# THE FEEDING HABITS OF ANADROMOUS ARCTIC CHAR, (*SALVELINUS ALPINUS* L.) IN FROBISHER BAY, BAFFIN ISLAND IN THE EASTERN CANADIAN ARCTIC: DIET, PARASITES AND STABLE ISOTOPES.

BY

IKECHUKWU COLLINS ISINGUZO

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

DEPARTMENT OF BIOLOGICAL SCIENCES (ZOOLOGY)
UNIVERSITY OF MANITOBA
WINNIPEG, MANITOBA

COPYRIGHT © 2009

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

*****

COPYRIGHT PERMISSION

# The Feeding Habits of Anadromous Arctic Char, (Salvelinus alpinus L.) in Frobisher Bay, Baffin Island in the Eastern Canadian Arctic: Diet, Parasites and Stable Isotopes

BY

Ikechukwu Collins Isinguzo

A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of Manitoba in partial fulfillment of the requirement of the degree

Of

Doctor of Philosophy

Ikechukwu Collins Isinguzo © 2009

Permission has been granted to the University of Manitoba Libraries to lend a copy of this thesis/practicum, to Library and Archives Canada (LAC) to lend a copy of this thesis/practicum, and to LAC's agent (UMI/ProQuest) to microfilm, sell copies and to publish an abstract of this thesis/practicum.

This reproduction or copy of this thesis has been made available by authority of the copyright owner solely for the purpose of private study and research, and may only be reproduced and copied as permitted by copyright laws or with express written authorization from the copyright owner.

# DEDICATION

This work is dedicated to the Holy Spirit, the Third Person, in the Holy Trinity…the Owner and Giver of wisdom, knowledge and understanding…the Beginning and the End…the One who makes something out of nothing, and somebody out of nobody.

## ABSTRACT

Chapter One tested the hypothesis that there is trophic structuring (TS) among Arctic char populations feeding in the marine environment based on published data and the hypothesis was rejected. A comprehensive study was undertaken to test the hypothesis further, by collecting data on diet, parasites and using stable isotopes. Anadromous Arctic char consume diet items that occur in different trophic levels and their endohelminth parasite community, transmitted by a broad range of food items, is consists of mostly non-host specific parasites. Based on 2002 data, char samples from several sites (Chapter Two) were similar with respect to length, weight age and sex and can be combined for statistical analyses. Moreover, male and female char diets were similar between sites and while diet varied among sample sites, char condition were comparable. Chapter Three compared char samples collected during 2002, 2004 and 2005 and assessed diet, parasites and stable isotope ratios (SIR) to determine if TS occurs. Diet and parasite data were unable to show clear cut evidence for TS as char were infected by non-host specific parasite species which in turn is a reflection of their diet. By contrast, stable isotope data were able to show TS in specific diet species. Selection of diet items based on particle size suggested a potential for TS and the correlation was dependent on a specific food species and its size range during its life stages. Furthermore, char that fed on invertebrates had a higher nitrogen signal than char that fed on sculpins and Arctic cod. Char feeding on Arctic cod had more $\delta^{13}C$ enrichment than char that fed on invertebrates and sculpin, respectively. There was no trophic shift by char feeding on Arctic cod but this may be related to the amount of time feeding on cod. Controlled feeding experiments

(Chapter Four) were designed to confirm if food particle size affected growth of char, if shifts in stable isotope values could be correlated with a diet shift and if the stable isotope half-lifes (HLs) from experimentally fed and wild char were comparable. Young-of-the-year (YOY) char were used because this is when char growth is considered the fastest and when the greatest shift in food particle size occurs in natural populations. Char length was not correlated with diet particle size for experimentally fed char but there was correlation for wild char feeding on *Mysis* spp., and *Onesimus littoralis*. My calculations found that experimentally fed YOY char and the larger older wild char had comparable specific growth rate (SGR) at similar temperatures. I conclude that HL of stable isotopes of C and N is dependent on char growth rate and not fish size. Stable isotopes HL were shorter for YOY but also relatively short for large wild char and can be contrasted with the much longer HLs reported in the literature for large old fish. Clearly stable isotopes can be used to predict intra-annual shifts in diets.

Since SGR of char is high in the marine environment, at low temperatures, the quantity and quality of food plus the length of time food remains in the intestine are needed to assess energy needs and possible shifts in diet preference (Chapter Five). Bomb calorimetry and proximate analysis of diet items found that the major food items varied in their nutrient content and could lead to a diet item preference but not a trophic shift. The relationship describing rate of gastric evacuations in YOY char is linear and this is similar to the results obtained from wild char in Chapter Three.

Data from my experimental studies, in general, corroborates my findings from wild char and provides further evidence that even if quality of diet and particle size

change there is little support for trophic structuring i.e. a permanent shift in diet, during the marine phase of char feeding, regardless of char size.

The predictability in char feeding makes it possible to calculate daily rates of diet consumption of wild marine char based on the model developed by Amundsen and Klemetsen (1988). I compared data from controlled feeding experiments (Chapter 5) with data from wild char and found a linear relationship between daily rate of diet consumption and temperature. Estimates of gross energy (GE) of diet items (Chapter Six) available to char showed that char growth is dependent on nutrient and total energy content and proportions of important diet items. The GE invested into growth by YOY was comparable to that of old wild char hence the similarity in their SGR. Furthermore, the stomach emptying time of old wild char is comparable to that of YOY since both groups have comparable rates of gastric evacuation. Results from Chapter Six agree with the findings in Chapter Three which showed that growth is dependent on protein, fat and total energy content of the most important diet items in char stomachs.

Contrary to my hypothesis 1 (stating absence of trophic structuring), my results have shown that TS occurs in wild char but this cannot be generalized, since it was dependent on specific diet type (e.g. *Mysis* spp., *O. littoralis* and Arctic cod). The homogenization of diet as a nutrient source and as transmitters of endohelminthes assures stability and predictability of feeding patterns of Arctic char in the marine environment. Moreover, the homogenization processes and apparent stability of feeding indicates that predictive energy models for Arctic char will likely work in a changing Arctic environment.

# ACKNOWLEDGEMENTS

I thank you, Precious Holy Spirit for everything. I was nothing, had nothing and knew nothing, but your mercy, grace, guidance, strength and wisdom took over from my fears, frailties, weakness and dullness. I could not have made it without your continual Presence and teachings. I can never thank you enough!

From the first day of our meeting to date, my supervisor, Professor Terry A. Dick, has not ceased to be a father. When I freshly arrived from Nigeria, he granted me enough time to adjust to my new environment and that really helped me. I was not quick at understanding the details of my research and could not have been able to do anything meaningful without Prof. Dick's great patience and unwavering commitment to my study. His thoughtfulness, teachings, advice and sincere criticisms are greatly appreciated.

Professor Dick's motivation, stimulating scientific discussions, sincere excitement at new discoveries as well as exciting extra-curricular discussions are deeply appreciated and will be missed dearly. It is amazing that Prof. Dick knows so much about Nigeria and particularly, my tribe, the Igbos. Very importantly, Prof., thank you so much for your great support during my wife's visa application and our permanent residence application processes. I will never forget that! I also thank Mrs. Kathleen M. Dick for her amazing kindness and for equipping me with all stationery needed for thesis writing.

I sincerely thank all my advisory committee members; Dr. L. C. Graham, Dr. Mike Papst and Dr. Martin Nyachoti for their genuine interest in my thesis, stimulating discussions and meaningful intellectual contributions. I also thank members of my candidacy examining committee; Drs Mark Abrahams and Kevin Campbell.

I am grateful to Faculty of Science for scholarships. I thank Natural Sciences and Engineering Research Council of Canada for funds through NSERC Northern Research Chair to Prof. Terry A. Dick. I enjoyed the friendship of all academic staff of Zoology unit of the Department of Biological Sciences. Again, I thank Drs Nate Lovejoy and Kevin Campbell for their warm friendship. I could not have made it without the support of non-academic staff. I will always remember Madeleine, Claire, Urmilla, Alison, Tara, John Stoyko, Terry Smith, Tracy, Lisa, Jacquileine, Shawn and Jaime. I also thank the library staff of UoM and DFO Winnipeg who assisted to source academic materials even when they were not within their reach.

I thank Colin Gallagher for helping and teaching me in so many ways. I thank Aihui Yang for helping in feeding and weighing fish during my experimental series. My colleagues (past and present) in tha lab made it all fun. I thank Chandra, Kate, Marina, Shree, Arpita, Amanda and Susan. Dean Jeske's kindness will always be remembered. Thanks Dean for taking me to grocery especially during the winter when I had no car. I thank Brenda Grabowski for being a good friend. I thank Prof. N. Kenkel for his kindness.

I thank all members of University community who donated books to my Community library project.

I am very grateful to my uncle, Dr. K. C. Asagwara and his wife, Doris, for all they did for me. I could not have been in Canada today without them. They gave me shelter and food, in addition to time and personal resources they invested towards my admission and visa procurement. Thank you very much.

I thank Sir (Dr.) A. O. Uhiara for the significant roles he played in my BSc and MSc degrees. His life and kindness had impacted me in so many positive ways. I thank Mr. Adam Nwaeze for supporting my academic pursuit without knowing anything about me. I thank Prof and Mrs L. C. Amajor for always being there for me. I greatly appreciate their passion and support in all matters of great interest in my life and family. I thank Dr. Ken Nwosu for his help during my student visa application. Prof. J. K. Udonsi, (of blessed memory) my BSc supervisor, did me so much favour. My MSc. Supervisor, Professor K.N. Don-Pedro is greatly acknowledged and thanked for his mentoring and kindness.

I thank Mr. Chukwudi Orji, Miss. Sonia Onuoha, Mr. and Mrs. Affiomah, Mr. and Mrs. Esonu, and Mr. and Mrs. Abegunde, Mr. and Mrs. Agboola Cole, Lucky Ugwoeje, Chuks Ajuzie and Chuka Nwoko for their financial support.

My adopted parents, Mr. and Mrs. Eze Onwuneme deserve my honour. They have done so much for me that there will not be enough space to write all. Bekei and Nene, your place in my heart is treasured.

I acknowledge, my late father, Chief Jumbo O. Isinguzo, with utmost honour. Papa, you laid the foundation for this success through your teachings and resources. I will always miss you! I am indebted to my mother, Chinyere Doris Isinguzo. Mama, thank you for your sacrifices, prayers, teachings and faith in me. Thank you also for all the money I borrowed from you and never really paid back as I promised. I thank Ugboaku and Ugochukwu, my younger ones for standing strongly by my side through all my academic pursuit. I am grateful to my late step-mother, Hannah Isinguzo for all she

taught me. I thank all my step-brothers (Chuka, Emeka, Ifeanyi and Chigozie) and step-sisters (Ngozi and Adanne) for all their love and support.

I have saved the "best for the last and the last for the best." Grace, my beautiful and lovely wife, made all this possible. As they say; "people don't chase rodents when houses are on fire!" Gin, I could never have finished this program had you not come to Canada and had there been no peace at home. Your love, support, encouragement, great understanding, respect and prayers kept me sane, healthy and focused. Thank you so much for everything and for putting up with my long nights and even absence from home most nights. Nmesomachukwu Bethel and Ulomachukwu Grace, my twin girls, who God gave my wife and I at the tail end of my study had also added to my joy in my academic pursuit and it is indeed, my pleasure, to acknowledge them in my thesis.

Lord Jesus, all the glory is yours! Thank you once again!

TABLE OF CONTENTS

Dedication.....i

Abstract.....ii

Acknowledgements..... v

List of Tables..... xiv

List of Figures.....xvii

GENERAL INTRODUCTION.....1

CHAPTER ONE. A review of literature to determine if the evidence supports trophic structuring of salmonids in the marine environment.
Introduction.....6
Materials and Methods.....8
Results.....10
Discussion.....12

CHAPTER TWO. Feeding and conditions of anadromous Arctic char based on sample location, diets, sex and age.
Introduction.....33
Materials and Methods.....36
Results.....42
Discussion.....50

CHAPTER THREE. Feeding patterns of anadromous Arctic char: growth, diet, parasites and stable isotopes.
Introduction.....73
Materials and Methods.....80
Results.....92
Discussion.....102

CHAPTER FOUR. Food particle size, growth and stable isotope signatures of the young-of-the year Arctic char under experimental conditions.
Introduction.....186
Materials and Methods.....189
Results.....195
Discussion.....201

CHAPTER FIVE. Gastric evacuation of young-the-of-the-year Arctic char: fish length and weight,temperature, time and model.
Introduction.....218
Materials and Methods.....222
Results.....225
Discussion.....227

CHAPTER SIX. Hypothetical estimations of energy requirements of anadromous and experimental Arctic char: daily rates of diet consumption, gastric evacuation rates, and testing of Amundsen and Klemetsen's model.
Introduction.....238
Materials and Methods.....241
Results.....246
Discussion.....249

GENERAL SUMMARY.....268

LITERATURE CITED.....274

APPENDICES.....306

(Chapter Two)
Appendix 1. List and codes of variables used in pCCA and CCA analyses in Chapter Two.....307

Appendix 2. Principal component analysis (PCA) of the relationship between mesh sizes,fish weight, fork length and age.....308

Appendix 3. Combinations used in data analysis in Chapter Two.....309

Appendix 4. Presence of food species by sample locations.....310

Appendix 5. Summary of dependent t-tests for weight among age classes among sex using 2002 samples.....311

Appendix 6. Summary of MANOVA results of male and female char weight, length, age and ratios of visceral fat, liver weight and gonad weight to fish weight in July over time. .....312

Appendix 7. Summary of MANOVA results of male char weight, fork length, age and ratios of visceral fat, liver weight and gonad weight to fish weight in August over time. .....313

Appendix 8. Summary of MANOVA results of female char weight, length, age and ratios of visceral fat, liver weight and gonad weight to fish weight in July over time.....314

Appendix 9. Summary of MANOVA results of female char weights length, age, and ratios of visceral fat, liver weight and gonad weight to fish weight in August over time. .....315

Appendix 10. Mean ± SD of ratio of visceral fat weight and fish weight of male and female char over time.....316

Appendix 11. Mean ± SD of ratio of liver weight and fish weight of male and female char over time.....317

Appendix 12. Mean ± SD of ratio of gonad weight and fish weight of male and female char over time.....318

Appendix 13. Intra-annual diet species abundances among male and female char in 2002 and 2004.....319

Appendix 14. Summary of dependent (paired) t-tests of stomach fullness and content data of male and female char over time.....320

Appendix 15. Mean ± SD of ratio of weight of stomach fullness and fish weight of male char over time.....321

Appendix 16. Mean ± SD of ratio of weight of stomach contents and fish weight of male and female char over time.....322

Appendix 17. Mean ± SD of $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios based on location. .....323

(Chapter Three)

Appendix 18. List of abbreviations used in Chapter Three.....324

Appendix 19. Mean of means (± SD) of fish weight, fork length and age for the 3 sampling years.....325

Appendix 20. Intra-annual fish length of char by age classes (7, 8 and 9) based on 2002 samples.....326

Appendix 21. Multiple comparisons based on Bonferroni post-hoc tests among effects (char condition and indices) and sample periods.....327

Appendix 22. Analysis of variance (ANOVA) results of condition factors for the 3 sampling years.....328

Appendix 23. Multiple comparisons of condition factors based on Bonferroni post-hoc tests for the 3 sampling years.....329

Appendix 24. Summary of mean ± SD of condition factor (K) for the 3 sampling years.....330

Appendix 25. Mean ± SD of fish condition data for the 3 sampling years.....331

Appendix 26. Multiple comparison based on Bonferroni post-hoc tests for the 3 sampling years.....332

Appendix 27. Summary of one-way ANOVA results of ratio of stomach contents/fish weight, GSI, LSI and VSI for the 3 sampling years.....333

Appendix 28. $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios of invertebrates based on 2004 samples.....334

Appendix 29. $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios of Arctic cod based on 2005 samples.....335

Appendix 30. Fractional contribution of most important diet items to char $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios based on 3-source mixing model.....336

(Chapter Four)
Appendix 31. Specific growth rates of young-of-the-year char in Experiment 1.....337

Appendix 32. Flow chart showing the design of experiments 1 and 2.....339

(Chapter Five)
Appendix 33. Mean ± SD ratio of weight of stomach contents to fish weight of small and large char.....340

(Chapter Six)
Appendix 34. Hypothetical estimation of mean amount of diet consumption per 1 °C rise/decline in temperature.....341

List of Tables

Page

Table 1. Common food species of the Salmoniformes.....21

Table 2. Summary of common parasites of Salmoniformes.....24

Table 3. Summary of common parasites of the genus *Salvelinus* in North America.....26

Table 4. Parasite species richness of members of the genus *Salvelinus* in North America. .....27

Table 5. Age data of male and female Arctic char over time.....60

Table 6. Changes in fork length over time in male and female Arctic char.....61

Table 7. Mean and standard deviation (Mean ± SD) of weight of male and female Arctic char over time.....62

Table 8. Diet items abundances among male and female char in 2002 and 2004 char samples.....63

Table 9. Specific growth rates of anadromous char by age classes.....125

Table 10. The weight and length ranges and mean ± SD of fish weight, fork length and stomach contents of the age classes of 2002 samples of char.....126

Table 11. The weight and length ranges and mean ± SD of fish weight, fork length and stomach contents of the age classes of 2004 samples of char.....127

Table 12. The weight and length ranges and mean ± SD of fish weight, fork length and stomach contents of the age classes of 2005 samples of char.....128

Table 13. Multivariate analysis of variance (MANOVA) tests of mean weight of fish, fork length and weight of stomach contents of Arctic char for the 3 sampling years. .....129

Table 14. MANOVA results of test of between-subjects effects (mean fish weight, fork length and weight of stomach contents) for the 3 sampling years .....130

Table 15. Summary of regression equations between mean weight of stomach contents and mean fish weight, fork length and fish age for the 3 sampling years .....131

Table 16. Inter-annual percentage proportion of wt. of diets consumed relative to total mean (± SD) fish weight for the 3 sampling years .....132

Table 17. Intra-annual fish growth by age classes (ages: 7, 8 and 9) based on 2002 samples.....133

Table 18. Intra-annual percentage proportion of diets consumed relative to total mean (± SD) fish weight based on 2002 samples.....134

Table 19. Multivariate comparison based on Bonferroni post-hoc tests of Lv, VF and VSI for the 3 sampling years.....135

Table 20. Intra-annual changes in fish condition.(VSI, LSI and GSI) based on 2002 and 2004 samples.....136

Table 21. The mean ± SD of wet weight and length ranges of key natural diet species of char.....137

Table 22. Percent frequency occurrence (%O), percent by number (%N) and percent by volume of each prey category for the 3 sampling years.....138

Table 23. The index of relative importance (IRI) and percent index of relative importance (%IRI) of the food species for the 3 sampling years.....139

Table 24. The total energy values of some key diet items of anadromous Arctic char .....140

Table 25. Proximate compositions (dry matter) analyses of key natural food species of Arctic char in the marine environment.....141

Table 26. Prevalence, mean (± SD) intensity and abundance of parasite species recovered from Arctic char for the 3 sampling years.....142

Table 27. Mean $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios according to length classes for the 3 sampling years .....143

Table 28. Mean $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios according to age classes for the 3 sampling years.....144

Table 29. Multiple comparison of carbon [C] and nitrogen [N] (C/N) ratio of food species and Arctic char based on Bonferroni post-hoc between-subjects tests based 2002 and 2005 samples.....145

Table 30. Daily growth rate constant (k), daily metabolic tissue replacement (m) and half-life (HL) (days) of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes of Arctic char based on 2002 samples.....146

Table 31. Particle size, amount and moisture contents of char test diets.....207

Table 32. Summary of ANOVA results on char growth for a period of 114 days based on total individual weight in Experiment 1.....208

Table 33. Mean ± SD of stable isotope ratios of test diets fed char and in muscle tissues of char consumed these diets over time (days) in Experiment 1.....209

Table 34. Mean ± SD of stable isotope ratios among switched test in muscle tissues of char over time (days) after char were switched diets in Experiment 2.....210

Table 35. Proximate and total energy analyses of the test diets fed char in Experiments 1 and 2.....211

Table 36. Mean ± SD of char weight over time (days) in diet switching experiment (Experiment 2).....212

Table 37. Significance values from Bonferroni corrected MANOVA analysis among test diets.....213

Table 38. Daily growth rate constant (k), daily metabolic tissue replacement (m) and half-life (HL) (days) of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes of the young-of-the-year (YOY) Arctic char in Experiments 1 and 2.....214

Table 39. Linear regression equations/constants, stomach emptying time and rates of gastric evacuation.....231

Table 40. General linear equations and model constants describing the relationships between gastric evacuation, temperature and time.....232

Table 41. Estimated rates of daily diet consumption in anadromous char at different temperatures.....257

Table 42. Hypothetical estimation of gross energy of diet items recovered from a single anadromous char in 2002 .....258

Table 43. Hypothetical estimation of gross energy of the 3 most important diet items of char when these diet species occur exclusively in char stomachs.....259

List of Figures

Pages

Figure 1. Phylogenetic tree of Salmonidae.....29

Figure 2. Phylogenetic tree of the genus *Salvelinus*.....31

Figure 3. Map of study area.....65

Figure 4. Partial canonical correspondence analysis (pCCA) of pooled food species and sample locations.....67

Figure 5. pCCA of sample locations and fish condition.....69

Figure 6. Canonical correspondence analysis (CCA) of fish condition, sampling periods and mesh sizes.....71

Figure 7. Model for interpretation of 3-D graphical representation of stomach contents analyses.....148

Figure 8. Frequency distribution of length categories in 2002, 2004 and 2005 samples of char.....150

Figure 9. Frequency distribution of age categories of 2002, 2004 and 2005 samples of char.....152

Figure 10. von Bertalanffy growth curves of Sylvia Grinnell River Arctic char in different study years.....154

Figure 11. The relationship between mean weight of stomach contents (MWS) and mean fish weight (MFW) over time and the general model describing this relationship using pooled data.....156

Figure 12. The relationship beween MWS and mean fork length (MFL) over time and the general model describing this relationship using pooled data.....158

Figure 13. The relationship between MWS and age and the general model describing this relationship using pooled data.....160

Figure 14. Intra-annual changes in fish growth in 2002 and 2004.....162

Figure 15. The relationship between weight of visceral fat and liver weight over the time and the general model describing this relationship using pooled data.....164

Figure 16. Inter-annual changes in char condition.....166

Figure 17. Intra-annual changes in char condition.....168

Figure 18. The relationship between liversomatic index (LSI) and fish fork length and between visceralfatsomatic index (VSI) and fish fork length over time.....170

Figure 19. The relationship between char fork length and particle size size of key diet items.....172

Figure 20. 3-D graphical representation of stomach content analysis of 2002, 2004 and 2005 samples of char.....174

Figure 21. Bar charts of stomach content analyses showing variations in food habits in 2002, 2004 and 2005 samples of char.....178

Figure 22. The mean ± SD $\delta^{13}C$ and $\delta^{15}N$ of diet species and char.....180

Figure 23. The relationship between $\delta^{15}N$ ratios and char length.....182

Figure 24. The relationship between $\delta^{13}C$ and $\delta^{15}N$ of invertebrates and Arctic cod recovered from char stomach samples.....184

Figure 25. Mean and standard error of fish weight over time of YOY char fed diets of Artemia (AR), frozen bloodworm (BW), frozen brine shrimp (BS) and commercial feed (CF) in Experiment 1.....216

Figure 26. Stomach emptying time of YOY char at 4, 7 and 10 °C in freshwater.....234

Figure 27. Stomach emptying time of YOY char in 23‰ salinity at 7 °C.....236

Figure 30. General vertebrate bioenergetic pathway.....261

Figure 31. The relationship between daily rate of food consumption and temperature.....263

Figure 32. The gross energy of char when *Mysis* spp. and *Themisto libellula* are consumed in varying (%) proportions.....265

Figure 33. The gross energy of char that fed on all diet items excluding Arctic cod (2002/2004) and char that fed 100% on Arctic cod excluding char that fed exclusively on invertebrates (2005).....267

# GENERAL INTRODUCTION

Arctic char, *Salvelinus alpinus* L, (Family: Salmonidae; Order: Salmoniformes) has a holarctic and circumpolar distribution and is adapted and restricted to cold-water habitats, resulting in distribution in higher latitudes than any other freshwater or anadromous fish species (Behnke 1984, Johnson 1980). The long term use of Arctic char estuarine fisheries by Inuit communities is well known. Arctic char estuarine fisheries have been identified as key fisheries by Nunavut Fisheries Management (NFM) study in 2004. According to NFM (2004), about 500,000 char are consumed annually by residents of Arctic communities. Arctic char estuarine fisheries are vulnerable to over fishing, of which an example is Sylvia Grinnell River fishery.

Arctic char is considered a key freshwater species because of its ability to utilize diet items in both freshwater and marine environments as sources of energy. The adaptation of char in harsh Arctic freshwater systems with low food resources, their ability to utilize diet items in both freshwater and marine environments as sources of energy and their economic importance as a food fish make them potentially vulnerable to climate change.

Studies by Amundsen (1994), Hobson and Welch (1995), Hammar (1998) Gulseth and Nilssen (2001) and Chakraborty (2007) had revealed trophic structuring among freshwater populations. Extensive studies of anadromous char by Grainger (1953), More and More (1974), More (1975), Johnson (1980), Dutil (1983, 1984, 1986), Adams et al. (1989), Adams and Huntingford (1997), Jørgensen et al. (1997), Rikardsen and Amundsen (2005), Finstad and Heggberget (1993), Rikardsen et al. 2000), focused more-

or-less on feeding, growth, reproduction and condition while only a few (e.g. Power et al. 2002, Reist et al. 2006) examined environmental influences on anadromous char. There is a scarcity of published information on trophic structuring among anadromous char populations in the marine environment.

Trophic structuring among freshwater char populations had been revealed through diet analysis (Hammar 1998, Klemetsen et al. 2003), endohelminth parasite communities (Frandsen et al 1989, Knudsen et al. 1996, Hammar 2000, Chakraborty 2007) and stable isotopes (Hobson and Welch 1995, Guiguer et al. 2002, Adams et al. 2003, McCarthy et al. 2004, Chakraborty 2007).

A combination of these three methods (diet analysis, endohelminth and stable isotopes) was used in this thesis to investigate trophic structuring among anadromous char populations in the eastern Canadian Arctic. Experimental studies were carried out under laboratory conditions using young-of-the year (YOY) char to determine if feeding and growth patterns of YOY char are comparable with wild anadromous char. Further, theoretical estimations of energy budget and daily food consumption and gastric evacuations of anadromous char were done in order to speculate on effects of temperature changes on char feeding habits. This is the first time these approaches are employed to examine trophic structuring in Arctic char populations from the eastern Canadian Arctic.

