation between individuals within the two size classes of males. Dominant males and sneaker males differed most in their traits of sexual colouration and kype growth: smaller males were more similar to females in both these traits. One would expect

that characters that might have a functional advantage during male-male encounters would differ between dominant and sneaker males if two strategies did exist. Dominant males engaged in aggressive encounters with other large males use behaviours such as ramming, biting, chasing and lateral displays. A large well developed kype, and bright coloration, may be of advantage in these encounters. Perhaps, because it increases the opportunity to inflict damage on other males, but also it may provide visual intimidation. If a large kype aids in chasing off other males, the advantage of a kype is obvious. Usually, small males are not the winners of aggressive encounters in salmonids (Kitano et. al 1994; Gross 1996) and, therefore, large kype size may be of no functional advantage to a small male. Also, a small male with a well developed kype might be perceived as a threat by a dominant male, causing the larger male to attack the smaller male in an asymmetrical contest that may result in injury to the smaller male. In Atlantic salmon, small males are sometimes killed by large males (Hutchings and Myers 1987).

My principal component analyses (PCA) showed that male types differ in their kype development. The initial PCA (with all characters included) showed that although most of the variance was accounted for in the first PC, which is usually the size vector, the character loadings in the first eigenvector indicated that kype depth was a significant contributor and, in fact, dominated the first principal component (Table 6). Subsequent analysis showed this character, as well as eye diameter and adipose fin base length, did not follow the typical size increases with growth. Once these variables were removed from the analysis, the two types of males had the same shape regardless of size, which is what one would expect if there were not two size independent kinds/morphs of males on the spawning grounds.

Dominant and sneaker males also differed significantly in their spawning colouration on the belly, throat, ventral fins, and back area. In these areas, small males were more similar to females than dominant males. Analysis of the intensity of the red, green and blue wavelengths of light indicated that the belly and ventral fins of male bull trout are the most brilliantly coloured areas during spawning. Dominant males had belly a colouration that tended towards orange or red and had black ventral fins, while sneaker males had a belly colouration that towards white and the ventral fins were more lightly coloured than those in the dominant males. Females also had white bellies and grey fins.

Fabricus and Gustafson (1953) demonstrated that in the Arctic char (*S. alpinus*) male colouration during spawning was related to aggressive behaviour and dominance: larger more aggressive males were more brightly coloured than their non-aggressive counterparts. It is thought that the brightly coloured belly area of bull trout males also signals dominance to other males (McPhail and Murray 1979; Kitano et al. 1994; James and Sexauer 1997), and for the genus *Salvelinus* in particular this phenomena of two types of mature males of different sizes and sexual colouration is common: Arctic char (Jonsson and Hindar 1982; Sigurjonsdottir and Gunnarsson 1989); Dolly Varden (Maekawa et al. 1993); miyabei char (Maekawa and Onozato 1986). In bull trout a functional relationship between colour, aggression, and size is suggested by my data on colour differences between large and small males, and behavioural observations made at redd sites. Dominant males attacked other larger, more brightly coloured males to a greater extent than they did smaller, non-coloured males (almost a 2:1 ratio). Although this result was not statistically significant, it is most definitely biologically significant. These data suggest that bright male colouration elicits attack by a dominant male. Because of the size variation between the coloured and non-coloured males, however, I could not exclude the possibility that size was the factor that influenced the aggressive behaviour of dominant males towards other males.

To control for body size, I conducted experiments with different coloured models of the same size. These trials effectively removed size variation, and showed that red colouration in the belly region, and black colouration on the pectoral and pelvic fins were enough of a sufficient visual stimulus to cause dominant males to exhibit aggression towards a model. In 1994, when my work in the Chowade River first started, I became interested in colour variation among males. Originally, I sexed many captured individuals as small females. This was based on their colouration, and I was surprised to observe a release of sperm from one of my supposed females when I ran my fingers along its belly. I wondered whether or not small males might be mimicking females in colouration, and the original intent of my model experiment was to make a "male-like" model and a "female-like" model, and try to assess whether small males coloured like females experienced reduced aggression of dominant males towards them. My data clearly showed that "female-like" models induced far less aggression from dominant males than "male-like" models of the same size (Figure 18).

Female mimicry is a strategy that is common in other fish species such as the ninespine stickleback (*Pungitius pungitius* - Morris 1952), and the bluegill sunfish (*Lepomis macrochirus* - Dominey 1980; Gross 1991). In salmonids, this strategy has not been positively identified, but was suggested for pink salmon in Lake Superior where at high densities small sneaking males resembled females in morphology (Noltie 1990), and on the Pacific coast for chum salmon, *Oncorhynchus keta*, (Beacham and Murray 1987). Saetre and Slagsvold (1996) suggest that a possible benefit of female mimicry in the pied flycatcher (*Ficedula hypoleuca*) may be the ability of the female mimic to conceal information that may be vital to an opponent during a contest. If small males are mimicking females, the advantage would be to conceal information from a dominant male that the mimic is actually a male. In bull trout, this would reduce aggression from the dominant male, and allow the sneaker to get close to the redd. Although I have no data that show that non-coloured sneaker males were on average closer to redd sites than satellite males, my personal observations suggest that small males do get closer to a digging female than coloured males on the periphery of the redd. My behavioural data also show that these small non-coloured individuals receive less antagonistic aggression than satellite males. Another sign that suggests sneakers may be mimicking females is female aggression. Females rarely are aggressive to males, but they do show minimal aggression towards other females. My few behavioural observations of female aggression indicate females did attack small non-coloured males at redd sites. This suggests females may mistake small sneaker males for females.

Gross (1984) suggested that in intraspecific matings in fishes, smaller males may have a functional advantage at spawning sites owing to their ability to occupy refuge sites that larger males cannot use, or simply by not appearing as a threat to a dominant male because of their small size. Bull trout males are a highly aggressive salmonid that engage in fierce battles for access to, and defending a territory around, a female digging a redd. For bull trout, Gross' (1984) suggestion is supported. The dominant male bull trout at redd sites were more aggressive towards large brightly coloured bull trout that engaged in competition with the dominant males. By contrast, little aggression was directed towards smaller males that were not brightly coloured and appeared inconspicuous. Thus, my studies suggest that there are two strategies used by male bull trout in the Chowade River, and that there can be functional advantages to being a small

male. I have not addressed the reproductive success (fitness) of small males compared to large males. This is an area for future work. Genetic data on other species does suggest that sneakers are successful, at least in achieving high fertilization rates. By showing, however, that small males differ from dominant males in their colouration and morphology, I have identified possible mechanisms that may foster successful matings by these small males that cannot physically compete directly with larger males for access to females.

CHAPTER 3 - MICROHABITAT AT BULL TROUT REDD SITES AND THE EFFECT OF REDD SITE SELECTION ON EGG TO ALEVIN SURVIVAL

INTRODUCTION

If bull trout populations are to be maintained, then mature fish must be able to spawn in high quality habitat. Although remarkably little is known about the spawning requirements of this species, it is my impression that bull trout have the most specific habitat requirements for reproduction of any salmonid in B.C. (Baxter and McPhail 1996). In many systems, they use only a small portion of what appears to be kilometers of suitable habitat, and return to these specific areas year after year (e.g., Shepard 1985; Schill et al. 1994; Baxter 1995; Stelfox and Egan 1995). Site selection can be so specific that redd superimposition occurs in some systems, even though the size of the spawning population may be relatively small (Oliver 1979; Ratliff 1987; Baxter 1995).

Bull trout and other char, for that matter, appear to prefer areas of groundwater infiltration (Oliver 1979; Allan 1980; Shepard et al. 1984; Cunjak et al. 1986; Fraley and Shepard 1989). There is also anecdotal evidence that spawning areas may have slightly higher water temperatures during the winter months (Ted Euchner, Ministry of Environment, Lands and Parks, Fort St. John, British Columbia, pers. comm.); however, there has been no documentation that bull trout actually spawn in groundwater areas. For Arctic char (*S. alpinus*) and brook trout (*S. fontinalis*) upwelling groundwater has been linked to spawning site selection (Cunjak et al. 1986; Curry and Noakes 1995; Curry et al. 1995), and this relationship should be more closely examined for bull trout populations (Baxter and McPhail 1996).