Chapter One of my thesis is a review of literature which was aimed at searching for supporting evidence, based on published information, for trophic structuring in the genus *Salvelinus* in the marine environment. Since, char were sampled from different locations within the same locality, Chapter Two focused on determining if location of forage influences feeding, growth and condition of geographically associated char

populations. Further, in the second chapter, I also examined the data to determine if sex differences affected char feeding and growth and if I was sampling the same population given that char age was the same early in July and late August. The main objective of my thesis was to test the hypothesis that trophic structuring in anadromous char was possible and that char feeding in the marine environment was dependent on diet particle sizes, quality and quantity. This hypothesis was tested in Chapter Three.

A series of experiments was conducted in order to understand fully the results obtained from field data and to assess the application of experimental results to field studies. In the fourth chapter, the objectives of these experiments were to determine the growth of arctic char fed three natural diets and a commercial feed and the time for young-of-the-year (YOY) Arctic char, reared at 7°C in freshwater fed one diet item to, produce a shift in stable isotope signatures that stabilized. These experiments were conducted to determine the half life (HL) of the isotope signature in char tissue following a diet switch. HL is the estimated time (days) it will take a given stable isotope value from a previous diet to equilibrate with that when a fish switches to a new diet item. In other words, HL is the decay of a stable isotope in a specific tissue derived from individuals fed a specific diet item (Suzuki et al. 2005, Tieszen et al. 1983, Hobson and Clark 1992).

In the fifth chapter, further experimental studies were conducted to determine stomach emptying time of the YOY Arctic char reared under controlled conditions at different temperatures, to assess gastric evacuation rates of YOY Arctic char at different temperatures and to examine the effects of fish size on evacuation rates and to apply the

data from these experimental series to develop a model for predictions of gastric evacuation rates of YOY char at different temperatures in freshwater.

The sixth chapter used experimental data to model energy requirements of the YOY char fed a single diet item at 4 °C, 7 °C and 10 °C in freshwater and daily rate of food consumption and instantaneous rate of gastric evacuation of anadromous Arctic char at different temperatures by using stomach content data. Based on the model that was developed, I used 2002 and 2005 stomach contents data to estimate annual energy budgets of anadromous char and to predict changes in annual energetics of anadromous char in the event of changes in proportional food intake due to warming trends in the Arctic.

The usage of the term "anadromous Arctic char" in this thesis refers exclusively to Arctic char feeding in the marine environment.

# CHAPTER ONE

A review of literature to determine if the evidence supports trophic structuring of salmonids in the marine environment

# INTRODUCTION

Understanding phylogenetic relationships among the family Salmonidae, (Salmoniformes), may help describe their historical ecological associations and their propensity to develop trophic structuring in freshwater and marine environments. Two important variables are diet and the endohelminth communities If patterns are evident, it may provide evolutionary insights to trophic feeding relationships within and between taxa within the Salmoniformes. The subfamilies Coregoninae (Coregonids:- whitefishes), Thymallinae (graylings), and Salmoninae (Salmonids:- lenok, mekous, belvica, huchen, taimen, chars, trouts, and salmons) make up the Salmoniformes (Scott and Crossman, 1973, Stearley and Smith 1993, Sanford 1990).

Crespi and Teo (2002) suggested that evolution of anadromous and freshwater life histories in the Salmoniformes may have occurred after Pleistocene glaciations whereas the separation into genera (i.e. *Coregonus*, *Salmo*, *Hucho*, *Salvelinus* and *Onchorhynchus*) probably occurred 20 million years ago since fossil forms of extant Salmoniiformes such as sockeye, chum and pink appeared about 6 million years ago (Crespi and Teo 2002). According to Stearley and Smith (1993), the subfamily Coregoninae was the earliest branch in the family Salmonidae followed by Thymallinae, and Salmoninae. Based on the evolution of semelparity and morphological data, Crespi and Teo (2002), Cavender (1980) and Stearley and Smith (1993) respectively, confirmed the common ancestry of the Salmoniformes.

Studies on the feeding habits of the genera *Onchorhynchus* (e.g. Irvine and Northcote 1983), *Salmo* (e.g. Ringler 1979), *Coregonus* (e.g. Knudsen et al. 2003,

Amundsen and Kristoffersen 1990) and *Salvelinus* (e.g. Power 1980, More and More 1974, Fraser and Power 1989) in freshwater indicate trophic structuring based on particle size. Part of this structuring is driven by evolutionary associations (i.e. phylogenetics of the Order) and part by historical ecological associations. Limited food resources and inter and intraspecific competition also play a role in freshwater systems. Intraspecific competition is especially true for Arctic char which often occurs as the only fish species in small Arctic lakes.

If feeding habits of Salmoniformes in the marine environment are predictable given the abundant and diverse food available, can it produce trophic structuring? Chambers and Dick (2005) reported that diet provides information on feeding habits over a short term but endohelminth parasite species are a better predictor of diet over a longer time frame. Furthermore, endohelminth species connect predator and prey as prey often serve as intermediate hosts for parasites (Isinguzo and Dick, 2008).

Since trophic relationships of Salmoniformes in freshwater are well known, the objective of this study is to test the hypothesis that trophic structuring of *Salvelinus* in the marine environment is also possible given the diversity and abundance of food resources in the Arctic marine environment.

## MATERIALS AND METHODS

The phylogenetic trees of the Salmoniformes (Kendall and Behnke 1984) and genus *Salvelinus* (Stearley and Smith 1993), based on meristic and morphometric characters, were used to highlight the phylogenetic relationships among these fishes (Figs. 1 and 2).

Diets of Salmoniformes are based on reports by Grant and Noakes (1986), Bernard and Holmstrom (1978), Irvine and Northcote (1983), Newman and Waters (1984), Ringler (1979), Wankowski (1979), Wankowski and Thorpe (1979), More and More (1974), Fraser and Power (1989), Alanärä and Brännäs (1997), Dunbar (1942), Grainger (1953), Hammar (1998) and Chakraborty (2007). Diets of the Salmoniformes reported by Martin and Olver (1980), Johnson (1980), Power (1980), Scott and Crossman (1973), Scott and Scott (1988) were also reviewed (Table 1).

Parasite prevalence, mean intensities and relative abundance (Table 2) were compiled from Knudsen et al. (2003), Kennedy (1978ab), Eddy and Lankester (1978), Dick and Belosevic (1981), Muzzall and Bowen (2000), Frimeth (1987ab), Hammar (2000), Watson and Dick (1979), Saksvik et al. (2001), Kennedy (1995), Frandsen et al. (1989), Muzzall (1989), Karvonen and Valtonen (2004), Muzzall and Peebles (1986), Black (1981), Kennedy and Hartvigsen (2000), Pugachev (1984), Mudry and McCart (1976), Hicks and Threlfall (1973), Anderson (1993), Hanek and Molnar (1974), Kabata (1969), Mudry and Anderson (1977). General parasitological surveys included Arai and Mudry (1983), Scholz et al. (2003), Berveley-Burton (1978), Sandeman and Pippy (1967), Bangham and Adams (1954), Bangham (1955), Kennedy (1974), Margolis

(1965), Dechtiar et al. (1988), Dechtiar and Christie (1988), and Dechtiar and Lawrie (1988)) and, studies on parasite biogeography were by Black (1983), Carney and Dick (2000), Kennedy (1977) and Lankester and Smith 1980) and other published reviews and bulletins by Kennedy (1978c), Muzzall (1995), Margolis and Arthur (1979), McDonald and Margolis (1995), Scott and Crossman (1973), Scott and Scott (1988), Hoffman (1999) (Tables 2 and 3).

# RESULTS

## Phylogeny

The genera *Onchorhynchus* (Fig. 1) and *Salvelinus* (Fig. 2) have freshwater and anadromous populations (Scott and Crossman 1973) except for *Salvelinus namaycush*, lake trout. By contrast, *Coregonus* and *Thymallus* are exclusively freshwater species (Scott and Crossman 1973) and *Coregonus clupeaformis* (lake whitefish), *C. nasus* (broad whitefish), *C. canadensis* (Atlantic whitefish), *C. sardinella* (Least cisco), *C. laurettae* (Bering cisco), *C. autumnalis* (Arctic cisco), and *C. artedii* (lake herring) exhibit seasonal migration to coastal waters to feed.

## Diet

The diets of Salmoniformes in freshwater environments range from phytoplankton to fish species (Table 1). Mills (1971), Martin and Olver (1980), Brodeur (1990) and Quinn (2005) reported that freshwater diets of Salmoniformes are size-related. Juvenile Salmoniformes feed on algae, aquatic insects (Scott and Crossman 1973) but shift to large crustaceans and fish species at adult stages (Brodeur 1990, Quinn 2005). By contrast, Grainger (1953) and Johnson (1980) demonstrated generalist feeding behaviour among char in the marine environment (Table 1). This is expected given abundant and diverse sources of diet items in the marine environment.

## Parasites

Freshwater endohelminth parasite species common to Salmoniformes include 3 monogeneans, 6 arthropods, 7 trematodes, at least 6 cestodes, 8 nematodes and 7 acanthocephalans (McDonald and Margolis 1995). Changes noted in the food habits of

Salmoniformes in the marine environment are also reflected in their marine parasite communities. Marine parasites species of Salmoniformes include 1 monogenean, 3 arthropods, 5 trematodes, 1 cestode, 3 nematodes and 1 acanthocephalan. Most of the above-listed parasite species are transmitted by amphipods which are a major food of the Salmoniformes (Tables 1). Endohelminth parasite species common to Salmoniformes are summarized in Table 2. A summary of common parasites of the genus *Salvelinus* are presented in Table 3 while Table 4 shows the parasite species richness of this genus in North America (McDonald and Margolis 1995). Total parasite species richness is similar but the proportional freshwater and marine parasite species differ significantly, especially in Arctic char.

# DISCUSSION

## Phylogeny

The relationship of the genus *Salvelinus* to other members of Salmoniformes is well established (Stearley and Smith 1993, Sanford 1990, Crespi and Teo 2002) (Figs. 1 and 2). *Salvelinus* originated well before Pleistocene with the oldest known fossil from northwestern America reported *c.* 10 million years B.P. (Cavender 1980).

The genus *Salvelinus* is a monophylectic group consisting of *Salvelinus namaycush*, *S. confluentus*, *S. fontinalis*, *S. leucomaenis*, *S. alpinus* and *S. malma* (Stearley and Smith 1993). Stearley and Smith (1993) recognized *S. malma* (Dolly Varden) as the closest relative of *S. alpinus* (Arctic char) and Behnke (1984) postulated that Arctic char and Dolly Varden diverged from a common ancestor during early Pleistocene. The validity of these species is established by their reproductive isolation as reported by DeLacy and Morton (1943), McPhail (1961) and Behnke (1972, 1984).

Within the genus *Salvelinus*, only lake trout and brook char are indigenous to North America and Behnke (1972) suggested that lake trout and brook char diverged from a common ancestor during the Pliocene. Selection pressures are thought to have produced an ecologically well-adapted generalist species that exploits a wide range of diets and habitats and a highly specialized, deepwater, lacustrine predator, lake trout (Martin and Olver 1980). Although Arctic char, *S. alpinus*, has a continuous holarctic distribution with both anadromous and lacustrine populations, it is geographically restricted to a narrow coastal zone. Regardless of differences in geographical distributions among these species in North America their ranges overlap.

**Food habits and endohelminth parasite communities**

Parasites common to most of the Salmoniformes are presented in Table 2 and include *Discocotyle sagittata, Cyathocephalus truncatus, Diphyllobothrium* spp., *Eubothrium* spp., *Proteocephalus* spp., *Cystidicola farionis, Echinorhynchus* spp., and *Neoechinorhynchus rutili* whereas parasites common to the genus *Salvelinus* are listed in Table 3 (McDonald and Margolis 1995, Hoffman 1999). Similarly, Table 4 shows a summary of parasites species richness in the genus *Salvelinus*. It is worth noting that fungi and protozoans were not included in Table 2 and in parasite species richness calculations. Data presented in Table 2 do not equal that in Table 4 since the former focused only on parasites common to Salmoniformes and not the parasite species richness of this group. Parasite total species numbers within the genus *Salvelinus* are similar but species richness differs between freshwater and marine parasites reflecting the relative importance of the two environments to the fish hosts (Table 4).

Salmoniformes: The ability of Salmoniformes to maintain their parasite communities in freshwater systems is a reflection of predictable feeding. Lankester and Smith (1980) reported the presence of *Cystidicola cristivomeri* from lake trout in 17 lakes and noted that the stomach contents of 97% of lake trout examined were infected with *C. cristivomeri.* Lankester and Smith (1980) also noted that while the 97% of lake trout infected with *C. cristivomeri* had *Mysis relicta* as the common food species, no *Mysis relicta* was recovered from the remaining 3% of uninfected lake trout. Lankester and Smith (1980) reported that *M. relicta* was not found in lakes where *C. cristivomeri* was absent. Similarily, Dick and Belosevic (1981) attributed the absence of *C. cristivomeri* in

Nettling Lake and Koukdjuak River system on Baffin Island to the absence of lake trout and *M. relicta* in this region of Baffin Island.

*Coregonus*: A consistent pattern of feeding produces a common suite of parasites and may result in increased parasite abundances in the Salmoniformes. Watson and Dick (1979) reported that abundant copepods in the diet of cisco (*Coregonus artedii*) resulted in abundant copepod-vectored cestodes and low number of amphipods in the diet led to low numbers of amphipod-vectored parasites. Clearly, there is a high correspondence between the diet and endohelminth parasite communities of the Salmoniformes. Knudsen et al. (2003) also noted that historical feeding patterns of sympatric morphs of *Coregonus* revealed congruence in their parasite communities. The consequence of comparable patterns in parasites and diets, also recorded among sympatric morphs of Arctic char (Frandsen et al. 1989), is reflected in different trophic niches.

Two to three trophic levels among Salmoniformes in freshwater systems are well documented (Amundsen et al. 1995, Curtis et al. 1995, Knudsen et al 1996 and reflects differences in feeding preferences. Knudsen et al. (2003) separated whitefish populations into three trophic groups [pelagic (resides in open water habitats and feeds on zooplankton); benthic (feeds on benthic invertebrates); zooplankton benthic (which alternates between benthic and pelagic habitats)] based on differences in their prey abundances. Knudsen et al. (2003) noted that benthic morphs had more abundant benthic prey species than pelagic morphs and *vice versa*. A correspondence in their parasite prevalence and relative abundance according to Knudsen et al. (2003) is a reflection of long-term historical ecological associations common to Salmoniformes. Therefore,

endohelmith parasites are good indicators of historical ecological associations among fish host species as well as providing data on diet.

Historical ecological associations may be affected if a fish host changes its environment or if diet composition and abundance change. For example the normal definitive hosts of *Bunodera lucioperca* are *Perca flavescens* (yellow perch) and *Micropterus salmoides* (largemouth bass) but Hicks and Threlfall (1973) reported that *B. luciopercae* was the most frequently occurring parasites of Salmoniformes in Labrador. Further, the occurrence of *B. luciopercae* in northern pike *Esox lucius* (Hicks and Threlfall 1973) supports the argument that *B. luciopercae* could be associated with pike and that historical ecological association may not be the only factor shaping the parasite community of Salmoniformes.

Absence of either a fish host or intermediate host will impact a given parasite community as will the introduction or invasion of new fish or prey species or changes in water physicochemical parameters such as effluents or temperature (Karvonen and Valtonen 2004). Thus, anadromous Salmoniformes upon entering a marine environment will shift its diet and in turn its parasite assemblage.

*Salvelinus*: The extensive overlap in the food of the genus *Salvelinus* (Table1) reflects the role of historical association on the diet of *Salvelinus*. The absence of marine food from lake trout is expected since it is a well established lacustrine predator (Behnke 1972).

Closely related hosts are generally expected to have closely related parasites (Choudhury and Dick 2001) so an evaluation of trends in the parasite communities among members of the genus *Salvelinus* should give insights into the underlying factors shaping their parasite assemblages. Of 55 parasite species reported from lake trout, 54

were freshwater and 1 was a marine species (McDonald and Margolis 1995). Similarly, 58 out of 61, and 27 out of 30 parasite species reported from brook char and Dolly Varden (McDonald and Margolis 1995) respectively, were freshwater species. Only 3 marine parasite species were reported from both brook char and Dolly Varden (Sandeman and Pippy 1967, Frimeth 1987a, b, McDonald and Margolis 1995, Hoffman 1999).

Although dietary shifts in the marine phase of anadromous populations of *Salvelinus* are well documented, trophic structuring of the *Salvelinus* group in the marine environment is not documented. This reflects more on a generalists feeding behaviour of the genus than on an established trophic ecology. It likely relates to availability of food and absence of interspecific competition in the marine environment (Table 4).

Arctic char: Diets of freshwater Arctic char include algae, Chironomidae, Trichoptera, Ephemeroptera, Diptera, zooplankton, smaller char and sticklebacks (Hammar 1998). By contrast, Grainger (1953) reported 42 different diet items from approximately 30 different species groups from stomach contents of marine Arctic char from Frobisher Bay, Baffin Island. This wide range of food species of Arctic char is reflected in their rich marine parasite community (Table 4).

Of 46 parasites species reported from Arctic char in North America (McDonald and Margolis 1995) only 6 (*Diphyllobothrium* sp., *Eubothrium* sp., *Cyathocephalus truncatus*, *Proteocephalus* sp., *Crepidostomum farionis* and *Cystidicola farionis*) are common to Salmoniformes, 28 are marine species while the remaining 12 infect other freshwater fish hosts that are not in the Order Salmoniformes (Hanek and Molnar 1974, Mudry and McCart 1976, Dick and Belosevic 1981, McDonald and Margolis 1995, Hoffman 1999). Similarly, 7 freshwater parasite species were recorded for European

populations of Arctic char (Frandsen et al. 1989). This implies that current ecological associations also contribute to the parasite community structures of Salmoniformes. These observations agree with the conclusions of Knudsen et al. (2003) that host feeding behaviour is a major determinant of endohelminth community structure and the endohelminth parasites are indicators of both historical and current ecological associations among the Salmoniformes.

Dolly Varden: Although Dolly Varden is reported to be the closest sister taxon to Arctic char (Stearley and Smith 1993, Brunner et al. 2001) with a similar life history, its parasite community appears to be influenced by factors different from that of Arctic char. For example, 28 out of 46 parasite species of Arctic char in North America are marine parasites (Hanek and Molnar 1974, Mudry and McCart 1976, Dick and Belosevic 1981, McDonald and Margolis 1995, Hoffman 1999) but only 3 (*Brachyphallus crenatus*, *Lecithaster salmonis* and *Bucephalopsis olrikii*) of 30 parasite species of Dolly Varden are marine parasite species (Gibson 1996, McDonald and Margolis 1995). This supports the idea that parasite assemblages of the genus *Salvelinus* are shaped through current ecological associations rather than historical or phylogenetic associations since the 28 marine parasites acquired by Arctic char are non-host specific. It is apparent that parasite-host specificity among this group is at a higher taxon and not at the individual species level.

Brook char: Similarities in the parasite species richness in the genus *Salvelinus* in North America supports a common freshwater ancestry (Cavender 1980, 1984, Stearley and Smith 1993) and a historical relationship to other Salmoniformes (Table 4), but it does not explain how current ecological associations shape the parasite communities of

*Salvelinus* with respect to other Salmoniformes. For instance, all freshwater parasites of brook char appear to be common to the genus *Salvelinus* (Bangham and Adams 1954, Bangham 1955, Sandeman and Pippy 1967, Power 1980, Black 1981, Frimeth 1987a, 1987b). Although Sandeman and Pippy's (1967) description of *S. exsanguinata* as a new species that is host specific to brook char was supported by Hoffman (1999), Margolis and Arthur (1979) listed this parasite as a synonym of *S. edwardsii* and as such was not considered as a valid new species in both Margolis and Kabata (1988) and McDonald and Margolis (1995). Apparently, host specificity does not appear to shape the parasite assemblage of brook char.

Host specificity at the species level among members of the family Salmonidae is equivocal. Kennedy (1977) considered *Eubothrium salvelini* and *Salmincola edwardsii* to be specific to Arctic char and Vik (1963) noted that *E. salvelini* was found in lakes where Arctic char, *S. alpinus* was the only fish present. Black (1981), Frimeth (1987a) and Dechtiar et al. (1988) reported *S. edwardsii* from brook char from Moisie River (Quebec), Tabusintac River (New Brunswick) and Lake Huron respectively. Similarly, the occurrence of *S. edwardsii* in Dolly Varden, lake trout (e.g. Hicks and Threlfall 1973, Hanek and Molnar 1974, Arai and Mudry 1983, Bangham and Adams 1954), rainbow trout *O. mykiss*, cutthroat trout *O. clarki* (Bangham and Adams 1954) is well documented. By comparison, *Cystidicola cristivomeri* and *Salmincola siscowet* are reported primarily from lake trout, suggesting that host specificity at the species level does occur.

Lake trout: Black and Lankester (1984) believed that, *C. cristivomeri* probably evolved with lake trout *S. namaycush* and that post glacial movement of lake trout into Arctic

Canada, led to the infection of Arctic char. Furthermore, Black (1983) demonstrated that the common dispersal routes of both *C. cristivomeri* and lake trout support the hypothesis of their coevolution. The occurrence of *C. cristivomeri* in other hosts is more likely indicative of current ecological interactions rather than a phylogenetic relationship. Eddy and Lankester (1978) reported the presence of *C. cristivomeri* in the swim bladder of Arctic char which fed on infected freshwater *Mysis relicta*, an essential intermediate host of this parasite.

The presence of *S. siscowet* in lake trout and its absence in other salmonids shows its specificity to lake trout (Anderson 1993) but what else shapes the parasite community? Some of the parasite species have been maintained through historical ecological associations which are dependent on common diet items for transmission. Examples of parasites maintained through such association include *Crepidostomum farionis*, *Eubothrium* spp, *Cystidicola farionis*, *Neoechinorhynchus rutili*, *Echinorhynchus lateralis*, *Capillaria salvelini*, *Discocotyle sagittata*, *Cyathocephalus truncatus*, *Diplostomum spathaceum*, *Truttaedacnitis truttae*, *Proteocephalus* spp *Diphyllobothrium* spp (Arai and Mudry 1983, Bangham 1955, Bangham and Adams 1954, Muzzall 1989, Muzzall and Bowen 2000, Dechtiar and Lawrie 1988, Dechtiar et al. 1988, Dechtiar and Christie 1988). These parasites are common to Salmoniformes and likely infected some ancestral salmonid host species.

*S. namaycush* has omnivorous food habits which includes phytoplankton, annelids, crustaceans, insects, arachnids; mollusks and a wide range of fish species. Low parasite species richness of lake trout is well documented (e.g. Muzzall and Bowen 2000), but over time, it has maintained and acquired new species such as *Triaenophorus*

*crassus*, *Bunodera luciopercae*, *Capillaria salvelini*, *Eubothrium* spp, *Echinoryhnchus* spp. Acquisition of new parasite species is expected since interacting or overlapping host species consume common diet items regardless of host phylogenetic association.

**Conclusion**

Similar to the Salmoniformes as a group, anadromous Arctic char feeding in the ocean are infected by a non-host specific community of parasites. Consequently, I predict that endohelminth communities in Arctic char and diet will not likely reflect a trophic structuring of char in the marine environment, even if there is a change in food size.