Shepard (1985) lists variables such as higher order streams, stream bed composition, low channel gradients, areas with overhanging bank cover, maximum stream temperatures of less than 18°C, and areas of groundwater upwelling as important factors for bull trout spawning sites. Graham et al. (1981) found that a combination of stream order, channel gradient and percent of gravel and cobble substrate was significantly correlated with bull trout redd density in the upper

Flathead River Basin, Montana. They suggested that to minimize impacts on fisheries, land managers include data on bull trout spawning habitat in their long-term planning.

Because so little is known about bull trout spawning habitat, the overall objective of this component of my thesis was to describe the habitat used by bull trout during spawning, and to specifically investigate redd site selection. I hypothesized that if bull trout were keying to areas of groundwater discharge, then by selecting these areas females were increasing their reproductive success. To test these hypotheses, I measured egg to alevin (eggs hatched, but egg sac not completely absorbed) survival in areas that were used by spawners and in adjacent areas that were not used. Groundwater discharge measurements were also taken to determine if spawners were utilizing groundwater discharge sites.

MATERIALS AND METHODS

I. DATA COLLECTION

Redd Surveys

Bull trout redds were identified either through visual observation from the stream bank or from the air during aerial redd surveys in 1994 and 1995. Redds were easily identified visually as areas of recently disturbed gravel (e.g., Figure 19), and such sites were marked for subsequent microhabitat analysis. The following microhabitat features were measured at redd sites:

- a) water depth at head of redd pit (cm);
- b) nose velocity at 12 cm above (Bustard and Royea 1995) the substrate at the upstream end of the redd pit and mound ($\text{m}\cdot\text{sec}^{-1}$);
- c) 60 % water column velocity ($\text{m}\cdot\text{sec}^{-1}$);
- d) length of redd (pit and mound, greatest distance in m);
- e) width of redd (pit and mound, greatest distance in m);
- f) b-axis diameter (intermediate axis) of 30 transect sampled substrate pieces from the mound of each redd (mm);
- g) distance to nearest cover (m);
- h) cover type (by visual observation using the definitions given in Table 16).

For all redds sampled, summary statistics were calculated for each microhabitat variable.

Egg to Alevin Survival Studies

The methodology used in this experiment was to identify redd sites selected by spawning bull trout, and identify sites with qualitatively similar habitat attributes but that were not used for spawning. Once these sites were identified, a pair of bull trout were artificially spawned, and the newly fertilized eggs placed into capsules and buried in a redd and in an adjacent unused site. Temperature recorders were also placed into the substrate at both sites. The egg capsules were retrieved in early spring before ice breakup, and egg to alevin survival was assessed at the different sites.



Figure 19. Photographs showing bull trout (*Salvelinus confluentus*) redds from the air.

Table 16. Cover types associated with bull trout (*Salvelinus confluentus*) spawning redds in the Chowade River.

Code	Cover Type
1	Open pool
2	Surface turbulence
3	Undercut bank
4	Log jam
5	Large organic debris >1 m
6	Pocket water
7	Boulder

Site Selection and Microhabitat Measurement

During the bull trout spawning period in 1995, redd sites were identified through visual air and ground surveys. Once these sites were located, I chose bull trout selected sites amongst a concentration of bull trout redds, and the non-selected sites from habitat about 100-150 meters upstream of the selected sites. Both sets of sites had qualitatively similar habitat characteristics but, to assess whether or not the two areas had similar microhabitat characteristics to those described at actual redd sites, I measured (30 times at each site) the microhabitat variables of water depth (cm), 60 % velocity ($\text{m}\cdot\text{sec}^{-1}$), and substrate diameter (mm).

Spawning Procedure, Egg Capsule Placement, and Temperature Measurements

A single pair of mature bull trout (one male, one female) were captured with a tangle net on September 12, 1995, and held in flow through fish tubes. The male was 475 mm in fork length, and the female was 640 mm in fork length. After holding the fish for a short time, the female was anesthetized with MS-222. Once the female was fully anesthetized to stage V (loss of buoyancy, operculum movement slow and irregular, no response to external stimuli), she was lifted from the anesthetic bath, her vent and belly region wiped dry with paper towels, and the eggs were sprayed into a clean dry plastic bucket. The male was then removed from the fish tube, his ventral region wiped dry, and his milt mixed with the eggs. Both fish were then replaced into the fish tubes to recover. The eggs and sperm were then mixed gently using a dry hand. After 5 minutes water was added to the eggs, and they were left to water harden for 15 minutes.

Thirty eggs were placed into each of 50 capsules filled with gravel. Then the capsules were randomly allocated to redd sites and non-redd sites (25 in each category). Egg capsules used for this experiment were copied from a design by Cope (1996) and consisted of stainless steel cylinders 12 cm in length, with 2.3 mm diameter holes set at 2.0 mm centres. The ends were covered with orange test caps with drilled holes in them. To aid in retrieval, wire was run out of the top of the capsule. At each site capsules were buried at 10, 20, and 30 cm depths. Sites were marked with rebar and flagging tape, and the capsules left in the river over the winter. To estimate fertilization success, 41 eggs were preserved in Stockard's solution, and transported back to the laboratory.

At each site a ONSETTM digital temperature recorder was placed in the substrate with the capsules at a depth of 15 cm. These recorders measured water temperature every 48 minutes, for a total of 30 temperature measurements each day.

Capsule Retrieval

The egg capsules were retrieved from the river on March 23, 1996. At this time most of the river was still frozen, except for the area in which spawning was concentrated. Capsules at each site were pulled from the substrate, and the number of alevins counted in each capsule. For length analysis, a sub-sample of alevins (n~30) were taken from each depth at each site and preserved in 10 % formalin.

Alevin Length Measurement and Estimation of Fertilization Success

Total lengths of alevins (tip of snout to posterior end of caudal fin) were measured at the U.B.C. Fish Museum using digital vernier calipers accurate to 0.01 mm. Fertilization success of the field crosses was estimated by viewing the eggs through a dissecting scope at 20 times magnification. Fertile eggs were identified by the presence of the blastodisc (Gould 1987).

Groundwater Measurements

On September 18, 1996 I returned to the capsule sites and measured groundwater discharge. These measurements were taken to test the hypothesis that bull trout spawners were selecting areas of groundwater discharge. Similar to the previous year, bull trout were again spawning at the redd selected sites, and not spawning at the non-selected sites. Again, there was no qualitative difference in available spawning habitat between the two sites.

The test for groundwater as the key factor distinguishing the two sites in terms of reproductive habitat quality involved the use of a mini-piezometer (Lee and Cherry 1978). Mini-piezometers are used to measure the hydraulic head in geologic materials that are saturated under positive pressure (Lee and Cherry 1978; Freeze and Cherry 1979). The piezometer used for this study was constructed from clear polyethylene tubing (5.0 mm outside diameter, and 3.5 mm internal diameter (ID)) cut to a length of 1.30 m. The sampling end was slotted, and covered with

0.5 mm screening secured with electricians tape. Installation of the mini-piezometers followed the procedure of Lee and Cherry (1978). The mini-piezometers were placed in the substrate at sites in bull trout selected areas, and at non-selected sites. A 17 mm ID steel pipe with 14 mm lag bolts was pounded into the substrate with a sledgehammer. The piezometer tube was then inserted down the steel pipe, and held in place while the steel pipe was removed. The water level in the piezometer tube showed the head differential with respect to the water surface. If the head level was above the level of the surface water this suggested groundwater discharge (upwelling), while a head level below the level of the waters surface suggested recharge (downwelling).

At each site specific discharge (v , in $\text{cm}\cdot\text{s}^{-1}$) of the groundwater was estimated using Darcy's formula:

$$v = K \times dh/dl$$

where K is the hydraulic conductivity ($\text{cm}\cdot\text{s}^{-1}$), dh is the hydraulic head differential (cm), and dl is the elevation head differential (cm) (Curry and Noakes 1995). The hydraulic head differential was measured as the difference between the hydraulic heads of the groundwater and the surface water. This measurement was made with a meter stick, or a combination of a meter stick and manometer, if the difference between the heads was minimal. The elevation head differential was measured as the depth of the piezometer within the substrate. I attempted to calculate hydraulic conductivity using the falling head test (Lee and Cherry 1978), but because of the high permeability of the substrate this method did not work. Therefore, K was estimated, based on the average substrate size at the two sampling sites, from a table provided by Freeze and Cherry (1979).

II. DATA ANALYSIS

Microhabitat was compared between the selected and non-selected sites (i.e., the sites where the egg survival studies were carried out) using a two sample t-test. Differences in mean alevin survival, and mean alevin length at depth in each site were compared using a parametric one way analysis of variance (ANOVA), or Kruskal-Wallis one way ANOVA if the assumptions of the parametric test were not met. If there were no differences in mean alevin survival and mean

alevin length at the different depths at each site, data from each depth were pooled and differences in mean alevin survival and mean alevin length were compared between selected and non-selected sites using a two sample t-test. Statistical significance for all tests was assessed at $\alpha=0.05$. Summary statistics were also calculated for survival and alevin length at all depths in both sites.

Temperature data were analyzed by calculating the mean temperature for each day, and summing cumulative temperature units (CTU) from the daily temperatures over the incubation period following the procedure of Leitritz and Lewis (1976). The mean temperature during the incubation period was also compared using a two sample t-test with statistical significance assessed at $\alpha=0.05$.

Differences in specific discharge between sites in the selected and non-selected areas were compared using a two sample t-test with statistical significance assessed at $\alpha=0.05$.

RESULTS

Redd Surveys

Microhabitat measurements were made at 15 redd sites in 1994, and 39 redd sites in 1995. In both years, most of the redd sites were concentrated in specific areas, and there was a high degree of redd superimposition. The 1994, redd surveys were incomplete (because of the inexperience of the surveyors and short time available for the survey). On average, redds were 1.61 m long by 1.18 m wide, and water depth averaged 96.6 cm (Table 17). Nose velocity at redd sites averaged $0.39 \text{ m}\cdot\text{sec}^{-1}$, and redds were located close (5.4 m) to logjam cover (Table 17). Substrate at redd sites in 1994 consisted primarily of large gravel with a mean b-axis diameter of 34.2 mm (Table 17).

In 1995, mean water depth at the redd sites was 56.5 cm, and redds averaged 2.53 m long by 1.25 m wide (Table 18). Nose velocity averaged $0.35 \text{ m}\cdot\text{sec}^{-1}$ at the redd sites, while mean 60 % column velocity was $0.45 \text{ m}\cdot\text{sec}^{-1}$ (Table 18). Most redds were located fairly close to cover (average of 3.87 m), primarily in the form of undercut banks (Table 18). Substrate at the redd sites consisted, on average, of large gravel with a mean b-axis diameter of 39 mm (Table 18).

Egg to Alevin Survival Studies

Although there were significant differences in water depth ($t=2.29$, $df=58$, $P=0.03$) and 60 % water velocity ($t=9.78$, $df=58$, $P<0.0001$), but not in substrate diameter ($t=-1.26$, $df=58$, $P=0.21$), between the sites selected for the egg survival studies (Table 19), microhabitat measurements at both locations were similar to those measured at actual redd sites (Table 18). This suggests that there were no qualitative differences between the redd sites, and my experimental locations. Fertilization success from my experimental cross was estimated at 100 % (i.e., all of the 41 eggs examined had a prominent blastodisc).

All the retrieved capsules had alevins, but some capsules at the redd sites were lost, presumably, because of ice movements. The retrieved alevins were not feeding and still had a large yolk sac. These alevins were most probably at least 30 days away from absorbing their yolk

Table 17. Summary of microhabitat measurements at bull trout (*Salvelinus confluentus*) redd sites in the Chowade River in 1994.

	Length (m)	Width (m)	Water Depth (cm)	Nose Velocity (m·sec ⁻¹)	60% Velocity (m·sec ⁻¹)	Substrate (mm)	Distance to Cover (m)	Cover Type ¹
Mean	1.61	1.18	96.6	0.39	N/A	34.2	5.4	3
Range	0.5-2.50	0.6-2.00	55-150	0.22-0.61	N/A	1-185	3.7-7.0	1-5
SE	30.7	18.9	7.3	0.04	N/A	1.9	0.6	N/A
n	7	7	15	12	N/A	215 (7 redds)	6	6

¹ - See Table 16 for cover classification

Table 18. Summary of microhabitat measurements at bull trout (*Salvelinus confluentus*) redd sites in the Chowade River in 1995.

	Length (m)	Width (m)	Water Depth (cm)	Nose Velocity (m·sec ⁻¹)	60% Velocity (m·sec ⁻¹)	Substrate (mm)	Distance to Cover (m)	Cover Type ¹
Mean	2.53	1.25	56.5	0.35	0.45	39	3.87	3
Range	1.0-4.75	0.3-2.45	28-93	0.07-0.58	0.05-0.70	2-174	0-16	1-5
SE	0.14	0.07	2.3	0.02	0.03	0.73	0.61	N/A
n	39	39	39	39	39	900 (30 redds)	39	39

¹ - See Table 16 for cover classification

Table 19. Summary of mean (\pm SE) microhabitat characteristics at bull trout (*Salvelinus confluentus*) selected redd sites and non-selected sites used for the egg to alevin survival studies (*=statistical significance between sites, $P \leq 0.05$).

	Selected Sites	Non-selected Sites
Depth (cm)	45.4 (± 2.2)*	39.4 (± 1.4)*
60% Velocity ($\text{m} \cdot \text{sec}^{-1}$)	0.58 (± 0.02)*	0.33 (± 0.02)*
Substrate (mm)	35.6 (± 3.6)	44.1 (± 5.7)
Distance to Cover (m)	3.5	5
Cover Type ¹	3	1

¹- See Table 16 for cover classification

(Clyde Murray, Department of Fisheries and Oceans, Nanaimo, British Columbia, pers. comm.). There were no significant differences in mean alevin length at different depths at either the non-selected sites ($H=5.18$, $df=2$, $P=0.08$) or at the selected sites ($H=1.53$, $df=2$, $P=0.22$). Mean alevin length was not significantly different ($t=0.295$, $df=123$, $P=0.77$) between areas (Table 20). There were no significant differences in mean alevin survival at different depths at the non-selected sites ($F=0.486$, $df=2$, $P=0.62$) or at the selected sites ($F=1.82$, $df=2$, $P=0.21$), but there was a significant difference in mean alevin survival between sites ($t=-2.29$, $df=35$, $P=0.028$) (Table 21). The range in mean alevin survival was much greater at the non-selected sites (16.7-100 %) than at the selected sites (80-100 %) (Table 21).

The cumulative water temperature profiles between the non-selected and the selected sites were different (Figure 20): the selected sites had consistently higher temperatures than the non-selected sites. Overall the eggs at the selected sites were subject to more CTU's than the eggs at the non-selected site. Thus, there was a significant difference in mean water temperature between the areas over the incubation period (t-test, $P<0.03$) (Table 22).

At the sites within the spawning area, I measured both groundwater discharge and recharge. The sites within the non-selected area, however, were on average locations of surface water recharge (mean= $-35.43 \text{ cm}\cdot\text{s}^{-1}$, $SE=7.93$, $n=9$), while the sites within the selected area were areas of groundwater discharge (mean= $4.35 \text{ cm}\cdot\text{s}^{-1}$, $SE=5.20$, $n=15$). Overall there was a significant difference in groundwater discharge between the two sites ($t=4.38$, $df=22$, $P=0.0002$). In general, sites that were selected for spawning were areas of groundwater discharge (upwelling), while areas that were not selected for spawning were areas of surface water recharge (downwelling).