Table 1. Common food species of the Salmoniformes (Table 1 continues in pages 22 and 23). Sources (see p. 8), Legend: x = present and 0 = absent.

| Food Species | Examples | Whitefish (C. clupeaformis) | Cisco (C. artedii) | Lake trout (*S. namaycush*) | Brook char (*S. fontinalis*) | Arctic char (*S. alpinus*) | Dolly Varden (*S. malma*) | Brown trout (Salmo trutta) | Rainbow trout (O. mykiss) | Sockeye (O. nerka) | Coho salmon (O. Kisutch) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **FRESHWATER** | | | | | | | | | | | |
| Algae | | X | X | X | X | X | X | X | 0 | 0 | 0 |
| Higher plants | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Class Oligochaeta | Lumbricidae | X | X | X | X | X | X | X | X | X | X |
| | Sparganophilidae | X | X | X | X | X | X | X | X | X | X |
| | Opistocystidae | X | X | X | X | X | X | X | X | X | X |
| | Nadidae | X | X | X | X | X | X | X | X | X | X |
| | Tubificidae | X | X | X | X | X | X | X | X | X | X |
| | Haplotaxidae | X | X | X | X | X | X | X | X | X | X |
| | Lumbriculidae | X | X | X | X | X | X | X | X | X | X |
| Class Hirundinea | Leeches | X | X | X | X | X | X | X | X | X | X |
| Class Crustacea | | | | | | | | | | | |
| Conchostraca: | Limnadiidae | X | X | X | X | X | X | X | 0 | 0 | 0 |
| | *Eulimnadia* sp. | X | X | X | X | X | X | X | 0 | 0 | 0 |
| Cladocera: | *Daphnia* sp., | X | X | X | X | X | X | X | X | X | X |
| | *Holopedium gibberrum* | X | X | X | X | X | X | X | X | X | X |
| Eucopepoda: | *Cyclops* sp. | X | X | X | X | X | X | X | X | X | X |
| | *Epichura* sp. | X | X | X | X | X | X | X | X | X | X |
| | *Bosmina* sp. | X | X | X | X | X | X | X | X | X | X |
| | *Diaptomus* sp. | X | X | X | X | X | X | X | X | X | X |
| Mysidacea: | *Mysis relicta* | X | X | X | X | X | X | X | X | X | X |
| Isopoda: | *Asellus racovitzai* | X | X | X | X | X | X | X | X | X | X |
| | *Asellus aquatieus* | X | X | X | X | X | X | X | X | X | X |
| | *Lirceus* sp. | X | X | X | X | X | X | X | X | X | X |
| Amphipoda: | *Pontoporeia* sp. | X | X | X | X | X | X | X | X | X | X |
| | *Gammarus* sp. | X | X | X | X | X | X | X | X | X | X |
| Decapoda | | X | X | X | X | X | X | X | X | X | X |
| Class insecta | | | | | | | | | | | |
| | Orthoptera | X | X | X | X | X | X | X | X | X | X |
| | Plecoptera | X | X | X | X | X | X | X | X | X | X |

| Food Species | Examples | Whitefish (C. clupeaformis) | Cisco (C. artedii) | Lake trout (*S. namaycush*) | Brook char (*S. fontinalis*) | Arctic char (*S. alpinus*) | Dolly Varden (*S. malma*) | Brown trout (Salmo trutta) | Rainbow trout (O. mykiss) | Sockeye (O. nerka) | Coho salmon (O. Kisutch) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Ephemeroptera | X | X | X | X | X | X | X | X | X | X |
| | Odonata | X | X | X | X | X | X | X | X | X | X |
| | Hemiptera | X | X | X | X | X | X | X | X | X | X |
| | Homoptera | X | X | X | X | X | X | X | X | X | X |
| | Neuroptera | X | X | X | X | X | X | X | X | X | X |
| | Trichoptera | X | X | X | X | X | X | X | X | X | X |
| | Lepidoptera | X | X | X | X | X | X | X | X | X | X |
| | Coleoptera | X | X | X | X | X | X | X | X | X | X |
| | Diptera | X | X | X | X | X | X | X | X | X | X |
| | Hymenoptera | X | X | X | X | X | X | X | X | X | X |
| Class Gastropoda | | X | X | X | X | X | X | X | X | X | X |
| Class Pelecypoda | | X | X | X | X | X | X | X | 0 | 0 | 0 |
| Class Pisces | Fish egg | X | X | X | X | X | X | X | 0 | 0 | 0 |
| | Larval fish | X | X | X | X | X | X | X | X | X | X |
| | Alewife | X | X | X | X | X | X | X | X | X | X |
| | Ciscoes | X | X | X | X | X | X | X | X | X | X |
| | Fourhorn sculpin | X | X | X | X | X | X | X | X | X | X |
| | Cottids | X | X | X | X | X | X | X | X | X | X |
| | Ninespine stickleback | X | X | X | X | X | X | X | X | X | X |
| | Threespine stickleback | X | X | X | X | X | X | X | X | X | X |
| | Emerald shiner | X | X | X | X | X | X | X | X | X | X |
| | Rainbow smelt | X | X | X | X | X | X | X | X | X | X |
| | Minnows | X | X | X | X | X | X | X | X | X | X |
| | *Salvelinus* | 0 | 0 | 0 | X | X | X | X | 0 | 0 | 0 |
| | Johny Darter | X | X | X | X | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Leucichthys* sp. | X | X | X | X | X | X | X | X | X | X |
| | Grayling | X | X | X | X | X | X | X | X | X | X |
| **MARINE** | | | | | | | | | | | |
| Class Oligochaeta | | | | | | | | | | | |
| Polychaetes | | 0 | 0 | 0 | X | X | X | X | X | X | X |
| Class Crustacea | | | | | | | | | | | |
| Copepoda | *Calanus hyperboreus* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | *Calanus finmarchicus* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | *Pareuchaeta glacialis* | 0 | 0 | 0 | X | X | X | X | X | X | X |

| Food Species | Examples | Whitefish (C. clupeaformis) | Cisco (C. artedii) | Lake trout (*S. namaycush*) | Brook char (*S. fontinalis*) | Arctic char (*S. alpinus*) | Dolly Varden (*S. malma*) | Brown trout (Salmo trutta) | Rainbow trout (O. mykiss) | Sockeye (O. nerka) | Coho salmon (O. Kisutch) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Copepoda | *Pareuchaeta norvegica* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| Mysidacea | *Mysis oculata* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | *Mysis mixta* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| Amphipoda | *Themisto libellula* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | *T. abyssorum* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | *Onesimus littoralis* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | *Gammarus* sp | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | *Gammarus locusta* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | *Gammarus serosa* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| Euphausiacea | *Euphausia pacifica* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | *Thysanoessa inermis* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | *Thysanoessa raschii* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | *Meganyctiphanes norvegica* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| Class Cephalopoda | | | | | | | | | | | |
| | Squids | 0 | 0 | 0 | X | X | X | X | X | X | X |
| Class Pisces | | | | | | | | | | | |
| | Herring (*Clupea pallasi)* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | Lance (*Ammodytes* sp.) | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | Eulachon (*Thaleichthys* sp.) | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | Capelin (*Mallotus villosus*) | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | Arctic cod | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | Polar cod | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | Lantern fish (Myctophidae) | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | Lumpsucker | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | Prickleback | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | Pollock (*Theragra* sp.) | 0 | 0 | 0 | X | X | X | X | X | X | X |
| | Sculpin | 0 | 0 | 0 | X | X | X | X | X | X | X |

Table 2. Summary of common parasites of Salmoniformes (Table 2 continues in p. 25). Sources (see p. 8). Legend: x = present and 0 = absent.

| Parasite species | Whitefish (C. clupeaformis) | Cisco (C. artedii) | Lake trout (S. namaycush) | Brook char (S. fontinalis) | Arctic char (S. alpinus) | Dolly Varden (S. malma) | Brown trout (Salmo trutta) | Rainbow trout (O. mykiss) | Sockeye (O. nerka) | Coho salmon (O. kisutch) |
|---|---|---|---|---|---|---|---|---|---|---|
| **FRESHWATER** | | | | | | | | | | |
| **Monogenea** | | | | | | | | | | |
| *Gyrodactylus* sp. | 0 | 0 | 0 | X | 0 | 0 | X | X | X | X |
| *Tetraonchus* sp. | X | 0 | X | 0 | X | X | 0 | 0 | 0 | X |
| *Discocotyle sagittata* | X | X | X | X | X | X | X | 0 | 0 | 0 |
| **Arthropoda** | | | | | | | | | | |
| *Argulus* sp. | X | X | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 |
| *Ergasilus* sp. | X | X | 0 | X | 0 | 0 | 0 | X | X | X |
| *Actheres* sp. | X | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Salmincola extensus* | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *S. californiensis* | 0 | 0 | X | 0 | 0 | 0 | 0 | X | X | X |
| *S. edwardsii* | 0 | 0 | X | X | X | X | 0 | 0 | 0 | 0 |
| **Trematoda** | | | | | | | | | | |
| *Crepidostomum farionis* | X | X | X | X | X | X | X | X | X | X |
| *C. cooperi* | X | X | X | X | 0 | 0 | 0 | 0 | 0 | 0 |
| *Phyllodistomum* sp. | X | X | X | X | X | 0 | X | X | X | 0 |
| *Diplostomum spathaceum* | X | X | X | X | X | X | X | 0 | 0 | 0 |
| *Diplostomum* spp. (metacer.)* | 0 | X | 0 | 0 | 0 | 0 | 0 | X | X | 0 |
| *Bunodera luciopercae* | 0 | 0 | X | X | X | X | X | 0 | 0 | 0 |
| *Tetracotyle* spp. (metacer.) | X | 0 | X | X | X | X | 0 | X | X | 0 |
| **Cestoda** | | | | | | | | | | |
| *Cyathocephallus truncatus* | X | X | X | X | X | X | X | X | 0 | 0 |
| *Eubothrium crassum* | X | X | X | X | X | X | X | X | 0 | X |
| *E. salvelini* | X | X | X | X | X | X | X | X | 0 | 0 |
| *Diphyllobothrium* spp. | X | X | X | X | X | X | X | X | X | X |
| *Proteocephalus* spp. | X | X | X | X | X | X | X | X | X | 0 |
| *Triaenophorus crassus* | X | X | X | 0 | 0 | 0 | 0 | 0 | X | X |
| **Nematoda** | | | | | | | | | | |
| *Philonema* sp. | X | X | X | X | X | X | 0 | X | X | X |
| *Truttaedacnitis truttae* | X | 0 | X | X | X | X | X | X | X | 0 |
| *Cystidicola farionis* | X | X | X | X | X | X | X | X | X | X |

| Parasite species | Whitefish (C. clupeaformis) | Cisco (C. artedii) | Lake trout (S. namaycush) | Brook char (S. fontinalis) | Arctic char (S. alpinus) | Dolly Varden (S. malma) | Brown trout (Salmo trutta) | Rainbow trout (O. mykiss) | Sockeye (O. nerka) | Coho salmon (O. kisutch) |
|---|---|---|---|---|---|---|---|---|---|---|
| *C. cristivomeri* | X | 0 | X | X | X | 0 | 0 | 0 | 0 | 0 |
| *Capillaria salvelini* | X | X | X | X | X | X | 0 | X | 0 | X |
| *Rhabdochona sp.* | 0 | 0 | 0 | 0 | 0 | X | 0 | X | X | X |
| *Raphidascaris sp.* | X | X | X | X | 0 | 0 | 0 | X | 0 | 0 |
| *Contracaecum sp.* | X | 0 | 0 | 0 | X | 0 | 0 | X | X | X |
| **Acanthocephala** | | | | | | | | | | |
| *Echinorhynchus lateralis* | 0 | X | X | X | X | 0 | 0 | X | 0 | X |
| *E. leidyi* | X | X | X | 0 | X | 0 | 0 | X | 0 | 0 |
| *E. salmonis* | X | X | X | X | X | 0 | X | X | X | X |
| *E. salvelini* | | | | | | | | | | |
| *E. gadi* | X | X | X | X | X | 0 | 0 | 0 | 0 | 0 |
| *Neoechinorhynchus rutili* | X | X | X | X | X | X | X | X | X | 0 |
| *Pomphorhynchus bulbocolli* | X | X | X | X | 0 | 0 | 0 | X | X | X |
| **MARINE** | | | | | | | | | | |
| **Monogenea** | | | | | | | | | | |
| *Gyrodactylus sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | X | X |
| **Arthropoda** | | | | | | | | | | |
| *Argulus sp.* | 0 | 0 | 0 | X | 0 | 0 | 0 | X | 0 | 0 |
| *Ergasilus sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lepeophtheirus salmonis* | 0 | 0 | 0 | X | 0 | 0 | 0 | X | X | X |
| **Trematoda** | | | | | | | | | | |
| *Brachyphallus crenatus* | 0 | 0 | 0 | X | X | X | X | X | X | X |
| *Derogene sp.* | 0 | 0 | 0 | X | X | X | X | 0 | 0 | 0 |
| *Lecithaster sp.* | 0 | 0 | 0 | X | X | 0 | 0 | 0 | 0 | X |
| *Phyllodistomum sp.* | 0 | 0 | 0 | 0 | X | 0 | X | X | X | 0 |
| *Prosorhynchus sp.* | 0 | 0 | 0 | X | X | | | | | |
| **Cestoda** | | | | | | | | | | |
| *Bothrimonus sturionis* | 0 | 0 | 0 | X | X | X | X | 0 | 0 | 0 |
| **Nematoda** | | | | | | | | | | |
| *Ascrarophis skrjabini* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | X |
| *Hysterothylacium aduncum* | 0 | 0 | 0 | X | X | 0 | 0 | 0 | X | X |
| *Anisakis sp.* | 0 | 0 | 0 | X | 0 | 0 | 0 | 0 | X | X |
| *Acanthocephala* | | | | | | | | | | |
| *Corynosoma sp.* | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | X | X |

Table 3. Summary of common parasites of the genus *Salvelinus in* North America. Source: Hoffman (1999), Margolis and Arthur (1979) and McDonald and Margolis (1995). Legend: x = present and 0 = absent.

| Parasites Species | Lake trout | Arctic char | Brook char | Dolly Varden |
|---|---|---|---|---|
| *Salmincola* spp. | x | x | x | x |
| *Eubothrium* spp. | x | x | x | x |
| *Diphyllobothrium* spp. | x | x | x | x |
| *Proteocephalus* spp. | x | x | x | x |
| *Cystidicola farionis* | x | x | x | x |
| *Echinorhynchus lateralis* | x | x | x | x |

Table 4. Parasite species richness of members of the genus *Salvelinus* in North America. Source: McDonald and Margolis (1995)

| Fish species | Total no. of parasites in N. America | Total no. of freshwater parasites | Total no. of marine parasites |
|---|---|---|---|
| Arctic char | 46 | 18 | 28 |
| Dolly Varden | 30 | 27 | 3 |
| Brook char | 61 | 58 | 3 |
| Lake trout | 55 | 54 | 1 |

Figure 1. Phylogenetic tree of the family Salmonidae. Redrawn from Kendall and Behnke (1984)

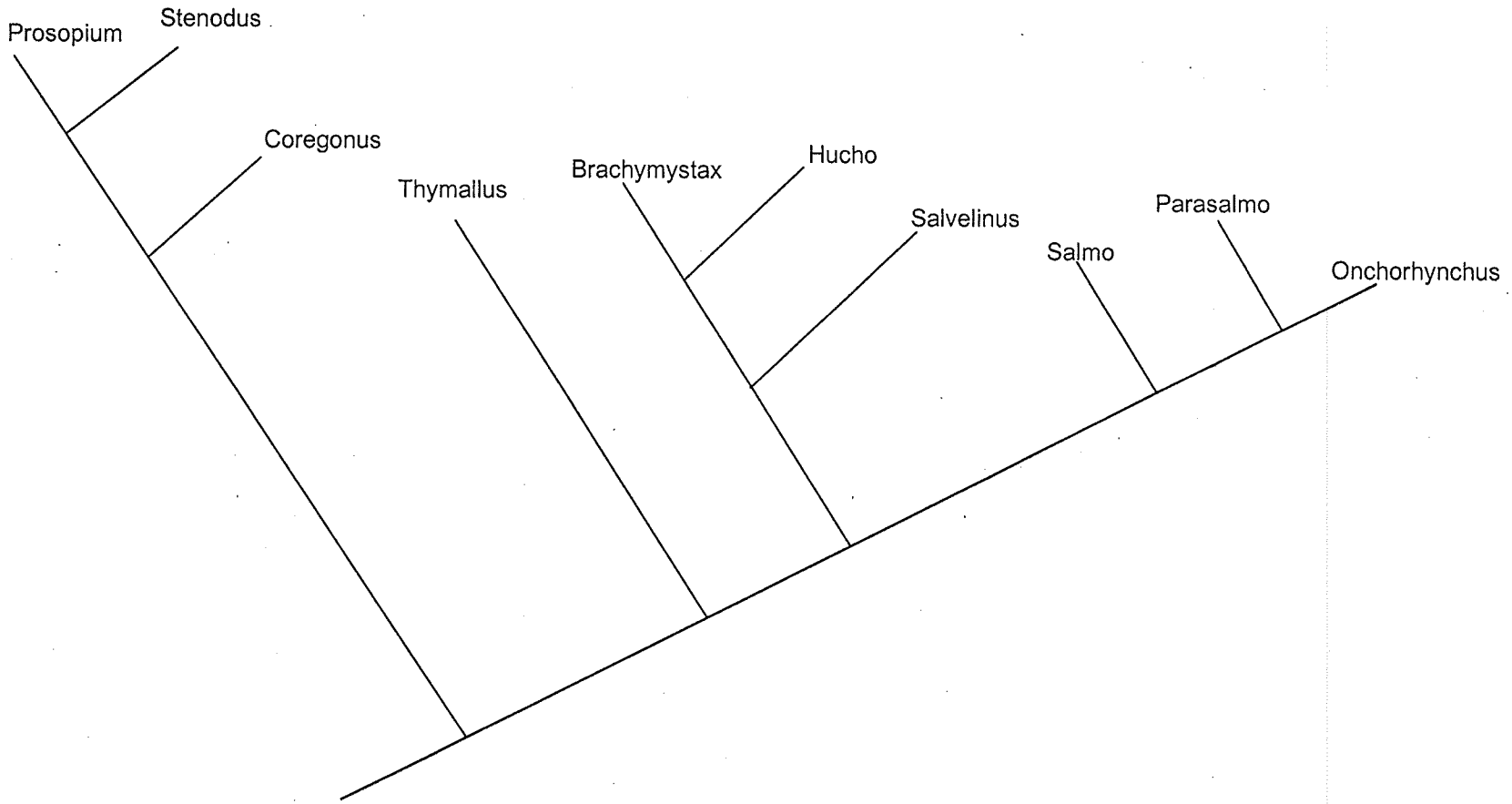
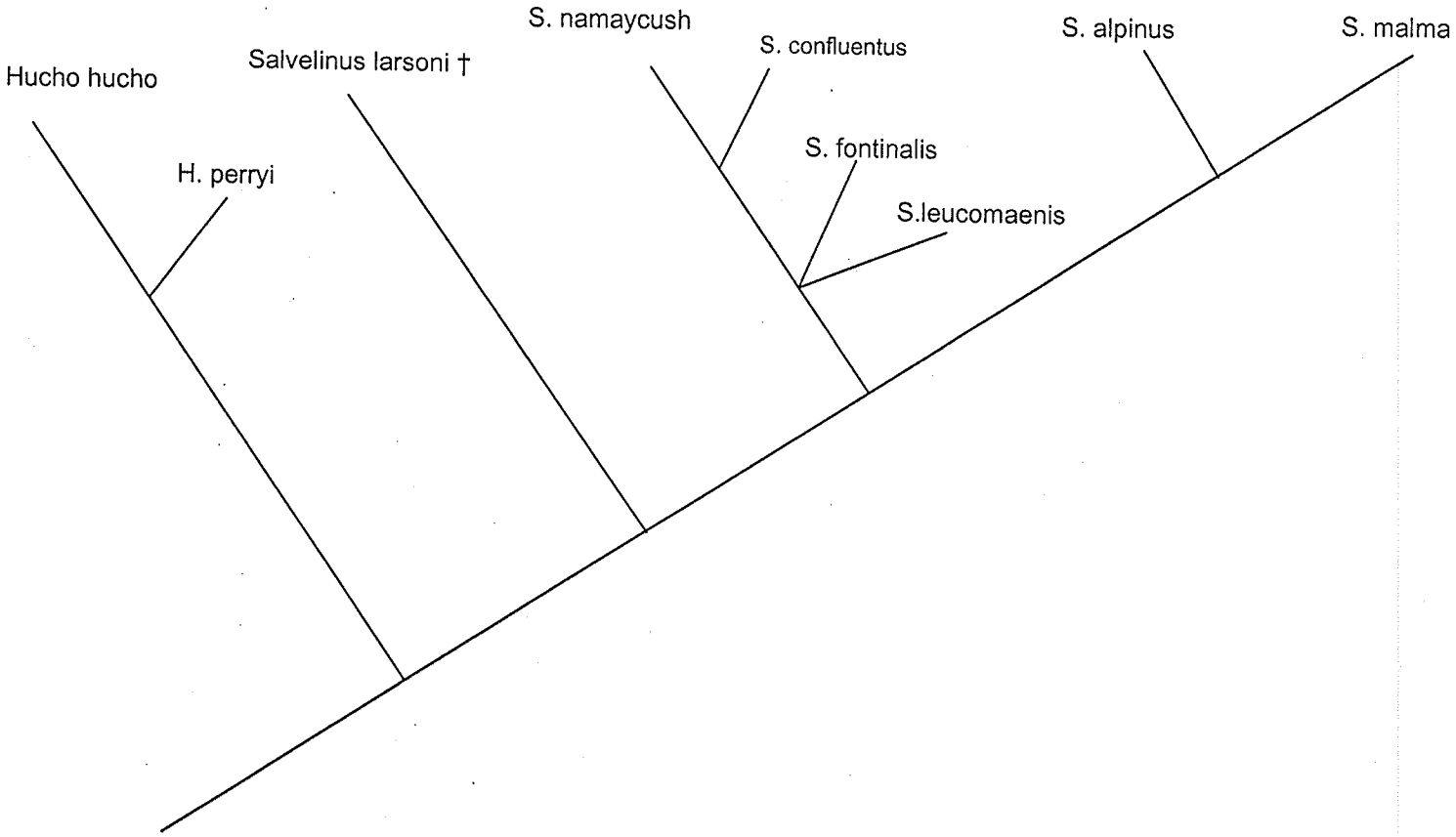

Prosopium
Stenodus
Coregonus
Thymallus
Brachymystax
Hucho
Salvelinus
Salmo
Parasalmo
Onchorhynchus

Figure 2. Phylogenetic tree of the genus *Salvelinus*. Redrawn from Stearley and Smith (1993)


Hucho hucho
H. perryi
Salvelinus larsoni †
S. namaycush
S. confluentus
S. fontinalis
S.leucomaenis
S. alpinus
S. malma

# CHAPTER TWO

## Feeding and condition of anadromous Arctic char based on sample location, diets, sex and age.

# INTRODUCTION

The feeding patterns of anadromous Arctic char have been reported by Grainger (1953), Johnson (1980) and Hammar (1998) but the influence of geographical variations in their feeding habits is not fully understood. Diet items of Arctic char in freshwater and marine environments are listed in Table 1 (Chapter One). Different and varying abundance of prey species occur in different locations in the marine environment (Grainger 1985; Dunbar 1942). According to conventional forage theory (Stephens and Krebs 1986), fish species and other predators prefer to consume available food resources in their immediate environment and might leave one location for another in search of prey species if food resources are depleted. Charnov's marginal-value theorem in conventional foraging theory (Charnov 1976) states that "a rate-maximizing forager will choose the residence time per each patch type (location) so that the marginal rate (energy derived) of gain at the time of leaving equals the long-term average rate of energy intake in the habitat" (Stephens and Krebs 1986). Although the ocean may not contain finite resources in terms of fish diet items, Rikardsen et al. (2004a) reported that spatial and temporal differences in prey availability within and between locations might influence post-smolt growth and survival of Atlantic salmon. Consistent feeding of an individual fish in a location may depend therefore, on abundance and type of diet items available (Rikardsen et al. 2004a). In essence, predators are likely to move from one location to another in search of food if depletion of resources occurs (Stephens and Krebs 1986).

Grainger (1971) observed differences in abundance and composition of zooplankton among sampling stations in Frobisher Bay. Similarly, Grainger (1971, 1985) demonstrated that zooplankton species composition varies with depth. This suggests a

possible variation in compound communities of prey species among different locations in marine environment. Dunbar (1942) noted significant differences in plankton communities between Disko Bay (west Greenland) and Home Bay (south of Clyde River, Baffin Island) despite the short distance between these two stations. Whereas *Themisto libellula* was more abundant in Baffin Island, the euphausiids, *Thysanoessa inermis* and *T. raschii* were more abundant in Disko Bay (Dunbar 1942). Perhaps the feeding patterns of char in marine environments may be influenced by the distribution of prey species within and among different locations in the marine environment.

Since char migrate to different locations with varying location-to-location distances and food species composition differs in the marine environment, there might be corresponding differences in fish condition over time among locations.

Within a population of anadromous char, some may travel considerable distances while others are much more localized in the marine environment relative to their freshwater origin. Restricted movement might be size-related (Gilliam 1982) or simply habitat preference (Dick Pers. Comm.). It is however, expected that highly active and mobile char that travel between locations will be exposed to and will feed on different food types with varying nutrient and total energy content, perhaps in a random pattern.

Considering the possibility of shifts in food species when char change feeding sites, it is necessary therefore, to incorporate the significance of sampling locations, distribution and abundance of key natural food species on fish growth and condition in studies of anadromous populations of Arctic char. The objectives of this chapter are to determine; a) if diet items vary among geographically closely associated char populations; b) if a shift in diet is reflected in growth and condition of char (see Chapter

Three for discussions on fish growth reflecting diet shifts); and c), if char of different sex and age have different feeding patterns and condition.

# MATERIALS AND METHODS

## Study area

The Sylvia Grinnell River originates in the interior of Baffin Island (Fig. 3), and it flows southwardly and empties near the northwestern extremity of Frobisher Bay at a latitude of about 63°44` N and longitude of 68°34`W (Grainger, 1953). Sylvia Grinnell Lake, is located about 20-35 miles inland from the mouth of the river and it is thought that char overwinter in this lake (Grainger, 1953, Pike and Dahlke, 1990; Kristofferson and Sopuck, 1983). Char were sampled from 7 different locations namely, Sylvia Grinnell River (1), Kagnitsuatsia (2), Causeway (3), Apex (4), Tarr Inlet (5), Foul Inlet (6) and Bay of Two Rivers (7) (Fig. 3)

## Fish data

Number (n) of samples used for age included: [2002 (July: 206; August: 240); 2004 (July: 197; August: 376)], for length: [2002 (July: 289; August: 392); 2004 (July: 185, August: 420)], and for weight: [2002 (July: 85; August: 120); 2004 (July: 182; August: 305)]. Number of samples used for diet abundances analysis based on 2002 data included for July (74) and August (73). Ninety-one samples from 2005 were used for comparative weight, length and condition analyses.

Fishing nets with various mesh sizes were used in sampling (Gallagher and Dick 2007). Variables measured from char included fish weight, fish length (fork, total and standard), age, weight of visceral fat, liver weight and gonad weight. Other variables measured included sampling date, mesh size, Julian dates of low and high tides and sampling locations. Fish otoliths were removed and aged after Grainger (1953).

Similarly, fish viscera and stomachs were removed and preserved immediately in a – 20 °C freezer until examined.

Calculations: *Condition factor* (K) = $(W \times 10^5)/L^3$ [1]

where W = fish weight (g) and L = fish fork length (mm)

*Gonadosomatic index* (GSI) = 100 x (Gd/W) [2]

where Gd = gonad weight (g) and W = fish weight (g)

*Liversomatic index* (LSI) = 100 x (Lv/W) [3]

where Lv = liver weight (g) and W = fish weight (g)

*Viscerosomatic index* (VSI) = 100 x (VF/W) [4]

where VF = weight of visceral fat (g) and W = fish weight (g) and

*Ratio of weights of visceral fat and gonad* (VG) = VF/Gd [5]

given that VF = weight of visceral fat weight (g) and Gd = gonad weight

**Weight and length**: - Fish weight in this thesis is the wet (i.e. round) weight of fish and is expressed in grams (g) while the length used in all the analyses was the fork length and referred to as fish length or length in accordance with the subject of discussion. The unit of the length used is millimeters (mm).

**Stomach content analysis**

Frozen char samples were thawed at room temperature, full stomach samples were weighed, and stomach contents removed. Empty stomachs, stomach contents and subsamples of individual food species were weighed. Stomach contents were then sieved (pore size = 0.1 mm) and rinsed into a beaker and allowed to settle for parasite count and identification. After rinsing, stomach contents were placed in large Petri dishes for identification, counting and measurement. Since some food species had lost some part of

their bodies, standard length measurements were done as follows: distance between head (i.e. the base of the antennae) to the base of the anus was measured as the length for amphipods and other crustacean food items, while for fish prey; it is the distance between the snout and the base of the caudal fin. These patterns of measurements were adopted because some of the food items had lost part of the caudal fin. Samples of each taxon were preserved dried or in 70% ethanol and stored in vials for further identification and reference purposes. The abundances of each taxon was enumerated and identified to species level. Keys used to identify stomach contents were Sars (1890, 1899), and Squires (1990) while fish species were identified using Scott and Crossman (1973) and Scott and Scott (1988).

**Statistical analyses**

Mean and standard deviations: The mean ± SD of fish weight, fork length, age, ratio of visceral fat/fish weight, ratio of liver weight/fish weight, ratio of gonad weight/fish weight, ratio of stomach fullness/fish weight and ratio of stomach contents/fish weight were calculated.

Diet abundance: Diet items were identified to species level were possible and those from the same genus were pooled. The abundance of diet species was calculated as the total number of diet items in individual char stomach/total number of char examined.

Multivariate Analyses: The multivariate analytical package used in these analyses (ter Braak and Šmilauer 2002) has species and environmental samples defaults. In other words, all data sets regardless of type would be classified either as species or environmental so that one data set would be able to predict the other. By this method,

interpretations of data and/or results are made easy by simple data classification. Multivariate analyses included canonical correspondence analysis (CCA), principal component analysis (PCA) and multivariate analysis of variance (MANOVA). Two types of CCA were used and included full CCA and partial CCA (pCCA).