Table 20. Summary of mean alevin length at bull trout (*Salvelinus confluentus*) selected sites and non-selected sites (*=statistical significance between sites, $P \leq 0.05$).

	Selected Sites	Non-selected Sites
Mean total length (mm)	22.29	22.33
SE	0.06	0.09
Range	20.87-23.17	19.09-23.45
n	51	74

Table 21. Summary of mean alevin survival at bull trout (*Salvelinus confluentus*) selected sites and non-selected sites (*=statistical significance between sites, $P \leq 0.05$).

	Selected Sites	Non-selected Sites
Mean alevin survival (%)	88.6*	76.1*
SE	1.9	3.6
Range	80-100	16.7-100

Table 22. Summary of mean incubation temperature at bull trout (*Salvelinus confluentus*) selected sites and non-selected sites (*=statistical significance between sites, $P \leq 0.05$).

	Selected Sites	Non-selected Sites
Mean incubation temperature (°C)	1.92*	1.83*
SE	0.01	0.01
Range	0.6-6.43	0.6-6.12

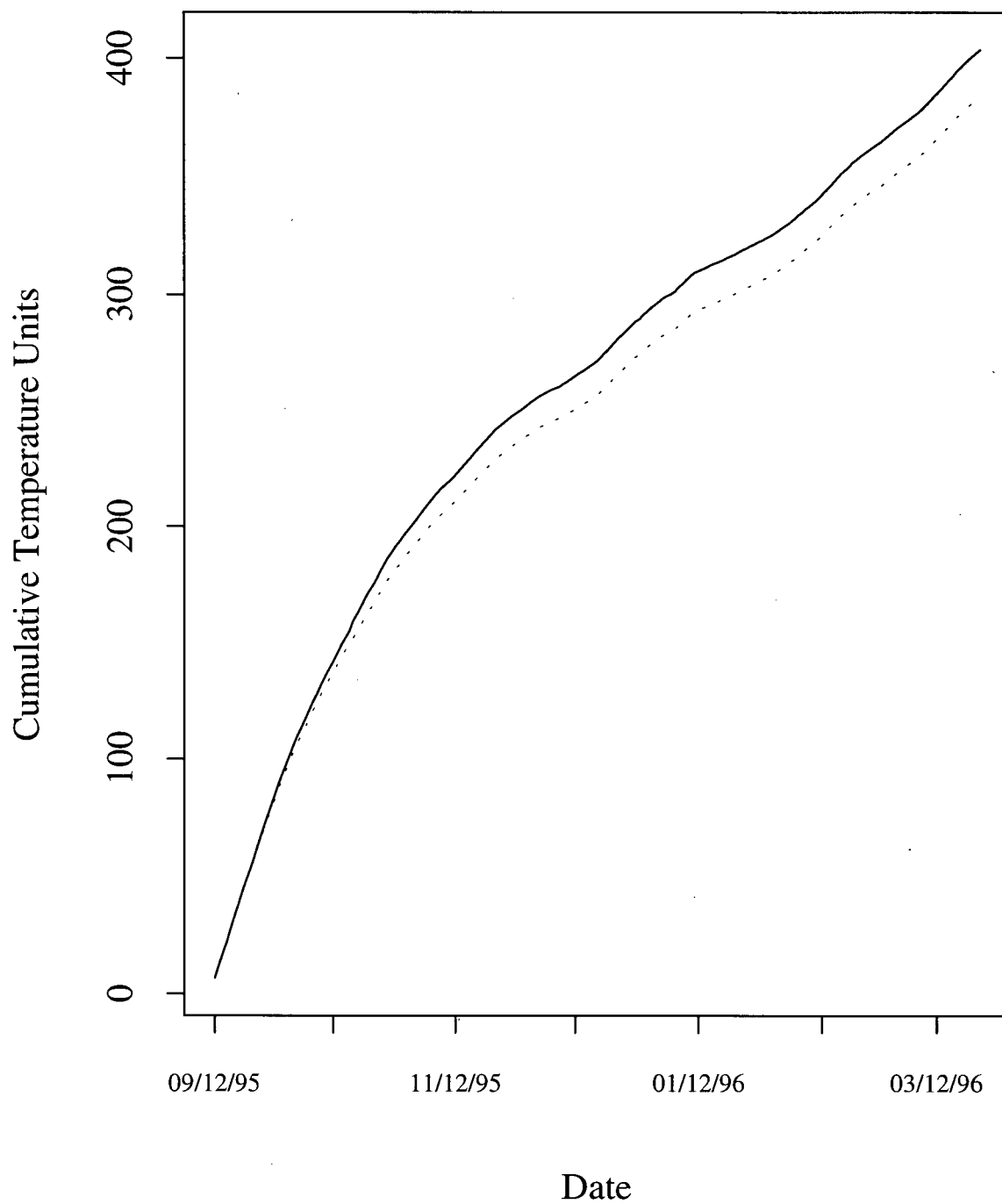


Figure 20. Cumulative temperature unit profile at egg incubation sites (solid line is profile of bull trout selected redd sites, dashed line is profile of adjacent non-selected sites).

DISCUSSION

Over the three years of study in the Chowade River, bull trout have been highly specific in the area of the upper river that they use for spawning. Site selection for spawning has been so specific that redd superimposition was common in 1995 and 1996. Despite the apparent abundance of suitable habitat throughout this 70 km long river, most spawning is concentrated in a stretch of less than 500 m. Microhabitat characteristics at bull trout redd sites in the Chowade River system were similar to those reported in other watersheds. Goetz (1989) gave extensive data on microhabitat characteristics at bull trout redd sites for several populations. Reported mean depth over redds ranged from 0.28 m in the Flathead River in Montana to 0.77 m in Meadow Creek in British Columbia. Mean velocity over redds ranged from 0.29 m·sec⁻¹ in the Flathead to 0.60 m·sec⁻¹ in Mackenzie Creek, British Columbia. Predominant substrate materials at redd sites were small and large gravel, followed by cobble.

Perhaps a better comparison for the Chowade River redd sites are the redd measurements made in the Kemess Creek watershed (also in the Peace River system) by Bustard and Royea (1995). This system is at a latitude comparable to the Chowade River, and has similar spawning timing. Bustard and Royea (1995) report the mean nose velocity at redd sites as 0.39 m·sec⁻¹, the mean depth of redds as 0.31 m, and a mean distance to cover as 5.4 m. They also report the mean diameter of spawning substrates as averaging between 2-4 cm. These results are consistent with the Chowade River data, and suggest that my measurements of bull trout spawning habitat use are typical for this region.

Apparently suitable spawning habitat, upstream and downstream of the redd sites, were not used by bull trout. These observations imply that spawning habitat may be limited, and that spawners are keying in on characteristics such as groundwater upwelling that enhance egg survival. The extreme site specificity in this region of the stream also suggests that such site selection is critical to an individual's (i.e., female) reproductive success.

My data support the hypothesis that bull trout actively key in on specific areas of groundwater influx in the Chowade River and that this increases egg to alevin survival. Certainly,

on average, bull trout spawn in areas of groundwater discharge. There is, however, some variability. Previously, ground water infiltration has been suggested as an important component in bull trout spawning site selection (Allan 1980; Shepard et al. 1984; Fraley and Shepard 1989); however, there are no reported data on actual groundwater measurements. Both brook trout (*Salvelinus fontinalis*) and Arctic char (*S. alpinus*) are known to prefer areas of groundwater discharge for spawning (Cunjak et al. 1986; Curry and Noakes 1995), and this may be a general phenomena for *Salvelinus*. Curry and Noakes (1995) suggest that brook trout use gradients created by discharging groundwater to home to spawning areas, but not for redd site selection. Although I have no contrary data for bull trout, in the Chowade River my observations suggest groundwater is used in site selection of redds. Spawning sites were strongly associated with groundwater discharge, while adjacent areas with similar microhabitat characteristics, but no influx of groundwater, were not used for spawning.

Other evidence also points to groundwater discharge as important for bull trout spawning areas. In the forest area surrounding the mainstem location with the highest redd densities I observed an upwelling spring, and in the winter when the egg capsules were pulled, the locations where bull trout had spawned were the only ice free areas on the river. These observations also suggest groundwater discharge, and coupled with the measured higher over winter temperatures and specific discharge measurements, conclusively show that the spawning area is influenced by groundwater (R. Beckie, Department of Geology, University of British Columbia, Vancouver, British Columbia, pers. comm.).

The Chowade River is a relatively long stream (about 70 km), and given the amount of apparently suitable spawning habitat, there appears to be too few spawners. However, it has been suggested that areas not used in any spawning system, even though they may appear suitable, probably have poor conditions for eggs and alevins (Hunter 1959). My experimental data support this contention. Although an average of 76 % of the eggs still survived to collection in the non-selected sites, the lowest survival of alevins was found in these areas. There were also significant differences in egg to alevin survival between the selected and non-selected sites. Over time, such differences in egg to alevin survival would select for site selective females. Cope (1996) suggested that incubation survival is influenced by two main factors; 1) how adults choose

incubation sites and, 2) the environment within those sites. The physical and biological data that I have collected in the Chowade River strongly suggest that bull trout select high quality incubation sites.

Temperature has been identified as a major physical factor that influences incubation success of salmonids (Velson 1987; Beacham and Murray 1990; Cope 1996) and, in general, interior populations of *Oncorhynchus* have faster development rates at colder temperatures than coastal populations (Brannon 1987; Beacham and Murray 1989). McPhail and Murray (1979) found that bull trout eggs from an interior population showed an increase in survival as incubation temperature decreased from 10°C, and a slight decrease in survival if temperatures dropped below 4°C. Colder temperatures also slowed embryonic development, but produced larger fry. They suggested that the embryonic development rates of char species are less retarded by low temperatures than those in other salmonids. Groundwater upwelling sites typically have warmer, more stable winter temperatures (Leman 1993), and the temperature data and physical lack of ice at redd sites suggests that this is also true in the Chowade River.

Cumulative temperature units (CTU's) are a way of measuring the temperature regime of incubating eggs, and provide a mechanism for estimating time to hatching (Leitritz and Lewis 1978). Eggs incubated in the bull trout selected redd environment were exposed to warmer temperatures throughout the incubation period than the eggs at the non-selected sites. Incubation in this type of environment might provide a number of developmental advantages. The primary advantage to eggs incubated at a warmer more constant water temperature would be a more stable rearing environment, and protection from potential freezing. Although both sites did reach temperatures close to 0°C, eggs in the non-selected area were exposed to temperatures closer to freezing, and for longer periods of time, than eggs in the selected area. The lower egg to alevin survival at the non-selected sites, may be a result of these lower temperatures. For brook trout, Curry et al. (1995) demonstrated that the lowest egg to fry survival was found at sites with the lowest sampled water temperatures and specific discharge (upwelling).

A second advantage for eggs incubated at warmer temperatures is their shorter hatching time and, thus, earlier date of emergence from the gravel than fry incubated at cooler

temperatures. The timing of fry emergence from the gravel may be extremely important for the survival of individuals within salmonid populations (Elliott 1989; Noakes 1989; Curry et al. 1995). The primary advantage is that fry that emerge early have the first chance to colonize refuge habitats, and begin external feeding, than fry incubated at cooler temperatures. The possibility also exists that a later time of emergence would be of disadvantage in that optimal rearing habitats might also be occupied, or emergence might occur at the beginning of spring freshet. The Chowade River is an extremely harsh environment during freshet, and fry that might emerge at this period would be washed downstream away from productive rearing areas in the upper river (Baxter 1995).

Given the lower survival of eggs incubated in sites that were not selected for spawning, and the fact that spawning site selection is limited to specific areas where a high degree of redd superimposition occurs, one aspect of the reproductive process in bull trout that was not addressed was the competition for redd sites among females, and the timing of spawning. In studies on sockeye salmon (*O. nerka*) spawning in northern environments, Cope (1996) found that earlier spawnings were more successful than late spawnings. He argues that this is because the embryos of earlier spawning fish hatch before freeze up and, thus, are able to move within the gravel and avoid freezing. For bull trout in the Chowade River this relationship between early and late spawners may be confounded by the high degree of redd superimposition that occurs. Early spawning females have a higher probability of their eggs being dug up than late spawning females, but still would give their eggs a thermal "head start" on development and emergence than late spawning females. This potential trade-off between early and late spawning females, and how this may affect fry recruitment, deserves further study.

One physical characteristic that I did not measure at redd sites, but that influences incubation success, is dissolved oxygen levels (Sowden and Power 1985; Curry et al 1995). In retrospect, I should have measured dissolved oxygen in the gravel at redd sites and adjacent non-selected sites. This measurement should be included in future studies of bull trout spawning areas. The high permeability of substrates in which bull trout spawn, however, suggests that intra-gravel dissolved oxygen levels would be high, and supply adequate amounts of water and dissolved oxygen to developing eggs.

My experiment supports the hypothesis that there is a significant relationship between spawning site selection by female bull trout and reproductive success. Areas other than those used for spawning may indicate low quality habitat. The small area in which these bull trout spawn within the Chowade River also brings up the question of adequate habitat protection to ensure population viability. Of all the Rocky Mountain Foothills streams that contribute bull trout to the Peace River population below the Peace Canyon Dam, the Chowade River accounts for most of the production (Baxter 1997a, 1997b, personal observations). This is based on my personal observations within the entire Foothills watershed, along with data we have gathered on population structure through out the region. If this is true, then to maintain the bull trout population in the region, it is essential to locate and protect these small areas of critical habitat. Resource extraction activities in these areas should be closely managed, if not restricted, to ensure spawning success.

CHAPTER 4 - CONCLUSIONS

SUMMARY AND AREAS FOR FUTURE RESEARCH

The studies undertaken in my thesis have clearly shown that, as in other animal mating systems, there has been the development of alternative mating strategies by individuals within the male bull trout population. I focused on studying the mechanisms (reduced sexual colouration and characteristics) that enable sneaker males to get within close proximity to a redd site to allow successful fertilizations. One aspect that I did not focus on, but which should be a priority for future research, is determining what percentage of fertilizations sneakers obtain through using this strategy, and whether or not they have an advantage at redd sites when the operational sex ratio is biased towards males. Such a study would clarify the selective forces that cause divergence in male strategies, and would also provide a field system to study the theory of negative frequency-dependent selection, and determine if it actually occurs (Gross 1991).

Another promising area for comparison of the two types of males is sperm competition. In Atlantic salmon (*Salmo salar*), small mature parr have different sperm characteristics (motility and period of viability) than large dominant males. This may explain how small sneaker males maintain their reproductive success even though they are at a competitive disadvantage relative to other males (Gage et al. 1995). This may also be the case in bull trout.

What exactly controls aggressive and territorial behaviour in bull trout males is unknown, but in other fish these types of behaviours have been linked to differences in androgen levels. Cardwell and Liley (1991) found that in the stoplight parrotfish (*Sparisoma viride*), non territorial males had lower levels of the androgens 11-ketotestosterone and testosterone than dominant males. Possibly examining these types of mechanisms might prove interesting in studying male behaviour in bull trout.

A continuation of the general population studies in the Chowade River will also benefit future study. Although ageing from scales suggested that males adopting the two different strategies follow different growth patterns, it is not known whether small males that are sneakers may grow into dominant males eventually through an ontogenetic shift in their growth pattern. I

suspect this is not the case, but monitoring the population, and continuing the tagging program, will enable these questions to be addressed. It will also provide information critical to proper management. Growth pattern differences between the types, and growth rates for individuals, could also be examined, and to date this type of information has not been reported in other studies. The Chowade River program could provide the major source of information on bull trout in relatively undisturbed systems.