Full Canonical Correspondence Analysis (CCA): This is a canonical form of Correspondence Analysis and a weighted form of Redundancy Analysis. CCA functions by using multiple regressions to select linear combinations of independent (environmental) variables that maximally explain variations in the dependent (species) variables (Legendre and Legendre 1998) (Appendix 3).

Application of full CCA: A CCA was used to determine if fish condition changed with time. Further, mesh sizes relative to fish weight, length and age were added in this analysis to determine if mesh sizes were able to sample across all sizes and ages of fish. Fish condition data was taken as species variables while all other variables except sample locations were referred to as "other environmental factors" and designated as environmental variables (Appendix 3).

Partial Canonical Correspondence Analysis (pCCA): Partial CCA (pCCA) is equivalent to CCA except that each synthetic gradient must be uncorrelated with the covariables. This means that the covariables represent gradients that have already been explained and extracted (Beasley and Kneale 2003) and as such, the resultant ordination diagrams display only the relationships between the variables of primary focus (ter Braak 1996). The variables-of-interest are locations, food species abundance and fish condition data (Appendix 3).

Partial CCA was used because food species contained large number of zero values (ter Braak and Šmilauer 2002, Legendre and Legendre 1998). Scaling was based on inter-species distances since interpretation among species was the primary aim of analysis using biplot scaling. Rare species were not downweighted. The statistical significance of response and explanatory variables was determined by a Monte Carlo permutation test.

All CCA/pCCA and Monte Carlo tests were performed using CANOCO 4.5 (ter Braak and Šmilauer 2002) programme. Prior to analysis, all data sets were imported into a CANOCO 4.5 format using CanoImp utility programme. The response, and explanatory variables and the covariables data were then selected for analysis using direct gradient analysis. The procedures and applications of the analytical package are explained by ter Braak and Šmilauer (2002).

Application of pCCA: 1): pCCA was used to determine the relationship between sampling locations and food species. In this analysis, sampling locations were regarded as environmental variables while diet data was taken as the response (species) variables. 2): pCCA was also used to determine the relationship between sampling locations and fish condition. Sampling locations data was used as species samples while fish condition data was used as environmental data set (Appendix 3).

Principal Component Analysis (PCA): The primary objective of PCA is to be able to represent an $x$-dimensional data space as new mutually perpendicular linear axes. In PCA, the first axis accounts for the most linear variation. Coordinates (environmental or species variables) that are closely associated will lie close to ordination (PCA) axes. The second PCA axis is perpendicular to the first indicating no relationships (Kenkel et al. 2002).

Application of PCA: This analysis was used to determine if there were relationships between mesh sizes, fish weight, size and age. This would indicate if mesh sizes used in the subsistence fishery were able to sample across all fish sizes collected with standard group of gillnets.

Multivariate Analysis of Variance (MANOVA): MANOVA was performed and corrected using Bonferroni *post hoc* tests to determine if there were gender-related significant differences in fish growth and condition over time. The 2005 data was only used in MANOVA. All other analyses were done using 2002 and 2004 data.

Dependent t-tests: Paired (or) dependent t-tests were performed in order to determine if there were significant sex differences in fish weight, size, age, ratio of weight/fish weight, ratio of liver weight/fish weight and ratio of gonad weight/fish weight over time. Data used in dependent t-tests were normalized using the square-root method and normality was tested using Kolmogrov-Smirnov (K-S) tests (Field 2005). Dependent t-tests and MANOVA were performed using SPSS 14.0 statistical package while mean ± STD were calculated using Microsoft Excel® package.

# RESULTS

## Fish

Length: Frequency distributions of anadromous length classes are presented in Figure 8 (p.150, Chapter Three). Length classes of 2002 and 2004 samples are comparable. Both 2002 and 2004 samples showed a unimodal size distribution (Fig. 8). Age: (see result on p.45). Preliminary CCA analysis showed that Julian date of high tide, height of low and high tides and mesh sizes did not affect the abundance of diet items. PCA analysis showed that the mesh sizes used sampled across all size and age categories and this observation is supported by the results of the frequency distribution plots (Appendix 2).

## Location

The ordination demonstrates that *Themisto libellula* and Polychaetes occur mostly in Kagnitsuatsia whereas *Calanus* species and sculpins are found extensively in Bay of Two Rivers and Foul Inlet (Fig. 4). Diet items, *Thysanoessa* spp., *Mysis* spp., and *Gammarus* spp. were similar among all sampling locations except Kagnitsuatsia and Bay of Two Rivers. By contrast, *Onesimus littoralis* was recorded from the stomachs of all fish samples in my study (Fig. 4, Appendix 4).

Partial CCA of sample locations and pooled diet items data: The ordination diagram of the pCCA of sample locations and pooled food species is presented in Fig. 4. Approximately 10% of pooled diet data is explained by the sampling locations. Fifty-nine percent of this 10% is summarized by axis 1 in pCCA. Bay of Two Rivers is the most positively correlated environmental variable. Bay of Two Rivers, Foul Inlet and

Kagnitsuatsia are strongly positively correlated. Other sampling locations which include the Causeway, Tarr Inlet and Sylvia Grinnell are negatively correlated with Bay of Two Rivers and Kagnitsuatsia. The contribution of Apex site to the overall trend in the data is not significant.

*Calanus* species and sculpins in the diet of char are most strongly positively correlated with Bay of Two Rivers and Foul Inlet whereas *Themisto libellula* and Polychaete species are strongly positively correlated with Kagnitsuatsia (Fig. 4). Other food species such as *Mysis* spp., *Thysanoessa* spp., *Gammarus* spp., and *Onesimus littoralis* are strongly negatively correlated with other sampling locations namely; Sylvia Grinnell, Causeway and Tarr Inlet.

Partial CCA of sample locations and fish condition: The ordination diagram of the pCCA of sampling locations and environmental variables is represented in Fig. 5. A total of 10.4% of sample location data is explained by fish condition data. About 62% of this 10.4% is summarized by axis 1 in pCCA. Total weight of stomach contents is the most positively correlated with condition data. Although weight of stomach contents and condition factor are strongly positively correlated with condition data, it is noteworthy that the condition data appear to be well distributed around the ordination center point as well as the sample locations (see discussion for interpretation).

**Sex difference**

Fork length: Changes in fish length over time are shown in Table 6. The mean ± SD of male and female char in July were 489.50 ± 74.30 vs. 439.50 ± 84.11 and 520.40 ± 88.40 vs. 474.80 ± 81.40 in 2002 and 2004, respectively, while in August fish male and female

char were 487.70 ± 79.20 vs. 442.50 ± 72.02 in 2002 and 462.50 ± 104.10 vs. 453.40 ± 68.90 in 2004 (Table 6).

There were significant differences (MANOVA: $P < 0.05$) between fish length in male char in July (Appendix 6) and none ($P > 0.05$) in August samples (Appendix 7) among all sampling periods. The July and August data on the length of female char were significantly different ($P < 0.05$) among years (Appendices 8, 9).

Fish weight: Mean ± SD for male and female fish weights, sex ratios, percent changes in their sex ratios from July to August are shown in Table 7. The mean weight ± SD of male and female char in July were 989.00 ± 435.50 vs. 731.00 ± 459.00 and 1680.50 ± 856.30 vs. 1323.10 ± 616.80 in 2002 and 2004, respectively. However, in August, the mean ± SD of male and female char were 1241.30 ± 634.60 vs. 1062.90 ± 490.60 and 1361.30 ± 771.40 vs. 1144.00 ± 532.50 in 2002 and 2004, respectively. There were no differences in sex ratios (Table 7).

MANOVA results showed no significant differences ($P > 0.05$) in fish weight in July among male char of 2002 and 2004 but highly significant difference ($P < 0.001$) between male char of 2004 and 2005, and between male char of 2002 and 2005 (Appendix 6). By contrast, there were no significant differences ($P > 0.05$) in fish weight in August in male char among all the sampling periods (Appendix 7). Highly significant differences ($P < 0.001$) were recorded in fish weight in July in female char among all the sampling periods (Appendix 6). Similar results were obtained in fish weight for female char in August except that there was no significant difference ($P = 0.266$) between 2004 and 2005 (Appendix 8).

Age: Preliminary results from dependent t-tests showed that there were no significant differences in fish age for both males and females in early July and late August in both 2002 ($P = 0.206$) and 2004 ($P = 0.515$) samples (see Table 5). The mean ± SD of age of male and female char in July were 10.60 ± 1.80 vs. 9.90 ± 2.60 for 2002 samples and 11.00 ± 2.60 vs. 11.00 ± 2.40 for 2004 samples whereas in August, the values were 10.80 ± 2.60 vs. 9.70 ± 2.30 and 10.00 ± 2.40 vs. 10.00 ± 2.00 in 2002 and 2004, respectively (Table 5). Sex ratios based on age data were the same over time (Table 5).

MANOVA results showed no significant differences ($P > 0.05$) in age in male char both in July and August over all the sampling years (Appendices 6, 7). However, significant differences ($P < 0.05$) in age data in July samples were recorded for female char between 2002 and 2005 but none between 2002 and 2004 and between 2004 and 2005, respectively (Appendix 8). Similar variations were observed in age data in August samples for female char where a significant difference ($P < 0.05$) was revealed between 2002 and 2004 but none between 2002 and 2005 and between 2004 and 2005 (Appendix 9).

Dependent t-tests to determine if there were significant differences in fish weight among age classes and between male and female char were performed using 2002 data. From these tests, there was no significant difference ($P = 0.341$) between age classes 8 and 9 (Appendix 5) but significant differences were recorded between age classes 8 and 10 ($P = 0.025$) and between 9 and 10 ($P = 0.020$) from July samples (Appendix 5). By contrast, no significant difference was observed among all the age classes from August (Appendix 5).

**Fish condition over time**

A CCA analysis was performed to determine if fish condition and growth changed over time. Twenty-one percent of fish condition data (analyzed as species) is explained by sampling periods and other environmental variables (Fig. 6). Approximately 64% of 21% is summarized by axis 1 in CCA ordination (Fig. 6).

The ratio of visceral and gonad weight, visceral/fatsomatic index and the weight of visceral fat were positively correlated with August sampling period whereas gonad weight and gonadosomatic index were positively correlated with July sampling period perhaps indicating the periods when these variables have greatest energy reserves. The central positions of weight of stomach content, weight of full stomach, fish (total, standard and fork) length and age relative to July and August sampling periods is indicative that subsistence sampling nets used both in July and August were able to sample across all ages and sizes of char with wide ranges of stomach contents (Fig. 8, Appendix 2).

**Fish condition and sex difference**

Ratio of visceral fat weight/fish weight: The mean ± SD of weight of visceral fat of male and female char in July were 0.0046 ± 0.0030 vs. 0.0065 ± 0.0043 in 2002 and 0.0076 ± 0.0045 vs. 0.0065 ± 0.0029 in 2004 while in August the values were 0.0085 ± 0.0060 vs. 0.0084 ± 0.0040 and 0.0118 ± 0.0041 vs. 0.0146 ± 0.0067 in 2002 and 2004 respectively (Appendix 10). Sex ratios based on ratios of weight of visceral fat weight/fish weight were apparently higher in 2004 than in 2002. Percent change in ratios of visceral fat weight/fish weight was highest in late July but lowest in late August (Appendix 10).

Significant differences ($P < 0.05$) in the ratio of weight of visceral fat/fish weight in all July samples over the sampling periods were observed for male char (Appendix 6). August samples of male char were different from July data. For example, there were significant differences ($P < 0.05$) in the ratio of weight of visceral fat/fish weight between male char of 2002 and 2004 and between 2002 and 2005 but none between the male char of 2004 and 2005 (Appendix 7). Changes in the ratio of weight of visceral fat/fish weight in July samples of female char were not significant between 2002 and 2004 samples but significant ($P < 0.05$) between 2002 and 2005 and between 2004 and 2005 (Appendix 8). Significant differences in the weight of visceral fat/fish weight.were recorded between 2002 and 2005 and between 2004 and 2005 samples but there were no significant differences between 2002 and 2004 among August samples of female char (Appendix 9).

Ratio of liver weight/fish weight: In July the mean (± SD) ratio of liver weight of male and female char were 0.0154 ± 0.0040 vs. 0.0188 ± 0.0113 and 0.0144 ± 0.0030 vs. 0.01860 ± 0.0058 in 2002 and 2004 respectively (Appendix 11). However, in August, the values were 0.0202 ± 0.0060 vs. 0.0198 ± 0.0056 and 0.01955 ± 0.0050 vs. 0.0233 ± 0.03660 (Appendix 11).

Results from MANOVA analysis showed that the ratios of liver weight/fish weight in male char among July samples over time were not significantly different between 2002 and 2004 but highly significantly different ($P < 0.05$) between 2002 and 2005 and between 2004 and 2005 samples (Appendix 6). By contrast, there were no significant differences in the ratios of liver weight/fish weight in male char from August samples (Appendix 7) and among female char from July samples (Appendix 8) throughout the sampling periods.

Ratio of gonad weight/fish weight: The mean ± SD of gonad weight/fish weight of male and female fish in July were 0.0009 ± 0.00075 vs. 0.0008 ± 0.00682 in 2002 and 0.0023 ± 0.0041 vs. 0.0150 ± 0.0141 in 2004 (Appendix **12**). Male char showed no significant difference over time in the ratios of gonad weight/fish weight (Appendices **6, 7**). However, male char were significantly different ($P = 0.007$) in the ratios of gonad weight/fish weight between 2002 and 2004 but not between 2002 and 2005 nor between 2004 and 2005 (Appendix **8**). Similarly, a significant difference was observed between 2002 and 2004 ($P = 0.005$) and between 2004 and 2005 ($P = 0.01$) but not between 2002 and 2005 ($P = 1.000$) among female char (Appendix **9**).

**Diet items abundance**

The abundance values of food consumed by male and female char over time are shown in Appendices **14, 15**. There was diet overlap between male and female. There were no changes in composition of food species however, changes in food species abundances were apparent over time. Male and female char consumed approximately equal amounts of diet items (Tables **8,** Appendix **13**).

Ratio of weight of stomach fullness/fish weight: Dependent t-tests for the ratio of weight of stomach fullness/fish weight among male and female char was significantly different ($P = 0.013$) between July and August samples for 2002 samples but not for 2004 (Appendix **14**). Mean ± SD calculations of the ratio of weight of stomach fullness/fish weight by sex also showed no apparent differences (Appendix **15**).

Ratio of weight of stomach contents/ fish weight: Results obtained from dependent t-tests showed no significant differences ($P > 0.05$) in the ratio of weight of stomach contents/fish weight in 2002 (July vs. August: $P = 0.290$) and 2004 (July vs. August: $P =$

0.714) among male and female char (Appendix **14**). Further, mean ± SD calculations of the ratio of weight of stomach contents/fish weight are in agreement with results obtained from dependent t-tests (Appendices **14, 16**).

# DISCUSSION

## Fish length

There are no differences in the length classes of char harvested using the subsistent gillnets in both 2002 and 2004 sampling periods suggesting that mesh sizes did not have any effect on sampling. Comparable length classes among char samples are important in the context of comparing fish growth and the amount or type of food species in char stomach by sampling locations. Overall, there was no change in the overall length (Fig. 8- p. 151, Appendix 2) (see Chapter Three for discussions on growth).

## Location

Sample locations and diet items: Some natural key marine diet items of anadromous Arctic char such as *Themisto libellula*, *Thysanoessa inermis*, *T. raschii*, *Gammarus* spp., *Calanus* spp., *Onesimus littoralis*, Polychaetes and sculpins have been listed in Chapter One.). These diet items are classified into pelagic (*Themisto libellula*), zooplankton (*Calanus* spp., *Thysanoessa* spp., *Mysis* spp., *O. littoralis*, *Gammarus* spp.) and benthic (Polychaetes) according to Dunbar (1942, 1946) and Percy (1993a,b). The correlation of *T. libellula* and Polychaetes with Kagnitsuatsia (Fig. 4) may either suggest the influence of tidal currents on the distribution of diet items in the marine environment given the differences in the natural habitats of these diet items or the depth at which char forage.

I calculated the mean $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios based on sample locations. Results showed slight variations in the $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios (Appendix 17). But Kagnitsuatsia and Foul Inlet had similar but slightly higher ratios

than the other locations. A preliminary analysis of the ratio of stomach contents to fish weight of char from these 2 locations revealed that Kagnitsuatsia had a higher ratio (0.0368, n = 60) than Foul Inlet (0.010709, n = 7) (see Chapter Three for discussions on $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios of char and diet items). Stable isotopes ratios are presented in Chapters Three and Four. Methods for stable isotope analysis are also presented in these chapters.

Differences in the correlation of the littoral diet items (*Calanus* spp., *Thysanoessa* spp., *Mysis* spp. *O. littoralis*, *Gammarus* spp.) and sculpin with the rest of the sampling locations is a reflection of differences in local distribution of diet items in the open sea. Rikardsen et al. (2004a) also noted spatial and temporal differences in prey avalaibility within and between locations. Figure 4 demonstrates that whereas *Calanus* spp., and sculpins were commonly found in the diet of char collected from Bay of Two Rivers and Foul Inlet, *Mysis* spp., *Thysanoessa* spp., *Gammarus* spp., were found mostly in Sylvia Grinnell estuary, Kagnitsuatsia, Tar Inlet and Causeway. By contrast, *O. littoralis* was recovered from the stomach of char collected from all sampling locations in Frobisher Bay. Both Bay of Two Rivers and Foul Inlet are shallower and exposed at low tides (Dick Pers. Comm.). This may be suggestive of the abundance of these diet items (*Calanus* spp., *Thysanoessa* spp., *Mysis* spp. *O. littoralis*, *Gammarus* spp. and sculpin) in these locations and/or the likelihood that char feeding may have been more inshore.

My results agree with Grainger (1971) who reported differences in the abundance and composition of zooplankton among sampling stations in Frobisher Bay. Similarly, Dunbar (1942) noted that plankton communities in Disko Bay (west Greenland) were different from Home Bay (south of Clyde River, Baffin Island) despite the short distance

between these two stations. Furthermore, Dunbar (1942) reported that *T. libellula* was more abundant in Baffin Island than in Disko Bay whereas *Thyssanoessa* spp., were more abundant in Disko Bay than along Baffin Island. The findings of this study are in agreement with the reports of Dunbar (1942) based on diet item distribution also reveal that stomach content analysis may be used to assess local distribution of food species in the marine environment.

Sample locations and fish condition: Rikardsen et al. (2004a) suggested that differences in feeding due to spatial and temporal differences in diet items might affect growth and survival of char post-smolt. However, my results show that predictability of fish condition by sampling locations (Fig. 5) is not apparent probably because char's key natural diet items were sufficiently nutrient-dense to meet normal growth and energy storage requirements. It is worth noting that char sampled from Bay of Two Rivers and Foul Inlet had higher condition factors than samples of char from other locations. Perhaps a diet of sculpins influenced growth since char from other locations fed primarily on crustaceans (Figs. 4, 5).

More and More (1974) observed that anadromous char in Cumberland Sound, in Baffin Island, grew at the same rate regardless of the capture location. Data from my study agrees with More and More (1974). Results of proximate analysis published by Percy and Fife (1980, 1981) showed that all char key natural food species had above the minimum fat and protein requirements (Fig. 6). Although multivariate analyses (Figs. 5, 6) found mean char weight and general condition were not predictable by location, these analyses also found that changes over time in char condition were not due to sex differences.

**Sex difference**

Fish length, weight and age: Although it is not known if a different population of similar aged char was sampled in the subsistence fishery in late August, both male and female char were the same in terms of weight, length and age from the beginning of their marine sojourn to the end (Tables 5-7, Appendices 3, 5). This is in agreement with the findings of Gulseth and Nilssen (2001) who reported no significant sex differences among all age classes of anadromous char from Dieset watercourse in Svalbard. Perhaps the slight variation in 2004 length and weight data was due to sampling errors (Table 6, 7). It is interesting to note that sex plays no role in char age classes both on arrival at the sea in July and in August (Appendix 5). Dependent t-tests analysis showed no significant differences in char weight among age classes 8 to 10 for males and females. Consequently, data can be combined for further analysis regardless of sex of individual char. However, dependent t-tests lacked the strength to determine the mean weight at age (see Chapter Three for calculations of and discussions on specific growth rates by age classes).

Sex ratios did not differ from unity in this study. Similar results were reported by Gulseth and Nilssen (2001) who observed apparent similarity in sex ratios among three morphs of anadromous char.

Results obtained from dependent t-tests in the ratio of weight of stomach fullness/fish weight showed significant difference ($P = 0.013$) among male and female char between July and August samples in 2002. Perhaps char consume diet items in proportion to their relative abundance in the marine environment (Table 8). More and More (1974) reported similar observations among char in Cumberland Sound area in

Baffin Island. Variations in weight of stomach contents are expected to be influenced by fish weight and not sex. For instance, More and More (1974) noted that the stomach contents of fish 10g in weight contained 1.5 times more food in their stomachs than char weighing 1000g. Perhaps this is the reason why there was no significant difference in the ratios of weight of stomach fullness/fish weight and weight of stomach contents/fish weight over time among male and female char except the variation between July and August samples in 2002 (Appendices **14, 16**).

**Fish condition and sex difference**

The condition of char plays an important role in its energy acquisition, storage or utilization during anadromy (Dutil 1984). Results of this study show that char condition is not influenced by location, sex or age (Fig. **6**). Hammar (1998) noted that diet availability and fish length rather than sex affect char condition in freshwater environment. Further, data from this study have shown that male and female char consume comparable amounts of food (see discussions below) and this lends support to the conclusion that sex does not play a role in fish condition. Based on diet items abundance, specific growth rate, total energy and energy requirements (see Chapter Three for discussions on these subjects) of char can be evaluated regardless of sex differences. Ratio of weight of visceral fat/fish weight: Variations in both male and female visceral fat percent increase may be due to sex differences (Appendices **6-9**).

Generally, the role of gender-related physiological differences in fish growth and condition is not fully understood. Data from this study showed that there were variations in growth among members of the same sex over time (Appendices **6-8**). But, since it is well known that lipid depletion is greater in female char than in males (Dutil 1984,

Jørgensen et al. 1997), it is also likely that the rate of lipid absorption might be higher in female than in male char. Adams and Huntingford (1997) reported a negative correlation between lipid reserves and growth and between lipid reserves and egg number in female char. This suggests that female char invest more lipids in gonadal development and exhibit greater depletion in lipid reserves than males. In other words, female char would probably require higher amounts of lipid than males since lipid levels that may be sufficient for males might be physiologically insufficient for females in terms of maturation and reproductive costs. This was clearly demonstrated in the ratios of weight of visceral fat/fish weight of male and female char in this study (Appendix 10).

Ratio of liver weight/fish weight: Liver is rich in glycogen but less so in lipids (Jørgensen et al. 1997, Dick Pers. Comm.). Food deprivation and restricted feeding lead to reduction in relative liver weight and fish weight. However, with availability of food resources and increased feeding efficiency, increases in liver weights are often recorded (Miglavis and Jobling 1989). Because of its importance in char swimming activity and its involvement in anaerobic activity (Van Dijk et al. 2005), glycogen levels are probably the first to be replenished in the marine environment. Miglavis and Jobling (1989) reported about a seven-fold increase in liver weight within sixteen weeks when char were transferred from restricted to satiation feeding regimes. It is expected therefore, that significant differences in the ratios of liver weight/fish weight in this study among male and female char between July and August (Appendices 6-8) should occur. Based on this observation, I conclude that char store some of their energy in the liver during anadromy. Similar results have also been obtained for roach *Rutilus rutilus* (Van Dijk et al. 2005).

Ratio of gonad weight/fish weight: Gonadal development in char does not take place in the sea (Appendices 6-9). Dutil (1984) categorized anadromous char population from Nauyuk Lake system according to their maturity and reproductive status. According to Dutil (1984), char that are ready to spawn in the fall of the current year are referred to as maturing fish while char that have spawned the previous year are known as postspawners until the following fall. But char that have previously spawned, not including maturing fish and postspawners are considered resting fish. Char that have not reached sexual maturity are referred to as immature fish.

Although this study was not designed to determine the effect of sexual maturity on char energy acquisition and mobilization, results suggest that while reproductive status of char might affect gonadal energy recovery and storage in female char, it does not to play any role in male char over time. This may be because char samples would have been represented by all reproductive classes except maturing char which do not migrate to the sea the year they spawn (Dutil 1984). These observations are in agreement with the findings of Jørgensen et al. (1997) who reported that females lost *c.* 80% of their body lipid during spawning and overwintering leading to great depletion of lipid reserves by early spring whereas only about 50-55% depletion of total lipid in male char was lost over the same period.

Dutil (1984) and Jørgensen et al. (1997) agree that the severity of energy lost in female char usually prevents females from spawning two years in succession. It is interesting to observe this pattern even in this study. Based on the variations of ratios of female gonad weight/fish weight over time (Appendices 8, 9) and the likelihood of a mixture of these reproductive classes of char in this study, the conclusion of Dutil (1984)

that two-month migration to the sea is not sufficient for full gonadal energy recovery of postspawners is upheld. For example, postspawners which are not considered resting until more than a year has passed since they last spawned, require more than a year to acquire and store the same amount of energy in their gonads as immature and resting fish (Dutil 1984). However, these results may even be more complicated since maturity may be deferred by char at adverse conditions (Dutil 1984).

Although reproductive status and changes in fish total energy content influence gonadal energy in female char but less so in males, the slight variations in gonadal energy reserve noted in this study were not related to sample locations or diet items consumed, but may be due to physiological differences between male and female char. I conclude that sample location and diet composition do not affect gonadal development among anadromous char population

**Diet items abundance**

Sex does not influence char feeding in the marine environment. Male and female char consumed equal amounts of diet items (Tables **8**, Apendices **13, 14, 16**). Several studies have reported feeding habits of anadromous char (Grainger 1953, Johnson 1980, Rikardsen et al. 2000, 2004a) but the present study is the first to investigate gender-related influence in diet consumption and its relationship to sample locations.

**Conclusions**

The location of char foraging in the marine environment does not affect their condition although relative abundance of diet species may differ from location to location. Char are exposed to abundant marine food species of similar overall energy and nutrient contents (see Chapter Three). Male and female char consume comparable amounts of diet items. This corresponded to their comparable length and weight values. This is understandable since they receive comparable amounts of nutrient contents from diet items. Although char migrate to the marine environment at different age classes, there is no sex related differences by age when they return to freshwater in late August.

Char growth and condition are high during the first 5 weeks but after this period, more energy is diverted into storage as visceral adipose fat and the weights also increase. There were no sex-related differences in the ratio of weight of visceral fat/fish weight. The ratio of weight of visceral fat/fish weight in August was about 61.29% higher than in July sample of char. Based on the fullness of char stomachs, feeding decreased with time and stomach fullness was inversely correlated with fat reserves. This is worth noting considering the fact that fat deposits are important energy reserves for reproduction, body building and maintenance etc.