In northern latitudes, bull trout spawn in unstable environments, and ensuring the survival of incubating eggs is critical to an individual female's reproductive success. This thesis has presented data that confirms bull trout in the Chowade River tend to spawn in areas of groundwater upwelling, and that these sites offer incubation environments that increase incubation success. In retrospect, this was a fairly general study: future research should focus on more detailed examinations of the relationship between water temperature and incubation success, and the selection of groundwater incubation sites. Looking at other variables such as dissolved oxygen levels within redd sites may also prove valuable.

Finally, I want to stress how small the spawning area is relative to the length of the river. A superficial study of the Chowade, and probably other rivers, would suggest ample spawning habitat is available. This would be a disastrous error. The only reliable way to identify spawning sites, is by finding spawning fish. Thus, as forestry activity increases in this region, it will be necessary to locate, and protect, spawning sites in other systems.

REFERENCES

- Allan, J.H. 1980. Life history notes on the Dolly Varden charr (*Salvelinus malma*) in the upper Clearwater River, Alberta. Alberta Energy and Natural Resources, Fish and Wildlife Division, Calgary, Alberta, 59 pp.
- Anderson, W.G., McKinley, R.S., and M. Colavecchia. 1997. The use of clove oil as an alternative anesthetic for fish and its effects on swimming performance of rainbow trout, *Oncorhynchus mykiss*. N. Am. J. Fish. Man. (in press).
- Baxter, J.S. 1994a. Adult bull trout (*Salvelinus confluentus*) surveys and assessment in the Chowade River (1994). Report to B.C. Ministry of Environment, Lands and Parks (Fort St. John), Fisheries Branch, British Columbia, 12 pp.
- Baxter, J.S. 1994b. Juvenile bull trout (*Salvelinus confluentus*) assessment and inventory in the Chowade River: preliminary surveys (1994). Report to B.C. Ministry of Environment, Lands and Parks (Fort St. John), Fisheries Branch, British Columbia, 8 pp.
- Baxter, J.S. 1995. Chowade River bull trout studies 1995: habitat and population assessment. Report to B.C. Ministry of Environment, Lands and Parks (Fort St. John), Fisheries Branch, British Columbia, 108 pp.
- Baxter, J.S. 1997a. Chowade River bull trout studies (1996). Report to B.C. Ministry of Environment, Lands and Parks (Fort St. John), Fisheries Branch, British Columbia, 47 pp.
- Baxter, J.S. 1997b. Upper Halfway River overview fisheries inventory: mainstem and tributary assessment. Report to B.C. Ministry of Environment, Lands and Parks (Fort St. John), Fisheries Branch, British Columbia.
- Baxter, J.S., and J.D. McPhail. 1996. Bull trout spawning and rearing habitat requirements: summary of the literature. B.C. Fisheries Technical Circular No. 98.
- Baxter, J.S., Taylor, E.B., Devlin, R.H., Hagen, J., and J.D. McPhail. 1997. Evidence for natural hybridization between bull trout (*Salvelinus confluentus*) and Dolly Varden (*S. malma*) char in a northcentral British Columbia watershed. Can. J. Fish. Aquat. Sci. (in press).
- Beacham, T.D., and C.B. Murray. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. Can. J. Fish. Aquat. Sci. 44:244-261.
- Beacham, T.D., and C.B. Murray. 1989. Variation in developmental biology of sockeye salmon (*Oncorhynchus nerka*) and chinook salmon (*O. tshawytscha*) in British Columbia. Can. J. Zool. 67:2634-2648.

- Beacham, T.D., and C.B. Murray. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. *Trans. Amer. Fish. Soc.* 119:927-945.
- Bilton, H.T., Morley, R.B., Coburn, A.S., and J. Van Tine. 1984. The influences of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity: results of releases from Quinsam River Hatchery, B.C. in 1980. *Can. Tec. Rep. Fish. Aquat. Sci.* 1306.
- Brannon, E.L. 1987. Mechanisms stabilizing salmonid fry emergence timing. Pages 120-124 *In* H.D. Smith, L. Margolis, and C.C. Wood, editors. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Can. Spec. Publ. Fish. Aquat. Sci.* 96.
- Bustard, D., and D. Royea. 1995. Kemess South Gold-Copper Project 1994 Fisheries Studies. Report of Dave Bustard and Associates and Hallam Knight Piésold Limited to El Condor Resources Limited and St. Phillips Resources Incorporated, Vancouver, British Columbia, 400+ pp.
- Cannings, S.G. 1996. Rare freshwater fish of British Columbia. B.C. Ministry of Environment, Lands, and Parks, Fisheries Branch, Conservation Data Centre, Victoria, British Columbia.
- Cardwell, J.R., and N.R. Liley. Androgen control of social status in males of a wild population of stoplight parrotfish, *Sparisoma viride* (Scaridae). *Hormones and Behaviour* 25:1-18.
- Carl, L.M., Kraft, M., and L. Rhude. 1989. Growth and taxonomy of bull charr, *Salvelinus confluentus*, in Pinto Lake, Alberta. *Environ. Biol. Fish.* 26:239-246.
- Cattell, R.B. 1966. The scree test for the number of factors. *Multivar. Behav. Res.* 1:245-276.
- Cavender, T.M. 1978. Taxonomy and distribution of the bull trout, *Salvelinus confluentus* (Suckley), from the American Northwest. *California Fish and Game* 64(3):139-174.
- Chebanov, N.A., Varnavskaya, N.V., and V.S. Varnavskiy. 1983. Effectiveness of spawning male sockeye salmon, *Oncorhynchus nerka* (Salmonidae), of different hierarchical rank by means of genetic-biochemical markers. *J. Ichthyol.* 23:51-55.
- Clutton-Brock, T.H., Guinness, F.T.E. and S.B. Albion. 1982. *Red Deer: The Behaviour and Ecology of Two Sexes*. University of Chicago Press, Chicago, Illinois.
- Cook, D.F. 1990. Differences in the courtship, mating and postcopulatory behaviour between male morphs of the dung beetle *Onthophagus binodis* Thunberg (Coleoptera: Scarabaeidae). *Animal Behaviour* 40:428-436.

- Cope, R.S. 1996. Responses of sockeye salmon (*Oncorhynchus nerka*) embryos to intragravel incubation environments in selected streams within the Stuart-Takla watershed. M.Sc. Thesis, University of British Columbia, Vancouver, British Columbia.
- Cunjak, R.A., Power, G., and D.R. Barton. 1986. Reproductive habitat and behaviour of anadromous Arctic char (*Salvelinus alpinus*) in the Koroc River, Quebec. *Rev. Ecol. Syst.* 113:383-387.
- Curry, R.A., and D.L.G. Noakes. 1995. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). *Can. J. Fish. Aquat. Sci.* 52:1733-1740.
- Curry, R.A., Noakes, D.L.G., and G.E. Morgan. 1995. Groundwater and the emergence of brook trout (*Salvelinus fontinalis*). *Can. J. Fish. Aquat. Sci.* 52:1741-1749.
- Davies, N.B. 1991. Mating systems. Pages 263-300 *In* J.R. Krebs and N.B. Davies, editors. *Behavioural Ecology*. Blackwell Scientific Publications, Oxford.
- Devries, D.R., and R.V. Frie. 1996. Determination of age and growth. Pages 483-512 *In* B.R. Murphy and D.W. Willis, editors. *Fisheries Techniques*. American Fisheries Society, Bethesda, Maryland.
- Dominey, W.J. 1980. Female mimicry in male bluegill sunfish-a genetic polymorphism? *Nature* 284:546-548.
- Elliott, J.M. 1989. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. I. The critical time for survival. *J. Anim. Ecol.* 58:987-1001.
- Endler, J.A. 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of the Linnean Society* 41:315-352.
- Fabricus, E., and K.J. Gustafson. 1953. Further aquarium observations on the spawning behaviour of the char, *Salmo alpinus* L. *Inst. Freshwater Research, Drottningholm Report* No. 35:58-104.
- Foote, C.J. 1988. Male mate choice dependent on male size in salmon. *Behaviour* 106:63-80.
- Foote, C.J. 1989. Female mate preference in Pacific salmon. *Animal Behaviour* 38:721-723.
- Foote, C.J. 1990. An experimental comparison of male and female spawning territoriality in a Pacific salmon. *Behaviour* 115:283-314.
- Foote, C.J., and P.A. Larkin. 1988. The role of male choice in the assortative mating of anadromous and non-anadromous sockeye salmon (*Oncorhynchus nerka*). *Behaviour* 106:43-62.

- Forsyth, A., and J. Alcock. 1990. Female mimicry and resource defense polygyny by males of a tropical rove beetle, *Leistotrophus versicolour* (Coleoptera: Staphylinidae). *Behav. Ecol. Sociobiol.* 26:325-330.
- Fraley, J.J., and B.B. Shepard. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead lake and river system, Montana. *Northwest Science* 63(4):133-143.
- Freeze, R.A., and J.A. Cherry. 1979. *Groundwater*. Prentice-Hall Inc., Englewood Cliffs, New Jersey.
- Gage, M.J.G., Stockley, P., and G.A. Parker. 1995. Effects of alternative male mating strategies on characteristics of sperm production in the Atlantic salmon (*Salmo salar*): theoretical and empirical investigations. *Phil. Trans. R. Soc. Lond. B* 350:391-399.
- Goetz, F. 1989. Biology of the bull trout, *Salvelinus confluentus*, a literature review. Willamette National Forest, Eugene, Oregon, 53 pp.
- Gould, W.R. 1987. Features in the early development of bull trout (*Salvelinus confluentus*). *Northwest Science* 61:264-268.
- Grewe, P.M., Billington, N., and P.D.N. Hebert. 1990. Phylogenetic relationships among members of *Salvelinus* inferred from mitochondrial DNA divergence. *Can. J. Fish. Aquat. Sci.* 47:984-991.
- Graham, P.J., Shepard, B.B., and J.J. Fraley. 1981. Use of stream habitat classifications to identify bull trout spawning areas in streams. Pages 186-190 *In* N.B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. Symp. Am. Fish. Soc. (Western Division), Portland, Oregon.
- Gross, M.R. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fish. Pages 55-75 *In* G.W. Potts and R.J. Wootton, editors. *Fish reproduction: strategies and tactics*. Academic Press, London.
- Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. *Nature* 313:47-48.
- Gross, M.R. 1991. Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. *Phil. Trans. R. Soc. Lond. B* 332:59-66.
- Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *TREE* 11(2):92-98.
- Gross, M.R., and E.L. Charnov. 1980. Alternative male life histories in bluegill sunfish. *Proc. Natn. Acad. Sci. U.S.A.* 77:6937-6940.

- Haas, G.R. 1988. The systematics, zoogeography and evolution of Dolly Varden and bull trout in British Columbia. M.Sc. Thesis, University of British Columbia, Vancouver, British Columbia.
- Haas, G.R., and J.D. McPhail. 1991. The systematics, zoogeography and evolution of Dolly Varden (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*) in North America. Can. J. Fish. Aquat. Sci. 48:2191-2211.
- Hagen, J. 1993a. Whitetail Creek fish population assessment, habitat description and enhancement plan, 1993. Report to BC Hydro and B.C. Ministry of Environment, Lands and Parks (Nelson), Fisheries Branch, British Columbia, 17 pp.
- Hagen, J. 1993b. Status of the Dutch Creek bull trout run. Report to BC Hydro and B.C. Ministry of Environment, Lands and Parks (Nelson), Fisheries Branch, British Columbia, 10 pp.
- Hagen, J., and J.S. Baxter. 1992. Bull trout populations of the North Thompson River Basin, British Columbia: initial assessment of a biological wilderness. Report to B.C. Ministry of Environment, Lands and Parks (Kamloops), Fisheries Branch, British Columbia, 37 pp.
- Harvey, P.H. 1982. On rethinking allometry. J. theoret. Biol. 95:37-31.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scand. J. Stat. 6:65-60.
- Hunter, J.G. 1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Bd. Canada 16:835-886.
- Hutchings, J.A. 1994. Age- and size-specific costs of reproduction within populations of brook trout, *Salvelinus fontinalis*. OIKOS 70:12-20.
- Hutchings, J.A., and R.A. Myers. 1987. Escalation of an asymmetric contest: mortality resulting from mate competition in Atlantic salmon, *Salmo salar*. Can. J. Zool. 65:766-768.
- Hutchings, J.A., and R.A. Myers. 1988. Mating success of alternative maturation phenotypes in male Atlantic salmon, *Salmo salar*. Oecologia 75:169-174.
- James, P.W., and H.M. Sexauer. 1997. Spawning behaviour, spawning habitat and alternative mating strategies in an adfluvial population of bull trout. Proceedings of the Friends of the Bull Trout conference, Calgary, Alberta, (in press).
- Jones, J.W. 1959. *The Salmon*. Harper and Row, New York, New York.
- Jones, B., and P. Michiel. 1996. Last stand of the big char. BC Outdoors, April:71-75.
- Jonsson, B., and K. Hindar. 1982. Reproductive strategy of dwarf and normal arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, western Norway. Can. J. Fish. Aquat. Sci. 39:1404-1413.

- Katano, O. 1990. Dynamic relationships between the dominance of male dark chub, *Zacco temminckii*, and their acquisition of females. *Animal Behaviour* 40:1018-1034.
- Keenleyside, M.H.A., and H.M.C. Dupuis. 1988. Courtship and spawning competition in pink salmon (*Oncorhynchus gorbuscha*). *Can. J. Zool.* 66:262-265.
- Kitano, S., Maekawa, K., Nakano, S., and K.D. Fausch. 1994. Spawning behaviour of bull trout in the upper Flathead drainage, Montana, with special reference to hybridization with brook trout. *Trans. Am. Fish. Soc.* 123:988-992.
- Lee, D.R., and J.A. Cherry. 1978. A field exercise on groundwater flow using seepage meters and mini-piezometers. *J. Geol. Ed.* 27:6-10.
- Leggett, J.W. 1969. The reproductive biology of the Dolly Varden char *Salvelinus malma* Walbaum. M.Sc. Thesis, University of Victoria, Victoria, British Columbia.
- Leggett, J.W. 1980. Reproductive ecology and behaviour of Dolly Varden charr in British Columbia. Pages 721-737 *In* E. K. Balon, editor. *Charrs, salmonid fishes of the genus Salvelinus*. W. Junk, The Hague.
- Leitritz, E., and R.C. Lewis. 1976. Trout and salmon culture. *Calif. Dept. Fish Game, Fish. Bull.* 164.
- Leman, V.N. 1993. Spawning sites of chum salmon *Oncorhynchus keta*: microhydrological regime and variability of progeny in redds (Kamchatka River Basin). *J. Ichthy.* 33:104-117.
- MacLellan, S.E. 1987. *Guide for sampling structures used in age determination of Pacific salmon*. Department of Fisheries and Oceans, Nanaimo, British Columbia.
- Maekawa, K., and H. Onozato. 1986. Reproductive tactics and fertilization success of mature male miyabe charr, *Salvelinus malma miyabei*. *Environ. Biol. Fish.* 15:119-129.
- Maekawa, K., Kitano, S., and S. Takeyama. 1993. Type-assortative mating of miyabe charr. *Japanese Journal of Ichthyology* 39:401-403.
- Maekawa, K., Hino, T., Nakano, S., and W.W. Smoker. 1993. Mate preference in anadromous and landlocked Dolly Varden (*Salvelinus malma*) females in two Alaskan streams. *Can. J. Fish. Aquat. Sci.* 50:2375-2379.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge University Press, Cambridge.
- McPhail, J.D., and C.B. Murray. 1979. The early life history and ecology of Dolly Varden (*Salvelinus malma*) in the upper Arrow Lakes. Report of the Institute of Animal Resource Ecology and Department of Zoology (University of British Columbia) to BC Hydro and Ministry of Environment, Victoria, British Columbia.