Sample location and diet composition do not affect gonadal development among anadromous char population. Different reproductive classes and the fact that char remain in freshwater during the year of spawning makes it difficult to correlate gonad weight with energy intake during anadromy. However, it is interesting to note that there might be different rates of energy acquisition, storage and utilization among different reproductive classes of char within the same sex and among sexes. Based on lack of differences among

samples the data can be combined. Further, multivariate analysis of the relative abundance of diet items from char collected from several locations in Frobisher Bay in Baffin Island found that local char diets were predictable.

Table 5. Age data of male and female Arctic char using 2002 and 2004 samples.

| Sex | Year | n | Total mean ± SD of fish age in July (Years) | n | Total mean ± SD of fish age in August (Years) |
|---|---|---|---|---|---|
| Male | 2002 | 29 | 10.60 ± 1.80 | 35 | 10.80 ± 2.62 |
| | 2004 | 110 | 11.00 ± 2.61 | 212 | 10.00 ± 2.38 |
| Female | 2002 | 177 | 9.90 ± 2.64 | 205 | 9.70 ± 2.30 |
| | 2004 | 87 | 11.00 ± 2.39 | 164 | 10.00 ± 2.00 |
| Ratio of total male/female fish age | 2002 | | 1.07 | | 1.11 |
| Ratio of total male/female fish age | 2004 | | 1.00 | | 1.00 |

Table 6. Changes in fork length (mm) between years in male and female Arctic char using 2002 and 2004 samples.

| Sex | Year | n | Total mean ± SD of fork length in July (mm) | n | Total mean ± SD of fork length in August (mm) |
|---|---|---|---|---|---|
| Male | 2002 | 98 | 489.54 ± 74.30 | 151 | 487.70 ± 79.22 |
| | 2004 | 92 | 520.40 ± 88.40 | 231 | 462.50 ± 104.10 |
| Female | 2002 | 191 | 439.50 ± 84.11 | 241 | 442.50 ± 72.02 |
| | 2004 | 93 | 474.80 ± 81.40 | 189 | 453.40 ± 68.90 |
| Ratio of total male/female fork length | 2002 | | 1.11 | | 1.10 |
| Ratio of total male/female fork length | 2004 | | 1.10 | | 1.02 |

Table 7. Mean ± SD of weight (g) of male and female Arctic char over time using 2002 and 2004 samples.

| Sex | Year | n | Total mean ± SD of fish weight in July (g) | n | Total mean ± SD of fish weight in August (g) |
|---|---|---|---|---|---|
| Male | 2002 | 29 | 989.00 ± 435.50 | 37 | 1241.30 ± 634.64 |
| | 2004 | 91 | 1680.50 ± 856.33 | 217 | 1361.34 ± 771.41 |
| Female | 2002 | 56 | 731.00 ± 459.00 | 83 | 1062.90 ± 490.61 |
| | 2004 | 91 | 1323.10 ± 616.80 | 188 | 1144.00 ± 532.50 |
| Ratio of total male/female fish weight | 2002 | | 1.40 | | 1.20 |
| Ratio of total male/female fish weight | 2004 | | 1.30 | | 1.20 |

Table 8. Diet items abundances among male and female char in 2002

| Food species | Year 2002 Male: July (n = 39) | Female: July (n = 35) | Male: August (n = 30) | Female: August (n = 43) |
|---|---|---|---|---|
| *Mysis* spp. | 204.20 | 139.60 | 212.30 | 334.10 |
| Sculpins | 1.62 | 3.22 | 13.00 | 11.10 |
| *Themisto libellula* | 19.50 | 30.70 | 128.00 | 116.00 |
| *Onesimus littoralis* | 15.10 | 11.00 | 23.60 | 5.80 |
| *Thysanoessa* spp. | 22.73 | 23.90 | 14.02 | 13.30 |
| *Calanus* spp. | 0.40 | 1.18 | 10.73 | 52.14 |
| *Gammarus* spp. | 2.22 | 7.00 | 0.21 | 0.20 |
| Polychaetes | 8.90 | 19.50 | 5.04 | 29.10 |

Figure 3. Map of the study area. Legend: 1 = Sylvia Grinnell River, 2 = = Kagnitsuatsia; 3 = Causeway 4 = Apex; 5 = Tarr Inlet; 6 = Foul Inlet and 7 = Bay of Two Rivers.

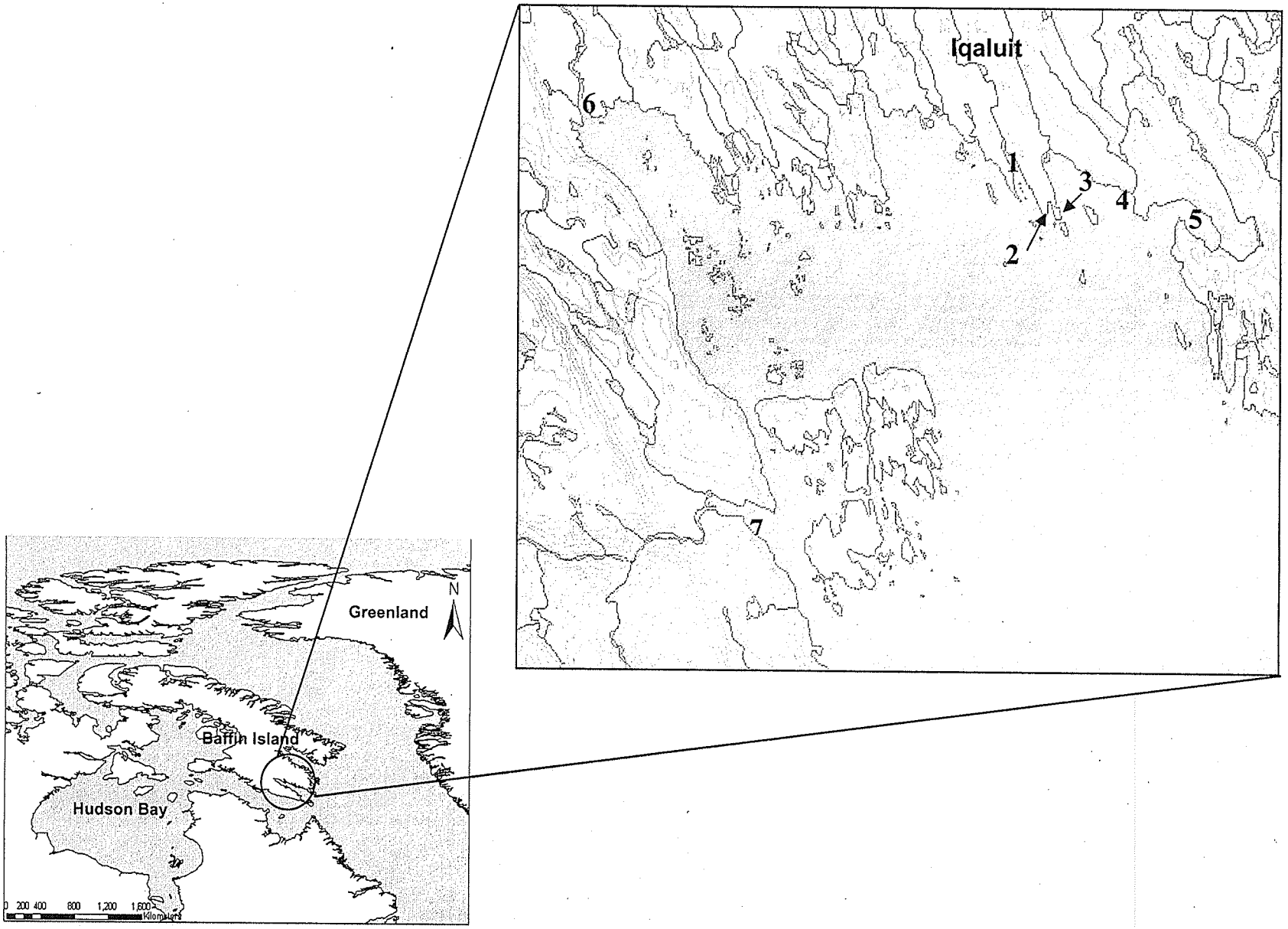

Iqaluit
1
2
3
4
5
6
7
Greenland
Baffin Island
Hudson Bay
N
0 200 400 800 1,200 1,600
Kilometers

Figure 4. Partial CCA of pooled food species and sampling locations. Diet items are represented by: *Py* = Polychaetes; *Them* = *Themisto libellula*; *Cal* = *Calanus* spp.; scp = sculpins; *Thys* = *Thysanoessa* spp.; *Mys* = *Mysis* spp.; *Ones* = *Onesimus. littoralis*; *Gam* = *Gammarus* spp. Sampling locations are represented by: KG = Kagnitsuatsia; BT = Bay of Two Rivers; SG = Sylvia Grinnell; TI = Tarr Inlet; FI = Foul Inlet; CW = Causeway; AP = Apex. Note: SG, CW, AP and TI are considered as a unit location considering their close proximity.

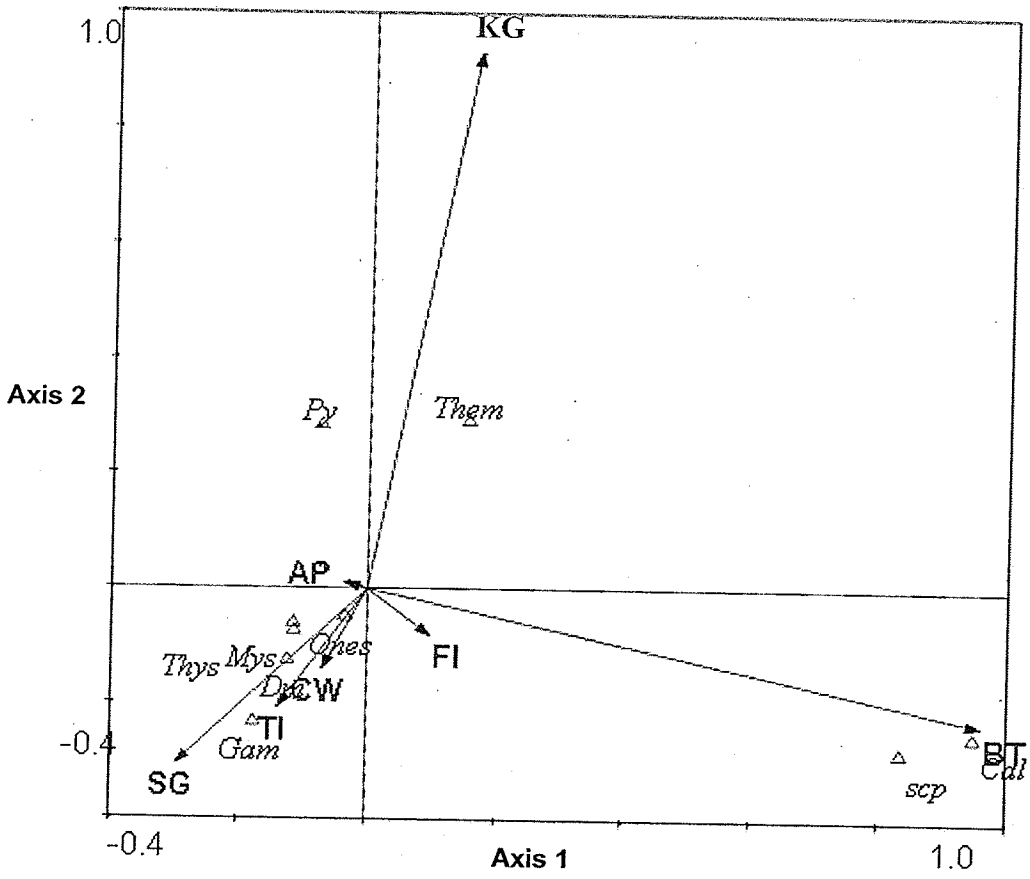

1.0
KG
Axis 2
Py
Thgm
AP
Thys
Mys
Ones
FI
DxCW
TI
Gam
-0.4
SG
BT
Cal
scp
-0.4
Axis 1
1.0

Figure 5. Partial CCA of sampling locations and fish condition. Sampling locations are represented by: KG = Kagnitsuatsia; BT = Bay of Two Rivers; SG = Sylvia Grinnell; TI = Tarr Inlet; FI = Foul Inlet; CW = Causeway; AP = Apex. Fish conditions are coded by: K = Condition factor; V = weight of visceral fat; Vsi = Visceralfatsomatic index; VG = ratio of weight of visceral fat and gonad; Lv = weight of liver; Lsi = Liversomatic index; Gd = Gonad weight; Gsi = Gonadosomatic index; Sc = Weight of stomach content.

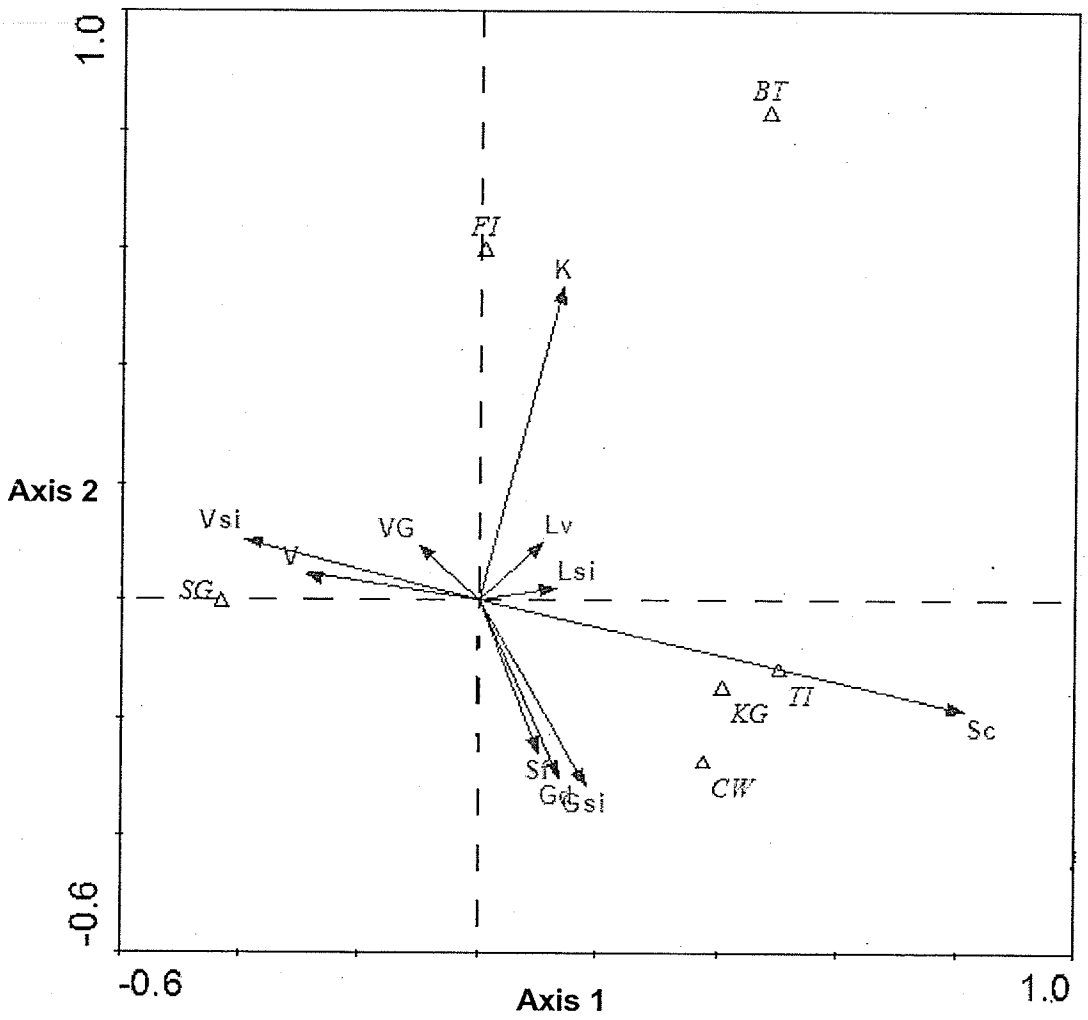
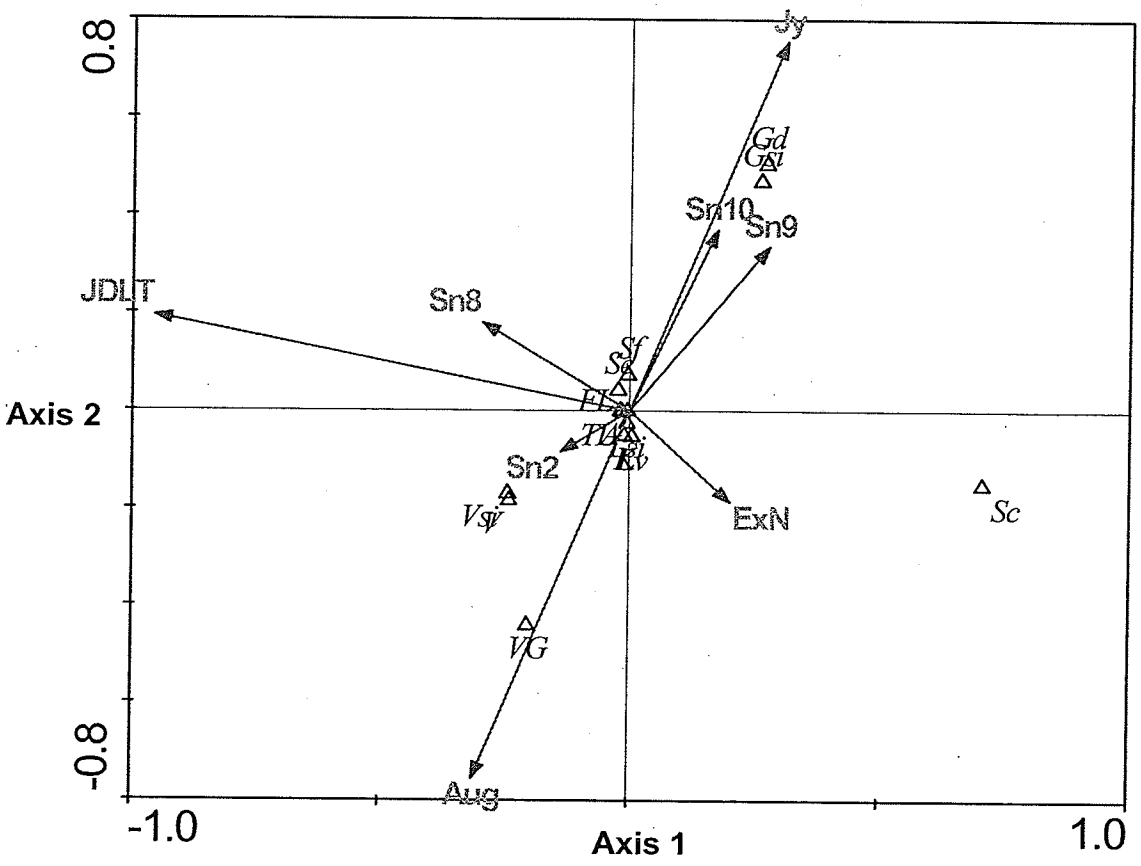

1.0
-0.6
Axis 2
-0.6
Axis 1
1.0
BI
FI
K
Vsi
VG
Lv
V
Lsi
SG
KG
II
Sc
CW
Gsi

Figure 6. CCA of fish condition, sampling periods and mesh sizes. Fish condition include: K = Condition factor; V = weight of visceral fat; Vsi = Visceralfatsomatic index; VG = ratio of weight of visceral fat and gonad; Lv = weight of liver; Lsi = Liversomatic index; Gd = Gonad weight; Gsi = Gonadosomatic index; Sc = Weight of stomach content; Sf = Weight of stomach fullness; Sampling periods are represented by: Jy = July; Aug = August and sampling nets with various mesh sizes are coded by: Sn2 = Subnet 2; Sn8 = Subnet 8; Sn9 = Subnet 9; Sn10 = Subnet 10. JDLT = Julian date for low tide.


0.8
-0.8
-1.0
1.0
Axis 1
Axis 2
Jy
Gd
Gl
Sn10
Sn9
JDLT
Sn8
Sf
Sa
El
Tl
Kb
Sn2
Vsp
ExN
Sc
VG
Aug

# CHAPTER THREE

## Feeding patterns of anadromous Arctic char: growth, diet, parasites and stable isotopes.

# INTRODUCTION

Chapter One discussed the evolutionary relationship among Salmoniformes, their ecological associations and propensity to establish trophic structure in freshwater where food may be limiting. At present, food appears to be less limiting in the marine environment (Johnson 1980) but there is a likelihood of alien species invasion as the Arctic warms and as a consequence, increased competition for food. The proportion and composition of food species of Artic char in the marine environment may change if warming trends in the Arctic continue. Therefore, it is important to understand the factors influencing Arctic char food habits in the marine environment since it is not clear if Arctic char in the marine environment show trophic structuring i. e. generalist or specialized feeding. Currently, it is not fully understood if char food habits in the marine environment are driven by particle size, quality [i.e. nutrient content (fat/protein) or total energy content], quantity (i.e. relative abundance) or trophic status of food items or that char are simply opportunistic feeders in the marine environment. Moreover, all the above factors affect growth.

**Growth:** The use of calculated growth curves in fisheries management is well known. This method has been employed for freshwater (von Bertalanffy 1957) and anadromous (e.g. Grainger 1953, Gallagher and Dick 2007) char populations. Grainger (1953) calculated growth curves for anadromous char by using otolith width relative to fish length in an equation expressed by: log (fish length) = -1.503 + 1.982 log (otolith width) but Gallagher and Dick (2007) employed the von Bertalanffy growth function expressed by: $[L_{(t)} = L\infty(1-e^{-k(t-t_0)})]$. Calculated growth curves are used to compare growth among

age/length/weight classes within a given population (Brett and Shelbourn 1975) or among populations of fish species or conspecifics (Rikardsen et al. 2000).

Specific growth rate (SGR): This is the rate at which fish grows within a given time period (Jobling 1994, Arnesen et al. 1994). Most growth studies involving fish species under controlled conditions calculate specific growth rates (SGR) among individual fish (Arnesen et al. 1994). SGR has also been used to compare growth among two char populations. For example, Finstad and Heggberget (1993) reported growth differences among hatchery-reared and anadromous char populations. Similarly, by using specific growth calculations, Arnesen et al. (1994) reported no significant difference between char held in freshwater and brackish water while the growth of these groups was better than that of char reared in seawater. Although SGR is widely used by fish biologists, its application to understand the feeding patterns of anadromous char population in the eastern Canadian Arctic and its usage to estimate metabolic turnover rates and half-life of $\delta^{13}C$ and $\delta^{15}N$ isotopes in anadromous char has not been reported.

Fish condition and indices: The use of Fulton's condition factor (K), liversomatic (hepatic) index (LSI or HSI), gonadosomatic index (GSI) and musclesomatic index (MSI) to examine fish condtion is well known (see Dutil 1984, Dutil and Lambert 2000, Hammar 1998, Chakraborty 2007). By contrast, only few studies (e.g. Johnson and Dick 2001, Chakraborty 2007, Chambers et al. (In press) used absolute values of liver weight, visceral fat weight and its index (visceralfatsomatic index- VSI) in trophic studies. Cavalli and Chappaz (1996) correlated feeding patterns of Arctic char in Muzelle Lake in France to GSI and HSI and concluded that char condition, reproductive capacity and population dynamics are associated with availability of food resources in freshwater

systems. Published information (based on long-term stomach contents data) on char condition/indices when char shift diets from freshwater to marine environment are lacking. Understanding the feeding habits of anadromous char may provide information on why char grow so rapidly in the marine environment. It may be a combination of diet quality and particle size.

**Diet particle size:** The influence of food particle size on food habits of the Salmoniformes in their natural freshwater systems is well documented and reported for Arctic char (*Salvelinus alpinus*) (Hammar 2000, Alanärä and Brännäs 1997, More and More 1974), brook char (*S. fontinalis*) (Allan 1981), lake trout (*S. namaycush*) (Martin and Olver 1980), sockeye (*Onchorhynchus nerka*) (Healey 1980), chum salmon (*O. keta*) (Brodeur 1990), pink salmon (*O. gorbuscha*) (Healey 1980). Furthermore, under controlled conditions in freshwater, size-dependent feeding had been confirmed for Arctic char (Tabachek 1988), brook char (Grant and Noakes 1986, Power 1980), and brown trout (*Salmo trutta*) (Ringler 1979). By contrast, stomach contents of anadromous Arctic char (Grainger 1953, Johnson 1980), adult sockeye (Pearcy et al. 1984), adult chum salmon (Andrievskaya 1957) and Atlantic salmon (Scott and Crossman 1973, Wankowski 1979) have revealed that the food habits of Salmoniformes in the marine environment are not size-related. Thus, suggesting that other factors might be playing a role in feeding patterns.

**Diet quality:** Total energy and nutrient content commonly, referred to as diet quality, are often considered to be the main driving force behind food habits of Salmoniformes during anadromy. Pearcy et al. (1988) reasoned that sockeye were feeding selectively on nutrient dense food organisms after they recovered pelagic fish and large squids from the

stomachs of adult sockeye. Similarly, Beacham (1986) and Craig (1987) reported that Chinook salmon (*O. tshawytscha*) and Coho salmon (*O. kisutch*), respectively, are predominantly piscivorous in coastal waters. While Craig (1987) noted that sand lance (*Ammodytes* sp.) was an important prey item of Coho salmon, Beacham (1986) observed that Chinook salmon tend to feed on the largest prey species available compared to other salmon species. From a study conducted under controlled conditions Jobling and Wandsvik (1983), noted that total energy and nutrient content of food organisms were the most important factors influencing Arctic char food intake and growth. Published information on the influence of food quality on char food habits during anadromy appear to be lacking.

**Diet quantity:** Although diet quality has been suggested to influence food habits of Salmoniformes, equally important in their feeding behaviour is food quantity (i.e. abundance). For example, Straty and Jaenicke (1980) discovered that sockeye preyed opportunistically on the most abundant large plankton that are available but switched to smaller prey when larger prey are less numerous. Similarly, Kaeriyama (1986) reported that juvenile Chum salmon consume hyperiids in relation to their abundance and did not feed on copepods and cladocerans based on their relative abundance. Similarly, Johnson (1980) reported that Arctic char are generalist feeders. While Johnson's (1980) results appear to agree with the findings of Grainger (1953) on generalist feeding behavior of char based on the variety of food items recovered from char stomachs, it lacked the linkage of diet to char as a predator based on trophic status of the diet species. This is important since diet species also serve as intermediate hosts to parasites and the latter in

turn, serve as links between predator and prey species (Chambers and Dick 2005, Isinguzo and Dick 2008).

**Endohelminth parasite species:** Whereas stomach content data provides information on feeding habits over a short term, endohelminth parasite species are good indicators of food species consumed by predators over a relatively longer period of time (Chambers and Dick 2005, Johnson and Dick 2001). Overall, endohelminth parasite species are the connecting links between predator-prey relationships given that prey species which serve as food items to predators also serve as intermediate hosts to the parasite species (Isinguzo and Dick 2008). By using summer diet and food-related endohelminth parasite intensities, Hammar (2000) reported discrete ontogenetic niche shifts in char modal groups. Similarly, Knudsen et al. (2003) reported three trophic levels among sympatric whitefish (*Coregonus lavaretus*) morphs based on diet and endohelminth parasites transmitted by the prey species.

**Stable isotopes:** Historical records of food consumed over time are commonly studied using stable isotopes ratios. Although stable isotope ratios are good indicators of food types eaten over a long time, results can be misleading as isotope signals are dependent on how fast a fish grows (Hesslein et al. 1993). According to Hesslein et al. (1993), stable isotope signals would be reflective of the growth rate of a fast-growing fish whereas it could take several years for a new isotopic equilibrium to be reached in a slow-growing fish if feeding shifted from one diet to another. Studies on stable isotopes ratios of Arctic char such as those of McCarthy et al. (2004), Adams et al. (2003), Guiguer et al. (2002), and Hobson and Welch (1995) have focused on the freshwater phase of char. Similarly, stable isotope studies of other sister taxa such as brook char *Salvelinus fontinalis* (Power

et al. 2002) and brown trout *Salmo trutta* (Grey 2001) had examined freshwater populations.

Metabolic turnover rates: Changes in isotopic ratios when fish switch diets are either due to growth or metabolic replacement commonly expressed as a turnover rate (Hesslein et al. 1993). Isotopic changes due to growth can easily be established once metabolic turnover rates are estimated. Hesslein et al. (1993) calculated metabolic turnover rate of 0.1-0.2 $\%d^{-1}$ for growing broad whitefish (*Coregonus nasus*) while Suzuki et al. (2005) estimated a turnover rate of 0.0031 $\%d^{-1}$ for Japanese temperate bass (*Lateolabrax japonicus*). High metabolic turnover rates are indicators of high growth rates while slow-growing fish would have low metabolic turnover rates (Hesslein et al. 1993). Although this method has been applied to some freshwater salmonids (e.g. Hesslein et al. 1993) it has not been used to examine isotopic changes and growth rates of char in the marine environment.

The turnover of stable isotope ratios when a fish switches from one diet item to another can also be expressed as a half-life value (Suzuki et al. 2005). Half-life (HL) value is the estimated time (days) it will take a given stable isotope value from a previous diet to equilibrate with that when a fish switches to a new diet item (Tieszen et al. 1983, Hobson and Clark 1992). Stable isotope ratios of animal tissues are known to change gradually toward a new value to reflect the isotope ratios of a new diet and then stabilize (Suzuki et al. 2005). This method is an important tool for understanding fish migrations (e.g. Suzuki et al. 2005). Further, it can also be used to examine growth rates among fish populations (e.g. Hesslein et al. 1993). However, the half-life of $\delta^{13}C$ and $\delta^{15}N$ isotopes ratios, when char switches diets from freshwater to anadromous phases, has not been

reported. These data may help pinpoint a shift in diet and provide evidence for trophic structuring (i.e. if it exists) in char from the marine environment. Published information on potential trophic structuring of anadromous char based on stable isotope studies appears to be lacking.

It is well known that Arctic char feed voraciously and continuously in the ocean with attendant high energy reserves (Dutil 1984, Dick Pers. Comm) and that the enormous energy acquired is not totally utilized while in the ocean as char returning to freshwater systems consistently show high condition, visceral fat deposits and enlarged livers (Dutil 1984, Johnson 1989, Dick Pers. Comm.). But factors enhancing char's high energy reserves within this short period of time in the marine environment are not fully understood. Is this rapid growth of char influenced by diet particle size or trophic status-driven and/or dependent on diet quality and quantity?

Previous studies (e.g. Grainger 1953, Johnson 1980) approached this subject primarily from stomach contents analysis perspective. Since stomach content analysis reveals only short-term feeding habits of a consumer, it was the intention of this chapter to use a combination of diet analyses, endohelminth parasite species and stable isotope data to test the hypothesis that feeding habits of Arctic char in marine environment is dependent on diet particle size, quality and quantity of the diet.

# MATERIALS AND METHODS

## Fish data

Fish data as well as male and female char were combined for July and August for the 3 sampling years since results from Chapter Two revealed no significant differences in growth or age due to sex difference between early July and late August. Also, results from Chapter Two showed that the location of char foraging in the marine environment does not affect its condition although the relative abundance of diet species may differ from location to location. Consequently, fish data from all sample locations were used.

Data collected from the char included weight (g) and length (fork, standard and total). Char were dissected so that the viscera (i.e. internal organs) could be separated from the flesh of the fish. The viscera samples were bagged and given identification numbers and then frozen at –20 °C until examined. Char organs examined included gonad, gills and mouth, heart, stomach, gut, caecae, liver, spleen and swim bladder. Otoliths were also collected for ageing. List of abbreviations is presented in Appendix 18.

Number (n) of char used for char weight and length was 815 for 2002, 742 for 2004 and 81 for 2005 samples. Number of samples used for stomach contents and parasite species analyses was 370 for 2002, 203 for 2004 and 68 for 2005 samples. Number of samples used for stable isotopes analysis was 69 for 2002, 26 for 2004 and 20 for 2005 samples.

**Diet items data**

Stomach content analysis and food species identification: Analysis performed on diet items included bomb calorimetry and proximate analysis.

**Bomb calorimetry**

Total energy was determined for individual diet items (i.e.by species) recovered from Arctic char stomachs. (Norwest Laboratories, Lethbridge, Alberta using direct calorimetry) (Table 24). Direct calorimetry involves burning a sample in a water-jacketed chamber and measuring the rise in water temperature. The method was devised by Berthelot (and modified by Thornhill Productions Ltd. and Gallenkamp Inc.) and is called bomb calorimetry, because the weighed sample will be placed in a heavy steel "bomb", then charged with oxygen under pressure (at least 20 atmospheres). The energy content of the sample is computed from the rise in temperature (Brody, 1945).

**Proximate analysis**

Proximate analysis was done for six key natural diet items of anadromous Arctic char [Norwest Laboratories, Lethbridge, Alberta using AOAC's (Association of Official Analytical Chemists') (1990) official methods]. Proximate composition analyses included % ash, % crude fiber, % crude protein, % total fats, % nitrogen free extracts, % TDN (total dissolved nitrogen), DE (digestible energy), GE (gross energy) and ME (metabolizable energy) expressed in Mcal/Kg (Table 25). Norwest Laboratories used the following equations to calculate, %NFE, %TDN, DE, GE and ME of samples of diet items:

$$\% \text{ TDN} = [(\text{Cpro})*(\text{DC})] + [(\text{Cfat})*(\text{DC} * 2.25)] + [(\text{Cfib})*(\text{DC})] \quad [6]$$

$$\text{DE} = [5.76*(x1)] + [9.43*(x2)] + [0*(x3)] + [4.08* (x4)] \quad [7]$$

$$GE = [5.67*(z1)] + [9.50*(z2)] + [5.26*(z3)] + [4.16*(z4)] \quad [8]$$

$$ME = [4.88*(x1)] + [9.50*(x2)] + [0*(x3)] + [4.06*(x4)] \quad [9]$$

$$\%\ NFE = [2.40*(x1)] + [7.71*(x2)] + [0*(x3)] + [3.27*(x4)] \quad [10]$$

where * = multiplication sign, TDN = Total dissolved nitrogen, DE = Digestible energy, GE = Gross energy, ME = Metabolizable energy, NFE = Nitrogen free extract, Cpro = Concentration of protein, Cfat = Concentration of fat, Cfib = Concentration of fibre $x1$ = Digestible Cpro [= Cpro x DC for Cpro for product type (= 88% for marine invertebrates)], $x2$ = Digestible Cfat [= Cfat x Digestion Coefficient for Cfat for product type (= 95.0%)], $x3$ = Digestible Cfib = Cfib x Digestion Coefficient for Cfib for product type (= 0.0%)], $x4$ = Digestible NFE = NFE x Digestion Coefficient for NFE for product type, $z1$ = Cpro = Concentration of protein, $z2$ = Cfat = Concentration of fat, $z3$ = Cfib = Concentration of fibre, $z4$ = NFE and DC = Digestion coefficient (Table 25).

**Necropsy Procedures**

The mouth lining and body surface of each fish were examined for ectoparasites. The heart, gills, intestine, pyloric caecae, gonads, liver, urinary bladder and kidneys were then removed and placed in separate petri dishes with 0.6% saline. Mesenteries were examined for larval nematodes and encysted acanthocephalans. The surface of the heart, kidneys and liver were thoroughly checked before being compressed between glass plates. In addition, sections of muscle were examined for encysted parasites.

Eyes, esophagus, stomach, intestine, urinary bladder, and caecae were excised and the contents were scrapped into petri dishes containing 0.6% saline. The contents were examined for parasites using a NIKON SMZ-1 dissecting microscope which were identified, enumerated and fixed in AFA (a solution of 50 parts 95% ethyl alcohol, 10

parts of 37% commercial formaldehyde, 2 parts of glacial acetic acid and 40 parts of distilled water) or 70% alcohol. Copepods and nematodes were fixed and stored in 70% ethanol and trematodes, cestodes and acanthocephalans were fixed in AFA for at least 48 hours and then stored in 70% prior to staining and mounting.

**Staining and mounting of parasites**

Distilled water was added at the ratio of 1:1 (i.e. alcohol and water) to a 10 ml.vial containing parasites (trematodes, cestodes and acanthocephalans preserved previously stored in 70% ethanol) and left for 5 minutes. The specimens were then placed in a Petri dish containing acetocarmine: water (1:90 parts) and left for 6 – 12 hours (time was dependent on the interaction of staining). The stain solution was decanted and fresh water added, stirred and left for 2 – 3 hours. The stain was decanted into a beaker and replaced with water (1 change only). Then, the specimen was placed in small petri dish in distilled water and checked under the microscope.

Following staining, specimens were washed twice in fresh 70% ethanol, transferred into 95% ethanol for 2 changes of 5 minutes each and finally transferred through 2 changes of absolute ethanol, of 30 minutes each. Parasite was transferred from the second change of 100% ethanol to slide brite® and left for 10 minutes. This process was repeated twice and then the specimen was transferred to ½ slide brite®: ½ permount® in glass petri dish and left for 10 minutes. Finally, the parasite specimen was mounted on a slide in permanent Canadian balsam, labeled and identified.

**Stable isotope analysis**

Methods for stable isotope analysis were adopted from Thomas and Cahoon (1993). A dorsolateral sample of muscle tissue from each fish was collected and dried in an oven at 70°C. Once dry, samples were ground into a fine powder and used directly for carbon and nitrogen analyses. $\delta^{13}$Carbon and $\delta^{15}$nitrogen isotopic analyses on the muscle (protein) were accomplished by continuous flow ion ratio mass spectrometry (CF-IRMS) using a GV-Instruments® IsoPrime attached to a peripheral temperature controlled EuroVector® elemental analyzer (EA) (University of Winnipeg Isotope Laboratory, *UWIL*). 1.0 mg samples of oven-dried fish muscle were loaded into tin capsules and placed in the EA auto-sampler in accompaniment with internally calibrated carbon/nitrogen standards (Pharma cottonseed and casein proteins: $\delta^{13}$ C = -22.95 and -26.98 ‰ Vienna PeeDee Belemnite (VPDB); $\delta^{15}$ N = 5.00 and 5.94 ‰ Air, respectively). Batch files were set up as follows: 4 casein, 4 pharma, 10 samples (every 5$^{th}$ sample duplicated and every 15$^{th}$ sample was done in triplicate), 4 cottonseed, and 4 casein. Carbon and nitrogen isotope results are expressed using standard delta ($\delta$ notation in units of *per mil* (‰). The delta values of carbon ($\delta^{13}$ $C_{cell}$) and nitrogen ($\delta^{15}$ $N_{cell}$) represent deviations from a standard, such that:

$$\delta_{sample} = [(R_{sample}/R_{standard})-1]*10^3 \qquad [11]$$

where R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio in the sample and the standard. The standards used for carbon and nitrogen isotopic analyses are Vienna PeeDee Belemnite (VPDB) and IAEA-N-1 (IAEA, Vienna), respectively. Analytical precision, determined from analysis of duplicate samples, was ± 0.16‰ for $\delta^{13}$C and ± 0.18‰ for $\delta^{15}$N. Accuracy was obtained through analysis of laboratory standards used for calibration of results.

**Statistical analyses**

**Fish**

Statistical analyses were done using SPSS (versions 11.0.1 and 14.0), SAS (version 9.1) and Microsoft Excel Package.

Frequency distribution: Simple frequency distribution of size and age classes of fish from three (2002, 2004 and 2005) sampling periods were done to determine if the size and age classes across the sampling periods were (uni- or bi-modally) comparable.

Inter-annual variations in fish growth: The term "inter-annual variations" refers to variations among year *X* (e.g. 2002), year *Y* (e.g. 2004) and/or year *Z* (e.g. 2005). Mean and standard deviation (± SD) of fish weight, length (fork), age and weight of stomach contents were calculated for all the sampling periods (Tables **10-12**).

Intra-annual fish growth: The term "intra-annual" refers to within-the-year period of time of char residency (i.e. from early July to late August) in the marine environment in a given year. Changes in char growth intra-annually were determined by calculating mean ± SD of fish weight in July and August using 2002 samples. The 2002 data set was used because of its high n value and consistent sampling across 2 months in the ocean and while diet varied among sample sites it consisted primarily of *Mysis* spp. and *Themisto libellula* (see Tables **22, 23**). Intra-annual percent increases in fish weight and length were also estimated. Differences (not reported in thesis) in fish weight and length were assessed for early July and late July/August samples statistically.

Specific growth rate (SGR): After Jobling (1994):

$$SGR = 100*(\ln W_2 - \ln W_1) / t_2 - t_1 \qquad [12]$$

where $W_1$ = char weight from day 0 to day 15 of July (i.e. early July), $W_2$ = char weight from day 16 to day 31 of August (i.e. late August), and $t_2$- $t_1$: approximated time in the sea was taken as 60 days.

Weight of char and weigth of stomach contents: Multivariate analysis of variance (MANOVA) was performed on the mean fish weight (MW), mean fish length (ML) and mean weight of stomach content (MWS) to determine if there were significant differences in these variables among the 3 (i.e. 2002, 2004 and 2005) sampling periods. A one-way ANOVA determined if there were significant differences ($P < 0.05$) in the amount of food consumed by char over time. Post-hoc tests of weight of stomach contents over time were examined using a Bonferroni correction method. Simple regression analysis was used to determine the relationship between ML, fish age and food particle size. Regression analysis was used to determine the relationship between MW and MWS, ML and MWS, as well as between MWS and age categories.

Fish condition indices: Preliminary analyses (one-way ANOVA) and mean ± SD were done to determine if there were significant differences in condition factors (K) among sampling periods. MANOVA (Table 19, Appendix 26) were performed to examine inter-annual changes in GSI, LSI and VSI while one-way ANOVA was done to determine if there were significant intra-annual changes in GSI, LSI and VSI (Fig. 17, Appendix 27).

**Diet**

Regression analysis determined the relationship between fish fork length and particle size for the 6 most common diet items from the Sylvia Grinnel and Kagnitsuatsia char samples. These stomach contents of char samples from these locations were used in this analysis because of their high numbers (*n*).

Stomach content data were pooled according to food species and sampling periods. Percent frequency occurrence (%O), percent by number (%N), and percent by volume (%V) of stomach contents were calculated (Tables **22, 23**).

Percent frequency occurrence (%O): The number of stomachs containing one or more individuals of each category expressed as a percentage of all stomachs or all those containing food (Hynes 1950, Hyslop 1980) (Tables **22, 23**).

Percent by number (%N): The number of individuals in each food category for all stomachs and the total expressed as percentage proportion of the total individuals in all food categories (Hynes 1950, Hyslop 1980) (Tables **22, 23**).

Percent by volume (%V i.e. weight): The proportion of the weight of individual prey species *i* in individual char stomach multiplied by the number of $i^{th}$ prey species contained in the same unit stomach sample and expressed as percentage (Hynes 1950, Hyslop 1980, Starostka and Applegate 1970). Average %V of prey species *i...n* was calculated (Tables **22, 25**).

Index of relative importance (IRI and %IRI): In addition, index of relative importance (IRI) (Pinkas et al. 1971) and percent index of relative importance (%IRI) (Cortés 1997) were calculated to determine the relative importance of each prey taxon to the feeding habits of char (Tables **22, 23**).

$$IRI = (N + V) \times (F) \qquad [13]$$

where N = %N, V = %V and F = %O.

Similarly;

$$\%IRI = 100 [ IRI_i / \sum IRI_i] \quad [14]$$

where *i* is a specific food category and *n* is the total number of food categories considered at a given taxonomic level (Pinkas et al. 1971, Cortés 1997).

Three-dimensional (3-D) graphing described by Costello (1990) and Cortés (1997) was done by using calculated values of %O, %N and %V to determine the feeding strategies of char and relative importance of prey species. The determination of feeding strategies reveals generalist or specialist feeding patterns while determination of relative importance of prey species will show which food species are dominant or rare (Costello 1990, Cortés 1997).

Interpretation of 3-D graphing (Cortés 1997): Each point on the graph represents the percent occurrence and abundance (in V and N) for a diet category (Fig. 7). Any diet point located close to 100% O, 100% V, and 100% N is the dominant diet taxon or category (*a* in Fig. 7). Conversely, diet items located near the origin of the three axes represent rare diet items (*b* in Fig. 7). Any diet item located closer to the %N axis than to the %V axis along the horizontal plane indicates that counts contribute more than volume to the abundance of that item. Conversely, any diet item located closer to the %V axis than to the %N axis along the horizontal plane indicates that volume contributes more than counts to the abundance of that item. The other six vertices of the cube in Fig. 7 can be regarded as extreme cases pointing to either specialized or generalized diets. Thus, a cluster of points located close to 100% O and the origin of the other two axes (%V and %N) would indicate a generalized diet (most predators take several different prey taxa in

low abundance; *c* in Fig. 7). In contrast, a diet item close to 1% O, 100% V, and 100% N (*d* in Fig. 7) would indicate a specialized diet by char, which would take large numbers of heavy items or items that make up a very large proportion of the total number and volume of stomach contents. A point located close to 100% O, 100% N, and 1% V would be indicative of a light food item consumed by most char (*e* in Fig. 7). Conversely, a diet item close to 1% O, 1% N, and 100% V would indicate a specialized diet by a few char, which would take a few very heavy items or items that make up a very large proportion of the total weight of stomach contents (*f* in Fig. 7). A diet item located near 100% O, 100% V, and 1% N (*g* in Fig. 7) would indicate that most predators take a few heavy items or items that make up a very large proportion of the total weight of stomach contents. In contrast, a diet item close to 1% O, 1% V, and 100% N (*h* in Fig. 7) would indicate a specialized diet by a few predators, which would take very large numbers of light items.

Bomb calorimetry and proximate analysis: Mean ± SD were calculated for total energy values and proximate compositions of diet species (Tables **24, 25**).

**Parasite**

Calculations on parasite data include; Prevalence: (Number of hosts infected/Number of host examined)*100%; Mean intensity: Number of parasites/Number of infected fish and Abundance: Total number of parasites in a sample of hosts/Total number of host examined (Table **26**). Terminology was according to Margolis et al (1982).

**Stable isotopes**

Regression analysis was used to establish the relationship between $\delta^{13}C$ and $\delta^{15}N$ ratios of char, invertebrates and polar cod. MANOVA was done to determine if there were significant differences in stable isotope ratios of char across sampling periods, size classes, and age classes. Similarly, MANOVA was performed to determine if there were significant differences between C: N ratios of diet items and char. Mean ± SD of $\delta^{13}C$, $\delta^{15}N$ and C: N by age classes were also investigated (Tables **27-29**). Data for 2002 was used to examine the relationship between stable isotope ratios of invertebrates and char. This is because diet items used for stable isotopes analysis were obtained from 2002 char stomach samples. Data for *Myoxocephalus scorpius* (sculpin) was from Chambers et al. (in press). But data for char that fed on sculpins was from 2002 char samples. Data for Arctic cod and for char that fed on Arctic cod were from 2005 samples.

Tests of lipid-normalizing model: Inter- and intra-annual C: N ratios of char muscle tissues were calculated to determine if the sample needed to be corrected for its lipid content by using Kiljunen et al.'s (2006) model. Fish muscle tissue with C: N ratio ≤ 3.003 were not corrected (Kiljunen et al. 2006).

Trophic enrichment factor (TEF): After Michener and Kaufman (2007):

$$TEF = \delta_{char} - \delta_{diet\ item} = \Delta^{13}C, \Delta^{15}N \quad [15]$$

where $\delta_{char}$ = stable (C or N) isotope ratio of char and $\delta_{diet\ item}$ = stable (C or N) isotope of diet item.

Trophic level (TL): After Hobson and Welch (1992):

$$TL = 1 + (D_m - 5.4)/3.8 \quad [16]$$

where TL is the trophic level of a consumer (i.e. char) and $D_m = \delta^{15}N$ value of char's muscle tissue (‰).

Mixing models: The three most important diet items in 2002, 2004 and 2005 were used to estimate the apparent proportionate fractional contribution of each diet to char's $\delta^{13}C$ and $\delta^{15}N$ ratios. This is called apparent since char consumed more than three diet items. The mixing model described by Phillips (2001) was used and described as follows:

$$\delta J_D = f_A \delta J_A + f_B \delta J_B + f_C \delta J_C \quad [17]$$

$$\delta J_D = f_A \delta K_A + f_B \delta K_B + f_C \delta K_C \quad [18]$$

$$1 = f_A + f_B + f_C \quad [19]$$

where $\delta J$ and $\delta K$ are the isotopic ratios for $\delta^{13}C$ and $\delta^{15}N$; A, B, C and D are subscripts representing three food sources and the consumer respectively whereas $f_A$, $f_B$ and $f_C$ represent the fractional contribution of each food source to the consumer's diet.

Solutions to $f_A$, $f_B$ and $f_C$ were evaluated using the following expressions (Phillips 2001):

$$f_A = \frac{(\delta K_C - \delta K_B)(\delta J_D - \delta J_B) - (\delta J_C - \delta J_B)(\delta K_D - \delta K_B)}{(\delta K_C - \delta K_B)(\delta J_A - \delta J_B) - (\delta J_C - \delta J_B)(\delta K_A - \delta K_B} \quad [20]$$

$$f_B = \frac{(\delta J_D - \delta J_C) - (\delta J_A - \delta J_C) f_A}{\delta J_B - \delta J_C} \quad [21]$$

$$f_C = 1 - f_A - f_B \quad [22]$$

Metabolic replacement constant (m): Estimates the change in $\delta^{13}C$ and $\delta^{15}N$ ratios in char. The method used to model change in $\delta^{13}C$ and $\delta^{15}N$ ratios of char in the marine environment is described in Chapter 4.

Daily growth rate constant (k)(see Chapter 4)

Half life (HL) of $\delta^{13}C$ and $\delta^{15}N$ isotopes (see Chapter 4)

# RESULTS

## Fish

Fish length and age: The frequency distribution showed that age classes in the samples are unimodal except for 2005 samples which showed a bimodal distribution (Fig. 9C). Length classes of Arctic char sampled in 2002, 2004, and 2005 had been discussed in Chapter Two.

Inter-annual variations in fish weight, length and age: Mean ± SD of inter-annual variations in fish weight were calculated and presented in Appendix 19. Mean ± SD fish weight were 1046.00 ± 532.00 g, 1223.50 ± 452.00 g, and 1646.90± 776.00 g while the mean ± SD fork length were 420.00 ± 108.00 mm, 447.70 ± 88.00 mm and 503.60 ± 101.00 mm for 2002, 2004 and 2005 samples, respectively. The mean ± SD age for these samples were 10.50 ± 4.00 (years) for 2002, 10.00 ± 3.00 for 2004 and 9.71 ± 2.70 for 2005 samples (Appendix 19).

Intra-annual fish weight: Comparison of samples was for all of July vs. all of August. Mean (± SD) of changes in fish growth for char at the ages of 7, 8, 9 and 10 in 2002 is presented in Table 17. In July, the mean ± SD of fish weight were 400.60 ± 305.70g, 690.0 ± 217.0g, 837.90 ± 288.0g and 1057.0 ± 427.0g for age 7, 8, 9 and 10, respectively. In the same order of age categories, August weight values were 695.00 ± 413.0g, 1104.70 ± 326.50g, 1125.00 ± 413.80g and 1171.0 ± 573.80g (Table 17).

Specific growth rate: The estimated SGR of char at various ages are listed in Table 9. Char at ages 7 and 8 had higher specific growth rates at 0.72% $day^{-1}$ and 1.22% $day^{-1}$,

respectively, while char at ages 9 and 10 had 0.50% $day^{-1}$ and 0.40% $day^{-1}$ specific growth rates, respectively (Table 9).

Weight of fish and stomach contents: Results of the MANOVA analysis to determine if there were significant differences in char growth and weight of stomach contents across all years 2002, 2004, and 2005 are shown in Tables **13, 14** and Appendix **15**. Table **13** shows a significant difference in the weight and weight of stomach contents of char between 2002 and 2005 samples ($F(6, 56) = 3.59$, Wilk's lambda = 0.521, $P = 0.004$). Furthermore, Table **14** lists the results of test of between-subjects (MW, ML and MWS) effects and among the sampling years (i.e. 2002, 2004 and 2005) and these include; MW ($F = 11.37$, $P < 0.001$), ML ($F = 0.423$, $P = 0.659$ ($> 0.05$)) and MWS ($F = 10.38$, $P < 0.001$).

Bonferroni multiple comparison post-hoc tests between-subjects (MW, ML and MWS) effects and sample periods are shown in Table **15**. There was no significant difference ($P = 1.000$) between MW of 2002 and 2004 samples whereas a significant difference ($P < 0.001$) was observed between MW of 2002 and 2005 samples and between MW of 2004 and 2005 samples ($P = 0.002$). No significant difference ($P = 1.000$) in ML was recorded among all the sampling years. Furthermore, there was no significant difference between MWS of 2002 and 2004 samples ($P = 1.000$) whereas there was a significant difference in the MWS of 2002 and 2005 samples ($P = 0.001$) and between the MWS of 2004 and 2005 samples ($P = 0.001$) (Appendix **21**).