- McPhail, J.D., and E.B. Taylor. 1995. The Skagit char project. Report prepared for the Skagit Environmental Endowment Commission, 39 pp.
- McPhail, J.D., and J.S. Baxter. 1996. A review of bull trout (*Salvelinus confluentus*) life history and habitat use in relation to compensation and improvement opportunities. B.C. Fisheries Management Report No. 104.
- Meidinger, D., and J. Pojar. 1991. *Ecosystems of British Columbia*. Ministry of Forests, Victoria, British Columbia.
- Morán, P., Pendás, A.M., Beall, E., and E. García-Vázquez. Genetic assessment of the reproductive success of Atlantic salmon precocious parr by means of VNTR loci. *Heredity* 77:655-660.
- Morris, D. 1952. Homosexuality in the ten-spined stickleback (*Pygosteus pungitius* L.). *Behaviour* 4:233-261.
- Noakes, D.L.G. 1989. Early life history and behaviour of charrs. *Physiol. Ecol. Jpn. (Spec. Vol.)* 1:173-186.
- Noltie, D.B. 1990. Intrapopulation variation in the breeding of male pink salmon (*Oncorhynchus gorbuscha*) from a Lake Superior tributary. *Can. J. Fish. Aquat. Sci.* 47:174-179.
- Oliver, G. 1979. A final report on the present fisheries of the Wigwam River with an emphasis on the migratory life history and spawning behaviour of Dolly Varden char *Salvelinus malma* (Walbaum). Fisheries investigations in tributaries of the Canadian portion of Libby Reservoir. British Columbia Fish and Wildlife Branch, Cranbrook, British Columbia, 82 pp.
- Phillips, R.B., and K.A. Pleyte. 1991. Nuclear DNA and salmonid phylogenetics. *J. Fish. Biol.* 39(Suppl. A):259-275.
- Pimental, R.A. 1979. *Morphometrics. The multivariate analysis of biological data*. Kendall/Hunt Co., Dubuque, Iowa.
- Pratt, K.L. 1992. A review of bull trout life history. Pages 5-9 *In* P.J. Howell and D.V. Buchanan, editors. Proceedings of the Gerhart Mountain bull trout workshop. Oregon Chapter of the American Fisheries Society, Corvallis, Oregon.
- Quinn, T.P., and C.J. Foote. 1994. The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon, *Oncorhynchus nerka*. *Animal Behaviour* 48:751-761.
- R.L. & L. Environmental Services Ltd. 1994. Fish migrations in the Chowade River, B.C. - Fall 1994. Report to B.C. Ministry of Environment, Lands and Parks (Fort St. John), Fisheries Branch, British Columbia, 34 pp.

- Ratliff, D.E. 1987. Bull trout spawning report, Metolius River tributaries 1987. Portland General Electric, Portland, Oregon.
- Ratliff, D.E., and P.J. Howell. 1992. The status of bull trout populations in Oregon. Pages 10-17 *In* P.J. Howell and D.V. Buchanan, editors. Proceedings of the Gerhart Mountain bull trout workshop. Oregon Chapter of the American Fisheries Society, Corvallis, Oregon.
- Reiman, B.E., and J.D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. General Technical Report INT-302. United States Department of Agriculture: Forest Service, Intermountain Research Station, Ogden, Utah, 37 pp.
- Reiman, B.E., and J.D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. *Trans. Am. Fish. Soc.* 124:285-297.
- Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223-225.
- S-Plus. 1995. *Guide to Statistical and Mathematical Analysis*. MathSoft Inc., Seattle.
- Saetre, G., and T. Slagsvold. 1996. The significance of female mimicry in male contests. *American Naturalist* 147(6):981-995.
- Sargent, R.C., Gross, M.R., and E.P. van den Berghe. 1986. Male mate choice in fishes. *Animal Behaviour* 34:545-550.
- Schill, D., Thurow, R., and P. Kline. 1994. Seasonal movements and spawning mortality of fluvial bull trout in Rapid River, Idaho. Job Performance Report, Project F-73-R-15, Subproject II, Study IV, Job 2. Idaho Department of Fish and Game, Boise, Idaho, 31 pp.
- Schroder, S.L. 1982. The influence of intrasexual competition on the distribution of chum salmon in an experimental stream. Pages 275-285 *In* E.L. Brannon and E.O. Salo, editors. Salmon and Trout Migratory Behaviour Symposium. University of Washington, School of Fisheries, Seattle, Washington.
- Sexauer, H. A. 1994. Life history aspects of bull trout, *Salvelinus confluentus*, in the eastern Cascades, Washington. M.Sc. Thesis, Central Washington University, Ellensburg, Washington.
- Shepard, B. 1985. Habitat variables related to bull trout spawning site selection and thermal preference exhibited in a thermal gradient. Pages 18-19 *In* D.D. MacDonald, editor. Proceedings of the Flathead River basin bull trout biology and population dynamics modelling information exchange. B.C. Ministry of Environment, Cranbrook, British Columbia.
- Shepard, B., Pratt, K., and J. Graham. 1984. Life histories of westslope cutthroat and bull trout in the upper Flathead River basin, Montana. Montana Department of Fish, Wildlife, and Parks. Kalispell, Montana, 85pp.

- Sigurjonsdottir, H., and K. Gunnarsson. 1989. Alternative mating tactics of Arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. *Environ. Biol. Fish.* 26:159-176.
- Sinervo, B., and C.M. Lively. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* 380:240-243.
- Slagsvold, T., and G. Saetre. 1991. Evolution of plumage colour in male pied flycatchers (*Ficedula hypoleuca*): evidence for female mimicry. *Evolution* 45:910-917.
- Somers, K.M. 1986. Multivariate allometry and the removal of size with principal component analysis. *Syst. Zool.* 35:359-368.
- Soto, C.G., and C.G. Burhanuddin. 1995. Clove oil as a fish anaesthetic for measuring length and weight of rabbitfish (*Siganus lineatus*). *Aquaculture* 136:149-152.
- Sowden, T.K., and G. Power. 1985. Prediction of rainbow trout embryo survival in relation to groundwater seepage and particle size of spawning substrates. *Trans. Amer. Fish. Soc.* 114:804-812.
- Strahler, A.N. 1952. Hypsometric (area-altitude) analysis of erosional topograph. *Bull. Geol. Soc. Am.* 63:1117-1142.
- Strahler, A.N. 1964. Quantitative geomorphology of drainage basins and channel networks. Section 4-2 *In* Ven te Chow, editor. *Handbook of Applied Hydrology*. McGraw Hill, New York, New York.
- Stelfox, J.D., and K.L. Egan. 1995. Bull trout investigations in the Smith-Dorrien Creek/Lower Kananaskis Lake system. Alberta Environmental Protection, natural Resources Service, Fisheries Management Division, Calgary, Alberta, 148 pp.
- Turner, G.F. 1993. Teleost mating behaviour. Pages 307-331 *In* T.J. Pitcher, editor. *Behaviour of teleost fishes*. Chapman and Hall, New York, New York.
- van den Berghe, E.P., Wernerus, F., and R.R. Warner. 1989. Female choice and the mating cost of peripheral males. *Animal Behaviour* 38:875-884.
- Velson, F.P.J. 1987. Temperature and incubation in Pacific salmon and rainbow trout: compilation of data on median hatching time, mortality and embryonic staging. *Can. Data Rep. Fish. Aquat. Sci.* 626.
- Williams, J.E., Johnson, J.E., Hendrickson, D.A., Contreras-Balderas, S., Williams, J.D., Navarro-Mendoza, M., McAllister, D.E. and J.E. Deacon. 1989. Fishes of North America endangered, threatened or of special concern:1989. *Fisheries* 14(6):2-20.

Wootton. 1984. Introduction: strategies and tactics in fish reproduction. Pages 1-12 *In* G.W. Potts and R.J. Wootton, editors. Fish reproduction: strategies and tactics. Academic Press, London.