The relationships between MW and MWS and between ML and MWS were best described by exponential models (Figs. **11A, 12A,** Table **15**) and the relationship between fish age and MWS are shown in Fig. **13A**. The relationship between MW and MWS were

expressed by: $y = 8.8713e^{0.0012x}$ (where y = MWS and x = MW) ($r^2 = 0.62$) for 2002, $MWS = 3.0949e^{0.0018MW}$ ($r^2 = 0.69$) for 2004 and $MWS = 2.0222e^{0.0018MW}$ ($r^2 = 0.72$) for 2005 samples (Fig. **11A**, Table **15**). Further, relationship between ML and MWS can be expressed by: $MWS = 2.1665e^{0.0063ML}$ ($r^2 = 0.73$) for 2002: $MWS = 0.7645e^{0.0083ML}$ ($r^2 = 0.82$) for 2004: and $MWS = 0.0089e^{0.0165ML}$ ($r^2 = 0.63$) for 2005 samples (Fig. **12A**, Table **15**).

Contrary to exponential models describing the relationships between MWS and MW/ML, the relationships between fish age and MWS for all the sampling years were best described by logarithmic models: MWS = 34.135ln*Age – 39.949 ($r^2 = 0.68$) (2002); MWS = 29.397ln*Age – 31.437 ($r^2 = 0.43$) (2004); MWS = 201.19ln*Age – 397.38 ($r^2 = 0.72$) (2005) (Fig. **13A**; Table **15**).

The $r^2$ values of the relationship between MWS, MW and ML in 2002 and 2004 were similar (MWS vs. MW = 0.62 (2002), 0.69 (2004): MWS vs. ML = 0.82 (2002), 0.83 (2004)). The $r^2$ values of the regression analysis involving MWS vs. MW and MWS vs. ML were 0.72 and 0.63, respectively, for 2005 samples (Table **15**). The powers of the exponential models appear similar for the equations describing the relationships between MWS and MW and between MWS and ML for all the samples. These values are 0.0012, 0.0018, and 0.0018 for MWS vs. MW representing 2002, 2004 and 2005 samples, respectively, while the powers for MWS vs. ML for 2002, 2004 and 2005 are 0.0063, 0.01 and 0.0165 respectively. The same pattern was noted in the logarithmic models describing MWS and fish age (.Fig. **13A**, Table **15**).

Data for MWS, MW and ML were pooled for all the samples (2002, 2004 and 2005) and the general models describing the relationships between MWS and MW, MWS

and ML and between MWS and fish age were estimated (Figs. **11B, 12B and 13B**). The models $MWS = 5.1086e^{0.0014MW}$ (Fig. **11B**) and $MWS = 0.503e^{0.009ML}$ (Fig. **12B**) can be used to describe the relationships between MWS and MW and between MWS and ML whereas the model MWS = 45.437ln*Age – 61.717 (Fig. **13B**) is the general model describing the relationship between MWS and fish age for anadromous Arctic char.

**Fish condition and condition factor (K)**

Condition factor: There were no significant differences in K among all samples (ANOVA: F = 0.335, P = 0.716) [mean ± SD: 1.13 ± 0.24 (2002), 1.12 ± 0.22 (2004) and 1.13 ± 0.21 (2005)] (Appendix **24**).

Inter-annual variations in liver and visceral fat weight and condition GSI, LSI and VSI: The mean ± SD of liver weight, visceral fat weight, LSI, VSI and GSI are presented in Appendix **25**. The relationship between liver and visceral fat weight is shown in Figs. **15 A&B**.

The results of MANOVA analysis performed to determine if there were significant differences in char condition data which include liver weight (Lv), liversomatic index (LSI), gonadosomatic index (GSI), weight of visceral fat (VF) and visceralfatsomatic index (VSI) are shown in Tables **19** (for VF and VSI) and Appendix **26** (for LSI and GSI) .

The condition (Lv, LSI, GSI and VSI) data was not pooled. Bonferroni multiple comparison post-hoc tests among subjects (Lv, LSI, GSI and VSI) effects and the 3 sampling years are shown in Table **19** for Lv and VSI, and Appendix **26** for LSI and GSI. There were significant differences ($P < 0.05$) in Lv and VF across the 3 sampling years. Similarly, there were significant differences in VSI ($P < 0.001$) between 2002 and 2004,

2002 and 2005 (Table **19**). By contrast, there were no significant differences in LSI and GSI ($P > 0.05$) across the 3 the sampling years (Appendix **26**).

Intra-annual comparisons of fish condition (GSI, LSI and VSI): Mean ± STD of fish condition were calculated for 2002 and 2004 samples only and the results are shown in Fig. **14** and Table **20**. The 2002 and 2004 data were used because char were sampled in both early and late July/August in these sampling years but was sampled only late July and August (early and late) in 2005. Higher mean values for GSI, LSI and VSI were observed in 2004 data than in 2002 (Table **20**). In 2002 GSI was fairly constant within the first 45 days in the sea, but decreased late August. Higher variations were observed in 2004. By comparison, LSI and VSI consistently increased from early July to late August in both 2002 and 2004.

Apparently, there was no relationship between LSI and fish fork length among 2002 and 2004 samples ($r^2 = 0.01$ and 0.01) (Fig. **18A**) whereas a weak positive correlation was observed for 2005 samples ($r^2 = 0.02$). By comparison, there was a consistently positive correlation between VSI and fish fork length over time. The 2004 and 2005 samples had higher VSI values than did the 2002 samples (Figs. **18A&B**).

Positive linear equations described the correlations between visceral fat (VF) and Lv ($r^2 = 0.57(2002); 0.60(2004); 0.23(2005)$) (Fig. **15A**). A general equation using pooled data was developed to describe the relationship between visceral fat and liver weight and this is expressed as; $Y = 0.4753x + 0.7223$ ($r^2 = 0.50$) where $Y$ = weight of visceral fat (VF) and $x$ = liver weight (Lv) (Fig. **15B**). There were no correlations between the following: K and GSI; K and Lv; GSI and Lv; K and weight of stomach

contents; Lv and weight of stomach contents; gonad weight and weight of stomach contents.

**Char diet**

The results of stomach content analyses by diet items for 3 years are presented in Tables **22** and **23**, respectively.

Diet wet weight and particle size: Data for 2004 was used to calculate mean ± SD of diet particle size and wet weight of invertebrates only, while 2005 data was used for only polar cod. The mean ± SD of diet particle size and wet weight of key natural diet items of Arctic char in the marine environment are listed in Table **21**. The mean ± SD of wet weight of char key diet items ranged from 0.0070 ± 0.13 to 29.00 ± 12.62 (g) while the total length of these diet items varied from 6.13 ± 1.00 to 144.90 ± 29.74 (mm). While *Calanus* species (copepods) were smallest in terms of weight and length (0.0070 ± 0.00 g and 6.13 ± 1.00 mm), Arctic cod had the largest values (29.00 ± 12.60g and 144.90 ± 29.74 mm) of weight and length, respectively (Table **21**).

**3-D graphical representation of stomach content analyses**

A model for interpreting 3-D graphical representation of stomach content analyses is illustrated in Fig. 7. The 3-D graphing of the stomach content analyses of 2002, 2004 and 2005 are shown in Fig. **20**. Diet items are represented by numbers: *Mysis spp* = 1; *T. libellula* = 2; *O. littoralis* = 3; *Thysanoessa* spp = 4; *Calanus* spp = 5; *Gammarus* spp = 6; Arctic cod = 7 (Fig. **20**). According to the model (Cortés 1997) (Fig. 7), *Mysis* spp was the most important diet species among 2002 char samples. After *Mysis* spp, in the order of importance was *T. libellula* while *O. littoralis*, *Thysanoessa* spp, *Calanus* spp and *Gammarus* spp were represented as rare species. (Fig. **20A**, Table **22**).

*T. libellula* was the most dominant prey species followed by *Mysis* spp in the 2004 samples (Fig. **20B**). *Thysanoessa* spp, *Calanus* spp, and *Gammarus* spp were also represented as rare species. (Fig. **20B**, Table **22**). Even at a lower %O, *Mysis* spp and *T. libellula* still tended towards the dominance axis in 2005 samples (Fig. **20C**), while Arctic cod and *O. littoralis* perhaps due to high %O and %V, tended towards the generalized and specialized axes of the 3-D graphs in 2005 samples. Overall, Arctic cod was the most important diet species in 2005 samples and tended towards specialization for all 3 years (Figs. **20 A-C**; Tables **22, 23**).

**Proximate analyses and bomb calorimetry of key diet items:**

Total energy and proximate composition values of char key marine diet species are presented in Tables **24** and **25**, respectively. The total energy content of these diet species ranges from 17480-24200 $KJKg^{-1}$ (Table **24**). *O. littoralis* had the lowest (17480 $KJKg^{-1}$), while Arctic cod had the highest total energy content with 24200 $KJKg^{-1}$ (Table **24**). The proximate compositions of char diet items varied. *Thysanoessa* spp. and *O. littoralis* had lower fat content with 10.48% and 12.86%, respectively (Table **25**). Higher fat levels were found for Arctic cod (42.09%), sculpin (34.72%) and *T. libellula* (30.77%) (Table **25**)

Regression analysis showed a strong negative linear relationships between % ash vs. digestible energy (DE) ($r^2 = 0.77$), % ash vs. gross energy (GE) ($r^2 = 0.73$), % ash vs. metabolizable energy (ME) ($r^2 = 0.69$), % crude fibre vs. DE ($r^2 = 0.52$), % crude fibre vs. GE ($r^2 = 0.45$) and % crude fibre vs. ME ($r^2 = 0.44$).

Results from regression analysis showed that char had varied responses to diet items of different sizes (Fig. **19**). Char size was not correlated with food particle size of

*Themisto libellula* ($r^2 = 0.03$), *Thysanoessa* spp. ($r^2 = 0.004$) and Arctic cod ($r^2 = 0.02$). Char size was positively correlated with *Calanus* spp. ($r^2 = 0.10$), *Mysis* spp. ($r^2 = 0.42$) and *Onesimus littoralis* ($r^2 = 0.43$) (Fig. **19**).

**Parasites**

The prevalence, mean intensity and abundance values of parasite species recovered from char over the 3 years are shown in Table **26**. At least 9 parasite species were recovered from char and included 3 trematodes (*Brachyphallus crenatus*, *Derogenes varicus*. and *Prosorhynchus squatmatus*), 4 cestodes (*Diphyllobothrium* sp., *Bothrimonus sturionis*. *Proteocephalus* sp. and *Eubothrium salvelini*) and 2 acanthocephalans (*Corynosoma* sp. and *Echinorhynchus gadi*).

The abundance values for the 2002 samples were 380.55 for *D. varicus,* 27.06 for *B. sturionis* and 3.78 for *Corynosoma* sp. (Table **26**). The abundance values for the 2004 samples were 60.49 for *B. crenatus and* 38.38 for *B. sturionis*. Parasite species with the highest abundance values for the 2005 samples were *P. squamatus* (32.99) followed by *B. crenatus* (5.32) and *B. sturionis* (1.11). Except for *Diphyllobothrium* sp., the abundance values for the remaining 6 parasite species were < 1.00 (Table **26**).

**Stable isotope analyses**

The mean ± SD $\delta^{13}C$ and $\delta^{15}N$ ratios of char and diet items are presented in Fig. **22.** The mean ± SD $\delta^{13}C$ and $\delta^{15}N$ ratios of diet items were -19.36 ± 1.06; 13.76 ± 1.83 for invertebrates, -17.26 ± 0.60; 15.05 ± 1.23 for sculpins, and -21.29 ± 1.16; 12.60 ± 0.67 for Arctic cod. Char that fed on invertebrates had -18.90 ± 0.79; 14.52 ± 1.17, char that fed on sculpins had -19.36 ± 1.06; 13.76 ± 1.83 and char that fed on Arctic cod had -20.22 ± 0.95; 13.92 ± 1.66. There was no correlation between $\delta^{15}N$ and char length in

char that fed on invertebrates ($r^2 = 0.00$). Char that fed on sculpins showed a weak positive correlation ($r^2 = 0.06$). But char that fed on Arctic cod showed a strong positive correlation ($r^2 = 0.68$) between $\delta^{15}N$ and char length (Fig. 23).

Results of MANOVA analysis found no significant change in $\delta^{13}C$ and $\delta^{15}N$ ($F(2, 4) = 2.151$, Wilk's lambda = 0.927, $P = 0.075$) between the years. Between-subjects ($\delta^{13}C$ and $\delta^{15}N$) tests of MANOVA analysis found no significant difference ($P > 0.05$) across the 3 sampling years (see also Tables 27, 28).

Lipid-normalizing model (Kiljunen et al. 2006): Data showed that mean ± SD of C: N ratios of char muscle were 0.73 ± 0.11, 0.67 ± 0.06, 0.69 ± 0.10 for 2002, 2004 and 2005, respectively. The mean C: N ratios for early July were 0.65 ± 0.21 (2002; n = 11) and 0.59 ± 0.12 (2004; n = 13). There were no data for late August in 2002 but the mean for 2004 was 0.69 ± 0.06 (n = 15). Since all ratios were below 3, lipid-normalization was not applied (Kiljunen et al. 2006) (Table 27, 28).

The $\delta^{13}C$ and $\delta^{15}N$ ratios of char key diets items are presented in Fig. 24 and Appendices 28, 29. Invertebrates with higher $\delta^{15}N$ values have lower $\delta^{13}C$ values but the inverse was also noted. The $\delta^{13}C$ values of *T. libellula*, *Thysanoessa* spp., *Gammarus campylops* and *O littoralis* ranged from -20.30 to -19.00 whereas $\delta^{13}C$ values of *Mysis* spp. and *Gammarus pulex* ranged from -18.78 to -17.00.

Mixing models: Based on calculations using Phillips' (2001) mixing model, the estimated proportionate fractional contribution of the 3 most important diet items in 2002, 2004 and 2005 char samples for the $\delta^{13}C$ and $\delta^{15}N$ were 3.00, 23.10 and -25.10 (see p. 123 for discussion on the negative sign; Appendix 30). These results are approximations since

other diet species will contribute to the overall estimates of proportionate fractional contribution.

Metabolic replacement constants (m): The estimated m values for $\delta^{13}C$ and $\delta^{15}N$ isotopes were 0.00142 and 0.00107, respectively (Table 30).

Daily growth rate constant (k): The calculated daily growth rate constant was 0.006593 (Table 30)

Half life of stable isotopes: The estimated HL for the wild char was 86.50 days for $\delta^{13}C$ and 90.57 days for $\delta^{15}N$ isotopes (Table 30).

# DISCUSSION

## Fish

Regardless of age classes, Arctic char sampled in 2002, 2004 and 2005 (Fig. 8) had comparable length classes and this suggests absence of significant growth differences. Data from this char population presented by Gallagher and Dick (2007), revealed a similar pattern. Gallagher and Dick (2007) concluded that there are slightly more and larger char today than over the past 30 years (Fig. 10). The non-significant impact of the variation in the number of larger char on the overall population corresponded to non-significant differences in length classes over time (Gallagher and Dick, 2007; Fig. 10).

The age classes for char samples are unimodal except for 2005 samples which showed a bimodal distribution (Fig. 9). Perhaps this is due to sampling errors such as inconsistency in sampling time or low number of samples.

Inter-annual char weight and length: Discussions on growth curves of this population are presented in Gallagher and Dick (2007). Based on calculations of the proportional changes, char weight increased over the years sampled. Percent increase in char weight was correlated with inter-annual changes in food habits suggesting an influence of nutrient contents and total energy of key diet items although other factors may be involved (Figs. 20, 21, Tables 22, 23, Appendix 19).

Intra-annual char weight and length: Younger char (ages: 7, 8, and 9) had a greater proportional increase in weight than char at age 10. Percent increase in weight declined with char age and length. This agrees with Jobling (1983) who noted that char SGR of

cultured char declined as fish increased in length. Char (age 7) sampled in 2002 increased their weight by 74% while char (ages: 8, 9 and 10) increased their weight by 60%, 34% and 11%, respectively, from July to August (Table 17).

Mean percentage increase in char length by age class i.e. 7 (10%) and 8 (11%) was about double that of char at ages 9 (6%) and 10 (5%). Since this analysis was done by age class and not collectively, these results suggest consistent growth patterns among anadromous char populations. Based on these calculations, the mean percentage increase in weight of char over 2 months of foraging in the marine environment is between 34-45% by weight and *c.* 8% by length (Table 17, Appendix 20).

Adams et al. (1989) noted that small char had slightly higher diet consumption (in absolute terms) than larger fish. Similarly, Rikardsen et al. (2002) reported that regardless of low degree of stomach fullness, post-smolts had higher percent frequency occurrence of diet items. Considering the fact that both younger and older char consumed comparable proportions of diet (Table 17), it is possible that younger char grew faster because they had higher metabolic and assimilation rates. Rikardsen et al. (2000) reasoned that faster growth among anadromous char might result from their higher diet consumption and more efficient food assimilation. It is also probable that younger char (age: 7 and 8) might be below reproductive age since sexually immature char often has more weight than char that had spawned (see Dutil 1984). Results from this study are in agreement with these reports.

Berg and Berg (1989) observed that char that migrated earlier grew faster than char of the same size that migrated later to the sea the same year. Rikardsen et al. (2000) noted that younger char that migrated earlier stayed longer in the sea and as a result, had

a significantly higher percentage weight increase than smolts that arrived later. Rikardsen et al. (2000) recorded a 112% percentage increase in char weight in early migrating smolts (age: 4-5 years) and attributed this to a one week extra stay in the sea. These reports agree with traditional knowledge of anadromous char. According to the local subsistence fishers larger char are the last to migrate upstream in the fall (Dick Pers. Comm.),

Maximum growth in char is observed between late July and early August (Fig. **14**). Rikardsen et al. (2000, 2005) also demonstrated that char post-smolts exhibited fast compensatory growth within the first 2-3 weeks of their marine sojourn but almost stopped growing prior to their return to freshwater. These observations agree with the findings of Grainger (1953) who reported that deposition of char summer otolith ring commences shortly after entrance into the sea. Klemetsen et al. (2003) and Rikardsen et al. (2004b) reasoned that it is important for char to obtain quality diets as soon as they arrive in the sea to enable rapid growth which is an important factor for predator avoidance, parasite resistance and migration.

Specific growth rate (SGR): Specific growth rates of anadromous char were influenced by size and age. My observation agrees with the findings of Jobling (1994) from cultured char (Table 9). From natural feeding, anadromous char (age range: 7 - 10), a SGR range of 1.22 – 0.40 $day^{-1}$ was calculated during open water in the sea (Table 9). The mean (0.71 $day^{-1}$) SGR of anadromous char was comparable to experimentally reared young-of-the-year char at 7 °C in freshwater (see Chapter Four and Appendix 22). Although at a higher temperature (12 – 13 °C), Finstad and Heggberget (1993) reported similar findings

for anadromous char in Finmark, northern Norway. Finstad and Heggberget (1993) observed a SGR of 1.49, 1.11 and 1.03% $day^{-1}$ in 1989, 1990 and 1991, respectively.

Weight of fish and stomach contents: The role of fish weight in diet consumption in marine char is not fully understood. Do smaller and larger char consume the same amount of diet regardless of size (weight or length)? Results from my study have shown that the relationship between the weight of stomach contents and fish weight or length is exponential (Figs. 9, 11). Apparently, the amount of diet char can consume in the marine environment corresponds to increasing weight and length of char. However, smaller and larger char consumed proportionally equal amounts of diet by wet weight (see Chapter 5).

Char consumed an average of 3.8% of its total body weight in the first 30 days (i.e. July) of their marine sojourn, declining to 3.2% over the remaining 30 days (i.e. August) resulting in an overall mean of 3.4% (Tables 16-18). A similar result was reported by Amundsen and Klemetsen (1988) who found that char in Takvatn, northern Norway, consumed 3.4% of body weight in July and 3.8% in August leading to an annual mean of 3.6%.

It is estimated that char fed at *c.* 9.7% (mean wet weight) of total body weight per day in July but declined to *c.* 7.9% in August. Adams et al. (1989) reported that anadromous char from Ungava Bay consumed *c.* 7.5% (wet weight) of their body weight per day in early summer, decreasing to *c.* 5.5% prior to the return to freshwater. Data from this study are comparable with the report by Adam et al. (1989). The differences among these results may be a reflection of growth, age or diet differences between char populations of Frobisher and Ungava Bays.

**Fish condition**

Condition factor (K) is often used to compare fish populations in terms of their nutritional state and to assess the quality of habitat related to food availability (Lambert and Dutil 1997). Results from the 2002 data presented in Chapter Two (see Fig. **6**) revealed that char condition factors over time in the marine environment were not influenced by season (i.e. July or August) or changes in food habits. Higher condition factors [mean ± SD: 1.13 ± 0.24 (2002), 1.12 ± 0.22 (2004) and 1.13 ± 0.21 (2005)] showed that all diet items of char were nutritionally sufficient to meet char nutrient and total energy requirements over a short period of time in the marine environment. In my study, K did not correlate with the amount of food consumed, weight of liver and visceral fat deposits in anadromous char. No data is available on the relationships between K and these variables.

Significant variations in the weight of visceral fat (VF), visceralfatsomatic index (VSI) and liver weight over time were due to differences in the total fat content of the most important diet species (Table **19**). The effects of dietary fat on char growth are discussed under diet quality section (see p. 111).

The model describing the relationship between visceral fat and liver weight (Fig.**15B**; $r^2 = 0.23$) was developed by using the pooled data (n = 206) and expressed as a linear equation:

$$VF = 0.025Lv + 3.1445 \qquad [23]$$

where VF = visceral fat and Lv = liver weight. Although this equation does not account for all the lipids in char, its significant correlation suggests that it can be used to predict either variable (i.e. VF or Lv) in anadromous char. This result agrees with that of Jensen

(1980) that liver is a good parameter for quick evaluation of char condition. Although more field and laboratory studies are required to test the accuracy of this equation, indirect estimation of lipid levels has also been carried out by Rikardsen and Johansen (2003) who estimated char lipid levels by using a morphometric method.

Changes in char diet quality corresponded to consistent increases in liver and visceral fat weight over time (Tables **22**, Appendix **25**). For instance, percentage increases in liver weight (actual weight not ratio) were 44%, 30% and 61% from 2002 to 2004, 2004 to 2005 and between 2002 and 2005 samples, respectively. Similarly, increases in the weight of visceral fat were 43.89%, 42.46% and 85.70% between 2002 and 2004, 2004 and 2005 and between 2002 and 2005 samples, respectively (Appendix **25**). These results suggest that changes in fat content level of char key diet items influence the amount of visceral fat deposits stored per marine sojourn. The difference between total fat of *T. libellula* (i.e. diet item with highest %IRI in 2004) and *Mysis* spp. (diet item with highest %IRI in 2002) was able to produce remarkable shift in weight of visceral fat whereas the difference between the total fat of Arctic cod (diet item with highest %IRI in 2005) and *T. libellula* did not lead to significant increase in the weight of visceral fat. This result is suggestive that shift to diets with higher total fat level may slow down char feeding rate since they probably may have stored enough visceral fat.

Indices describing liver (LSI), visceral fat (VSI) and gonads (GSI) have been used to help define fish condition (Chakraborty 2007, Johnson and Dick 2001). Char diet quality influenced LSI and VSI. By contrast, it had no effect on GSI (Fig. **14**, Table **20**). Since maximum growth of char in the marine environment is recorded between late July and late August (this study), proportional increases in these indices were calculated using

early July data as day-0. Char GSI decreased from 123% in late July to 70% in late August in 2002 (Mean = 98%) and from 155% in late July to 77% in late August in 2004 (Mean = 97%). Apparently, it appears there is no change in gonad weight even as fish weight increases. By comparison, slight increases were recorded for LSI which showed that char increased from 104% to 111% (Mean = 103%) and from 115% to 134% (Mean = 128%) from late July to late August in 2002 and 2004, respectively. From late July to late August in 2002, VSI increased from 70% to 148% (Mean = 104%) whereas in 2004, it increased from 144% in late July to 253% (Mean = 203%) in late August. The consistencies in these results are indicative of corresponding consistency in physiological responses of char in the marine environment regardless of time (Table 20). Jørgensen et al. (1997) reported that total body lipid stores of char increased about 5 times in the sea. Data from this study supports these findings (Fig. 14, Table 20).

It is apparent that char invest more into energy storage than in gonadal development during the marine phase. This result agrees with the data in Chapter Two and with the findings of Dutil (1984) and Johnson (1989) who reported that char do not migrate to the sea the year of spawning. Dutil (1986) reasoned that since the spawning interval was directly proportional to threshold energy reserves and threshold body conditions, char are triggered to spawn early in the season and not during anadromy. Therefore, since threshold body condition is vital to gonadal development (Dutil 1986, Crespi and Teo 2002), energy acquisition and storage perhaps for gamete production during freshwater phase is important.

It was noted that between late August of 2002 and that of 2004, percent increase in LSI was 31% while an increase of 49% in VSI was calculated within the same period.

Superimposing these results on diet items proximate composition data, particularly the total fat content levels of *Mysis* spp. (16.87%), *T. libellula* (30.77%) and Arctic cod (42.09%), revealed mean changes in total fat content of 13.90% (i.e. 30.77 – 16.87%; *Mysis* spp. vs. *T. libellula*), 25.22% (Arctic cod vs. *Mysis* spp.) or 11.32% (Arctic cod vs. *T. libellula*) will lead to significant increases in LSI and VSI but not GSI values (Appendix **20**).

Reasons for variations in the relationship between LSI and fish size over time (Fig. **18A**) are not fully understood. Dutil (1986) noted that changes in energy storage might not be precisely estimated based on fish size but by using condition index. By comparison, the relationship between VSI and fish size was constant over time (Fig. **18B**) Perhaps there is a lipid level threshold for the liver below which significant increases in LSI will not be observed or beyond which remarkable increases in LSI with length will be apparent. This assumption is in agreement with Dutil (1986) who suggested a threshold energy reserve or threshold body condition below which it is impossible for char to recover from energy lost due to spawning.

**Char and food particle size**

Selection of diet items based on particle size suggested a potential for trophic structuring but the correlation was dependent on a specific diet item and its size range during its life stages. Although it is unknown if char feed preferentially on gravid amphipods or if maturity of diet items changes over time in the open water, Percy (1993b) noted that fecundity of *T. libellula* is significantly correlated with its size. This observation agrees with my results which revealed that char have an innate ability to distinguish diet items based on their quality and size (Fig. **19**, Table **25**). Similar findings

were reported by More and More (1974) who noted size-related feeding among anadromous char in Cumberland Sound area of Baffin Island but their observations were not correlated to proximate compositions of diet items.

Although there had been many studies on feeding habits of anadromous char (e.g. More and More 1974, Adams et al. 1989, Finstad and Heggberget 1993, Rikardsen et al. 2000, Gulseth and Nilssen 2001, Rikardsen and Amundsen 2005), this study is the first to examine the feeding habits of anadromous char based on individual particle size, nutrient composition and total energy content.

Collective assessment of stomach contents may result in misleading interpretations since preliminary analysis on pooled particle size data showed that feeding patterns of char in the marine environment are not influenced by sizes of diet items. Although it is unknown if char feed on diet items in their schools or as individual units, a comparison of sizes and proximate compositions of diet items gave a better understanding of the subject (Fig. 19, Table 21).

Grainger (1953) listed about 34 different diet items from stomach samples of 450 char. Further, based on a review of published data, Johnson (1980) also noted that char marine diet species range from amphipods to fish species. More and More (1974) observed high abundance of *T. libellula* (size range: 18-37 mm) in char stomachs from Cumberland Sound area of Baffin Island and de March et al (1977) recorded the occurrence of Arctic cod (size range: 94-200 mm) early in July and high abundance of *T. libellula* and *Mysis* species (size range: 20-32 mm) in late August in anadromous char returning to Stanwell-Fletcher Lake. Data from this study is in agreement with these reports on the basis of composition and diversity of diet items. However, except for More

and More (1974), results from my study do not support the hypothesis of an exclusively opportunistic feeding behaviour of anadromous char (see Fig. 19) as commonly reported by some workers (e.g. Johnson 1980, Table 21). More and More (1974) found that significant variation in composition of diet items in anadromous char of different sizes was due to size-dependent feeding.

**Diet quality and quantity**

Char feeding and growth is influenced by diet quality. Similar observations had been reported by Rikardsen et al. (2007) who noted that char feeding and growth patterns reflect the quality and diversity of diet species available in the marine environment over time. Char fed mostly on invertebrates in 2002 and 2004 (i.e. *Mysis* spp. and *T. libellula*, respectively) but proportions changed between 2002 and 2004 and in 2005 char fed chiefly on Arctic cod (Tables 22, 23). Similar observations have been reported by Rikardsen et al. (2007) who noted that anadromous char and brown trout shifted from sandlance and crustaceans to herring larvae when the latter was in high abundance. Results from my study have also shown that diet species abundance is directly proportional to diet index of relative importance (IRI) (Tables 22, 23). It is interesting to note that changes in char diet importance corresponded with positive changes in total fat content of diet items which in turn are reflected in char growth patterns and condition over time (Tables 22-25).

These results demonstrate that the lipid content of char's most important diet item influences char total weight, visceral fat and liver weight (Figs. 14-18, Tables 10-12, 25). Perhaps total energy of diet items are influenced by the proportion of total fat content.This assumption is in agreement with the observations of Miglavis and Jobling

(1989), van Dijk et al. (2005) and Hayward et al. (1997) who reported that compensatory growth and energy reserves were directly proportional to increased food intake for juvenile char, juvenile roach *Rutilus rutilus* and in juvenile hybrid sunfish (*Lepomis cyanellus* X *L. machrochirus*), respectively. Although the effect of dietary lipid levels on feeding and growth of anadromous char was not the focus of this chapter, data from this study are in agreement with Olsen et al. (1990), who found that char fed commercial diet with unsaturated fat content demonstrated a higher growth rate than char fed with coconut oil with comparatively saturated fat content. Further, data from my study agrees with the findings of Martino et al. (2002) who fed *Pseudoplatystoma coruscans*, a Brazilian carnivorous fish, four diets of constant protein (46%) and lipid (6%, 10%, 14, and 18%) and gross energy (GE) of 4440, 4650, 4840, and 5140 Kcal/Kg. Martino et al. (2002) reported a significant difference ($P < 0.05$) in fish proximate composition due to dietary lipid levels and also observed a significant increase ($P < 0.05$) in visceral fat content directly proportional to dietary lipid level. Tabachek (1986) and Gurure et al. (1995) reported that increasing dietary lipid increases the proportion of dietary protein utilized for growth in char under controlled conditions. This sparing effect has also been reported for other salmonids including rainbow trout (Watanabe 1977, Reinitz et al. 1978, Takeuchi et al. 1978) and coho salmon (Clarke et al. 1982).

Total energy and nutrient contents of char key marine diet items were all above minimum requirements of char (Dick and Yang 2002) (Table **24**). *O. littoralis* was reported as char's most important diet species (Grainger 1953) but, over time, its importance in char's diets shifted to other food items with higher total energy, % protein and % total fat values such as *Mysis* spp, *T. libellula* and Arctic cod (Fig. **20**, Table **22**).

Jobling and Wandsvik (1983) noted that char diet intake and growth under controlled conditions are not only influenced by the nutrient contents but also by the total energy content of the diet items. Similar findings have been reported by Alanärä and Kiessling (1996) who demonstrated that char fed high-energy (22.0 $MJKg^{-1}$) diets grew significantly faster than those offered low-energy (19.8 $MJKg^{-1}$) diets under culture conditions.

Char preference for diet species with higher total energy values appeared to increase over the three years in which samples were collected (i.e. 2002, 2004 and 2005) (Figs. **20, 21**; Tables **24, 25**). A correlation of relative diet importance and total energy content of diet species suggests that char food habits changed from *O. littoralis* (total energy = 17480 $KJKg^{-1}$) (re: Grainger 1953) to *Mysis* spp. (mean: 20830 $KJKg^{-1}$) in 2002 to *T. libellula* (22960 KJ $Kg^{-1}$) in 2004 and to Arctic cod (24200 $KJKg^{-1}$) in 2005 (Figs. **20**). The occurrence of *Mysis* spp. as the second most important diet species (and not *T. libellula)* followed by *O. littoralis* among stomach contents of char in 2005 (Table **23**), confirms the hypothesis that char feeding habits in the marine environment is affected by the quality and quantity of diet items. Rikardsen et al. (2007) noted a shift from crustaceans in the initial marine residence to fishes especially herring later in the period. Rikardsen et al. (2007) suggested that char might preferentially select herring when present in abundant numbers.

**Parasite data**

Laboratory analysis found that *Mysis* spp were the intermediate hosts of *B. crenatus*, *D. varicus*, and *P. squamatus*; *T. libellula* of *B. sturionis, Corynosoma* sp., and *Thysanoessa* spp. of *Echinorhynchus gadi* (T. Dick and I. Isinguzo and Personal

observations). High parasite prevalence and abundance in the 2002 and 2004 samples corresponded to high abundance of invertebrates (e.g. *Mysis sp.* and *T. libellula*) from these samples. By contrast, low parasite load among 2005 char samples was due to low abundances of amphipods in char stomach contents in 2005 (Tables **22, 23, 26**). This result is in agreement with Kennedy (1978b) who reported that levels of infection in any locality are directly proportional to abundance of intermediate hosts.

Char with polar cod in their stomachs (i.e. 2005 char samples) had low levels of infection compared to 2002 and 2004 char samples. This is not surprising given that Arctic cod is one of the definitive hosts and not the intermediate host of the parasites recorded in this study. However, Dick and Belosevic (1981) reported high prevalence and abundances of *B. crenatus*, *P. squamatus*, and *B. sturionis,* from char and expressed their potentials as good biological indicators for anadromous char. Results from this study are in agreement with this report. For example, high variations in parasite abundance data in 2005 corresponded with feeding patterns of char in that year. It is worthy to note that char fed mostly on *Mysis* spp. and *T. libellula* in 2002/2004 than in 2005. Based on this observation, parasite data was able to detect both diet shift and quality (Table **26**).

The parasites of Salmoniformes have been reviewed in Chapter One. The occurrence of *B. crenatus*, *P. squamatus*, and *B. sturionis* in hosts other than Salmoniformes and particularly char is worth noting. For instance, *P. squamatus* is commonly found in mussels *Mytilus edulis*, *M. galloprovincialis* (Matthews 1973), sole *Solea solea* (Laffargue et al. 2004), shorthorn sculpin *Myoxocephalus scorpius* (Coustau 1991), Greenland halibut *Reinharditus hippoglossoides* (Arthur and Albert 1994), ringed

seal *Phoca hispida* (McDonald and Margolis 1995, Dick Pers. Comm.), conger eel *Conger conger* (Matthews 1973) and painted eel *Echelus myrus* (Radujkovic et al. 1989).

*B. crenatus* has been reported from a wide range of hosts other than char and these include Arctic cod *Boreogadus saida,* Atlantic cod *Gadus morhua,* Atlantic herring *Clupea harengus,* Pacific herring *Clupea pallasi,* American plaice *Hippoglossoides platessoides*, rainbow smelt *Osmerus mordax*, saithe *Pollachius virens*, Greenland halibut and ribbed sculpin *Triglops pingeli* (McDonald and Margolis 1995). Similarly, *B. sturionis* has been described as one of the parasites of sturgeon Acipenseridae (Choudhury and Dick 2001) and flounders, Pleuronectidae (McDonald and Margolis 1995). This is a reflection of the broad range of host species of *B. sturionis* other than char.

The relationships of *P. squamatus, B. crenatus*, and *B. sturionis* to char and their wide ranges of marine host species are traceable to the corresponding wide ranges of their intermediate hosts. These (i.e. intermediate hosts) are in turn, diet species of the hosts. For example, the presence of *Mysis* spp., *T. libellula* and *Thysanoessa* spp. in the stomachs of ringed seal and Arctic cod confirms that *P. squamatus, B. crenatus*, and *B. sturionis* will be found in any intermediate and final host species that overlap with one another in their distributions (Dunbar 1942, Lønne and Gulliksen 1989).

My results showed that diet and parasite data were able to correlate diet shift to diet quality, but were unable to detect trophic structuring among anadromous char since char are infected by a broad range of non-host specific parasite species in several diet species.

**Stable isotopes data**

Char muscle tissues: Stable isotope values of consumers increase relative to their diet species and enrichment in $\delta^{13}C$ is approximately by 0-1.00‰ while that of $\delta^{15}N$ is by *c.* 3.4 ± 1.1‰ (Owens 1987, Minagawa and Wada 1984, DeNiro and Epstein 1978). The enrichment of $\delta^{15}N$ stable isotope ratios in the tissues of consumers relative to their diets leads to trophic structuring (Vander Zanden et al. 1997) and this demonstrates the relationships between predators and prey species in a given ecosystem. There was trophic structuring among char in the marine environment based on stable isotopes analysis but this was for char that fed on *Mysis* spp., and *O. littoralis* (see Figs. **19**, **22**).

Trophic structuring is often positively correlated with fish size and age among char in freshwater systems where diet selection, specialization and competition are maximal due to inadequate food resources (e.g. Hobson and Welch 1995, Chakraborty 2007). Positive relationships between fish size and $\delta^{15}N$ and $\delta^{13}C$ ratios among char morphotypes have been reported by Hobson and Welch (1995), Adams et al. (2003), Guiguer et al. (2002) and Chakraborty (2007) and among brown trout (Grey et al. 2002) in freshwater systems.

There was no correlation ($r^2 = 0.00$) between char length and $\delta^{15}N$ values in char that fed on invertebrates (based on pooled data), while char that fed on sculpins showed a weak positive correlation ($r^2 = 0.06$). By contrast, char that fed on Arctic cod showed a strong positive correlation ($r^2 = 0.68$) (Fig. **23**). These results suggest that $\delta^{15}N$ enrichment of char that fed on Arctic cod is particle size related but not in char that fed on invertebrates and sculpins. This is expected since mean ± STD length of *Mysis* spp. (26.67 ± 2.66 mm) and *T. libellula* (29.88 ± 5.23 mm) was similar (Table **21**). Further,

the slight tendency of positive correlation in char that fed on sculpins corresponded to slight variation in the sizes of sculpins recovered from char stomachs. Therefore, stable isotope results correlated with the particle size data since it showed that correlation (i.e. between char length and $\delta^{15}N$ values) was dependent on specific diet items (Fig. 23).

Calculations, based on Hobson and Welch's (1992) model (see eq. 11 p. 90) were used to calculate the trophic level of char relative to diet items. Char that fed on invertebrates had a trophic level of +3.4‰, which is indicative of its slightly higher $\delta^{15}N$ values than char that fed on Arctic cod and sculpin which had a trophic level of +3.2‰, respectively (Fig. 22). It is not known why char that fed on invertebrates shared the same trophic range with char that fed on Arctic cod/sculpin. Perhaps higher $\Delta^{15}N$ (see eq. 10, p.88) compensates for lower dietary protein. Char that fed on invertebrates had higher (5.07) $\Delta^{15}N$ value than char (1.32) that fed on Arctic cod. Although not expected, this result suggests that the stable isotopes signatures of *Mysis* spp. and *T. libellula* were high enough to dominate char stable isotopes signals, thus suggesting that diet quality plays a role (Fig. 22, Table 25). This assumption agrees with the findings of Michener and Kaufman (2007) who reported that $\delta^{15}N$ enrichment is dependent on diet quality and not quantity. It is also probable that the food habits of *Mysis* spp. and *T. libellula* were responsible for high $\delta^{15}N$ ratios of char that fed on these diet species (see discussion on p. 118, Fig. 24).

Dunbar (1946) reported that *T. libellula* is a cannibalistic amphipod that feeds also on other zooplankton such as copepods, copepod larvae, ostracods, decapods and nauplius larvae. Further, Percy and Fife (1981) noted *T. libellula* is a carnivorous amphipod that accumulates lipid in summer when its prey species are abundant. Similar

observations had been reported for *Mysis* spp. Viherluoto et al. (2004) reported that *Mysis* species grew faster when the proportions of copepods increase in their stomachs (Figs. **19 – 21**; Tables **27-29**).

Based on $\delta^{13}C$ values, char that fed on sculpins shifted to two trophic levels (i.e. the difference between the lowest and the highest $\delta^{13}C$ values, = 2.11‰), char that fed on Arctic cod had one trophic shift (1.07‰) while char that fed on invertebrates had no trophic shift (0.13‰) (Fig. **22**, see DeNiro and Epstein 1978). Although $^{13}C$ enrichments do not always correspond to increases in trophic levels (Michener and Kaufman 2007), my result is in agreement with the findings of Rau et al. (1983) who reported $\delta^{13}C$ trophic enrichment of 1‰ in a marine pelagic food web. Trophic shift in char that fed on sculpin is perhaps a reflection of $\delta^{13}C$ values of sculpin's key diet items (i.e. *O. littoralis* and *Gammarus* spp., see discussions on p. 119/120; Chambers et al. (In press)) and the low proportions of these diet items in char diets. This assumption supports the hypothesis that higher proportions of high fat diets will lead to lower $\delta^{13}C$ values in consumers while higher proportions of high protein diets will lead to higher $\delta^{15}N$ values (see Focken 2001). Overall, my result is in agreement with the reports of Bradstreet and Cross (1982) and Hobson and Welch (1992) who found that Arctic cod was an important energy link between primary producers and vertebrates that occupy higher trophic levels.

Lipid normalizing model: The mean ± SD C: N ratios of char muscle tissue ranged between 0.59 ± 0.12 and 0.73 ± 0.11. This indicates negligible variations in $\delta^{13}C$ and $\delta^{15}N$ ratios of char diet items (Fig. **24**) (Kiljunen et al. 2006) and also supports the hypothesis of absence of trophic structuring in anadromous char given that the presence

of trophic structuring would also have been reflected in distinct variations in C: N ratios of char muscle tissues.

Metabolic turnover rate constant (m): Anadromous char had high metabolic turnover rates for $\delta^{13}C$ to $\delta^{15}N$ isotopes (Table 33). This is expected given the estimated high SGR (Table 9). Hesslein et al. (1993) reported a direct proportionality between growth rate and rate of change of stable isotopes. Hesslein et al. (1993) reported metabolic turnover rates of 0.0018 $day^{-1}$ for both $\delta^{13}C$ and $\delta^{15}N$ isotopes for growing broad whitefish *Coregonus nasus*. Results obtained from my study support the findings of Hesslein et al. (1993) and for the young-of-the-year char. The m values for YOY char varied from 0.00001 to 0.0152 $day^{-1}$ and this variation corresponded with different growth rates which in turn are a reflection of diet type that char groups were fed (see Chapter Four).

Half life of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes: I estimated HLs of 86.50 days for $\delta^{13}C$ and 90.57 days for $\delta^{15}N$ isotope for char within the age range of 7 to 10 (Table 30). These are relatively short HLs considering the size (weight and length), age and cold environment of wild char. My results contrasted the findings of Hesslein et al. (1993) who reported that HL of $\delta^{13}C$ was longer than 1 year for 2.5 year old broad whitefish.

Short HLs of $\delta^{13}C$ and $\delta^{15}N$ isotopes is correlated with the high SGR and high metabolic turnover rates (0.00142; 0.00107 $day^{-1}$) calculated for char (Tables 9, 30; Appendices 28, 29). Hesslein et al. (1993) stated that slow-growing fish would have longer HLs while fast-growing fish will have short HL. Data from this study support this report since char had high SGR (mean: 0.71 $day^{-1}$) (Table 9).

Short HLs of anadromous char are comparable to HLs (Mean = *c.* 50 days) of YOY char reared under controlled condition which is a reflection of high SGR in wild

and YOY char (see Chapter Four). Recent studies (e.g. Logan et al. 2006) have shown that liver tissues turnover significantly faster than muscle tissues and give better estimates of HLs. Perhaps wild char would have shown shorter HLs values if liver tissues were analyzed.

Short HL values provide more recent information because the more rapid changes in tissues occur, the more likelihood of recent dietary uptake (Tieszen et al. 1983, Suzuki et al. 2005). Furthermore, short HLs imply that new and equilibrium $\delta^{13}C$ and $\delta^{15}N$ ratios would be reached after a short period of time post-diet switch e.g. from freshwater to marine environment (see Suzuki et al. 2005). Therefore, short HLs obtained from this study are indicative that $\delta^{13}C$ and $\delta^{15}N$ ratios were recently acquired in the marine environment and not a carry-over from the freshwater system. Since short HLs of $\delta^{13}C$ and $\delta^{15}N$ ratios represent recent changes in $\delta^{13}C$ and $\delta^{15}N$ ratios, the result obtained by plotting $\delta^{13}C$ vs. $\delta^{15}N$ ratios (Fig. 22) which showed no trophic structuring among char in the marine environment is validated.

This is the first study that had estimated metabolic turnover rates and HLs of $\delta^{13}C$ and $\delta^{15}N$ isotopes in anadromous char populations.

Char diet items: The trophic position of Arctic cod by $\delta^{13}C$ and $\delta^{15}N$ ratios is two levels higher than that of *O. littoralis* and *Gammarus* spp. but not *Mysis* spp., *T. libellula*, and *Thysanoessa* species. There were two sources of carbon resulting to two groups (here referred to as groups A and B) of Arctic cod based on $\delta^{13}C$ values (Fig. 24). Group A had lower $\delta^{13}C$ values (mean ± SD -22.48 ± 0.40, n = 5) while group B had higher $\delta^{13}C$ values (mean ± SD -20.44 ± 0.56, n = 7). Perhaps group B were feeding more on *O. littoralis* and *Gammarus* spp. since these diet species had higher $\delta^{13}C$ values (mean ± SD

-18.56 ± 1.31, n = 3). Although the food habits of *O. littoralis* are not fully understood, higher $\delta^{13}C$ signals is indicative of microphyte feeding (DeNiro and Epstein 1978). Grall et al. (2006) recorded highest $\delta^{13}C$ values of -16‰ to -18‰ for 5 bivalve species, 1 crustacean and 1 gastropod and observed that these diet species were filter feeders. My results support this report since *O. littoralis* and *Gammarus* spp. are both benthic and interface filter feeders (i.e. benthopelagic) that utilize both detritic sedimented particulate organic matter (POM) and benthic microphytes (Sainte-Marie 1986). Relative frequency occurrence (%) of stomach contents of *O. littoralis* revealed the presence of large carrion (31%), polychaetes (6.1%), arthropods (35.1%), crustaceans (18.4%) and detritus (34.2%) (see Sainte-Marie 1986). The swimming ability (mean speed 17 $cms^{-1}$) of *O. littoralis* may account for their opportunistic feeding behaviour (Sainte- Marie 1986). The consequence of such ability is acquisition of carbon from both benthic and pelagic sources and this may have influenced the result of this study.

Crawford and Jorgenson (1993) observed the presence of *Calanus* spp. (copepods), *O. gracialis* and *T. libellula* (amphipods) in their sampling nets, but reported that Arctic cod fed predominantly on *O. littoralis* and slightly on *T. libellula*. My data support this report because out of the three sampling years, *O. littoralis* had its highest %V value in char stomachs in 2005 which was the year Arctic cod was the most important diet item in char (see Table 22).

Although the carbon origin of group A is unknown, Lønne and Gulliksen (1989) reported high occurrences of calanoids (i.e. copepods) and *T. libellula* in stomach of Arctic cod samples. Perhaps Arctic cod with lower $\delta^{13}C$ values (i.e. group A) fed on calanoids and *T. libellula*. Laboratory analysis found exoskeletal tissues of copepods in

Arctic cod stomachs (Pers. Observation). It is probable that high fat content of calanoids and *T. libellula* influenced the $\delta^{13}C$ values of group A (see Table 25, Weslawski et al. 1994). Or, Arctic cod in group A fed on a mixture of phytoplankton and zooplankton (i.e. *Mysis* spp., *T. libellula* and *Thysanoessa* spp.). The lower $\delta^{13}C$ values (corresponding to high total fat content) of these diet species (mean ± SD -19.32 ± 0.76; n = 5) and phytoplankton (-22.4, n = 74) (see Grall et al. 2006) support this assumption (Table **25**). Further, the two groups are suggestive of two size classes of Arctic cod. Hobson and Welch (1992) found that larger Arctic cod (range 48-247 mm, n = 26) had higher (-18.9; 15.2) $\delta^{13}C$ and $\delta^{15}N$ values compared to smaller Arctic cod (range 14-16 mm, n = 1) (-19.8; 11.1). Similar results were obtained from my study. Larger (i.e. group B) Arctic cod (mean ± SD 153.33 ± 39.73, n = 7) had higher $\delta^{13}C$ (-20.44 ± 0.56) while smaller Arctic cod (mean ± SD 117.40 ± 14.52, n = 5) had lower $\delta^{13}C$ (-22.48 ± 0.40) values. This result supports the assumption that group B were feeding on amphipods since $\delta^{15}N$ values of both groups were the same (A = 12.92 ± 0.56; B = 12.38 ± 0.67).

Although there were no distinct variations in $\delta^{15}N$ values of the most important invertebrates (i.e. *Mysis* spp. and *T. libellula*) and Arctic cod, trophic shift occurred between Arctic cod and diet items such as *O. littoralis* and *Gammarus* species (Fig. **24**). Further, MANOVA results showed no significant differences ($P < 0.05$) in the ratios of $\delta^{13}C$ to $\delta^{15}N$ isotope ratios (C/N) between amphipods and Arctic cod and between these diet items to char among the year samples (Table **29**). Perhaps this indicates homogenization processes and apparent stability in feeding habits of char.

Mixing models: Estimates of apparent fractional contributions of individual diet species to char trophic positions using 3-food source mixing models (Phillips 2001) suggest that

diet item of higher quality may likely contribute more to the consumer's $\delta^{13}C$ to $\delta^{15}N$ isotope ratios (Appendix 30). Negative (-25.10) fractional contribution value estimated for Arctic cod suggests that the tissue turnover time for vertebrate fat might be longer than the duration of char in the sea. Alternatively, it might be reflective of intrinsic variations in physiological responses in animals (Ben-David and Schell 2001). Estimates of apparent fractional contributions correlated with diet quality (Fig. 19-21, Tables 22, 23). Overall, stable isotopes results supported diet and parasite species data.

**Conclusions**

Selection of diet items based on particle size suggested a potential for trophic structuring but the correlation was dependent on a specific diet item and its size range during its life stages. Char growth and condition were not dependent on the amount of diet consumed but on the quality of key diet items. Char diet and parasite species were unable to show trophic structuring as char were infected by a broad range of non-host specific parasite species which in turn is a reflection of their diet. However, parasite species are able to show recent feeding history of char even in the absence of diet species (i.e. intermediate hosts) since endohelminth parasites such as B. *crenatus*, *D. varicus* and *B. sturionis* appear to last longer in char stomachs. Further, parasite species provided strong prediction of diet shift, quality and quantity as the presence of Arctic cod correlated with low parasite loads. By contrast, high parasite abundance correlated with high abundance of amphipod diets

Stable isotopes results were able to show trophic structuring among marine char. But trophic structuring was diet item-specific and was found for char feeding on *Mysis* spp. and *O. littoralis*. $\delta^{13}C$ ratios of diet items can be used to predict spatial and temporal

variations in char carbon sources. Calculated HLs of $\delta^{13}C$ and $\delta^{15}N$ of char muscle tissues revealed that char in the ocean may require about 3 months to reflect a change in stable isotopes ratios. This is relatively short considering the size and age of char that migrate to the sea. Perhaps these HLs would have been shorter if liver tissues were used in analysis. Calculated metabolic rates and HLs of $\delta^{13}C$ and $\delta^{15}N$ ratios reflected high SGR and these were comparable to that of YOY char (see Chapter Four). Therefore, short HLs are dependent on fish growth rather than fish size. This observation contrasts the reports of Hesslein et al. (1993).

To summarize, I conclude that in the absence of abundant quality diet items, char may consume diet items that are more numerous in abundance while still retaining their innate instinct to feed preferentially on high quality larger diet items when these occur in great quantity. This is the first study that had combined diet, parasites and stable isotopes data to examine trophic relationships among anadromous char feeding in the marine environment.

Table 9. Specific growth rates of anadromous char by age classes. Data used was from 2002 samples.

| Age (Years) | n | Mean ± SD weight in early July (g) | n | Mean ± SD weight in late August (g) | Specific growth rate (% day-1)* |
|---|---|---|---|---|---|
| 7 | 7 | 412.14 ± 346.22 | 15 | 634.00 ± 160.42 | 0.72 |
| 8 | 7 | 509.29 ± 335.91 | 33 | 1058.19 ± 315.05 | 1.22 |
| 9 | 12 | 803.75 ± 294.04 | 29 | 1065.45 ± 392.73 | 0.50 |
| 10 | 4 | 837.50 ± 332.23 | 22 | 1048.64 ± 519.00 | 0.40 |
| **Average** | | | | | **0.71** |

*Approximated residency time in the sea = 60 days
Early July = day 0 - day 15
Late August = day 16 - day 31

Table 10. The weight (g) and length (mm) ranges and mean ± standard deviation (SD) of fish weight (MW), length (ML) and weight of stomach contents (MWS) of the age (Years) classes of 2002 samples of Arctic char.

| Age (Years) | n | MW ± SD | ML ± SD | MWS ± SD | Weight range | Length range |
|---|---|---|---|---|---|---|
| 4 | 5 | 65.4 ± 17.91 | 184.80 ± 22.95 | NA | 37-80 | 144-199 |
| 5 | 23 | 149.0 ± 12.00 | 233.68 ± 46.97 | 3.93 ± 2.66 | 30-417 | 142-350 |
| 6 | 29 | 313.0 ± 194.00 | 292.43 ± 59.99 | 8.63 ± 7.49 | 35-655 | 138-395 |
| 7 | 66 | 654.0 ± 411.00 | 366.85 ± 62.14 | 24.92 ± 18.91 | 80-2900 | 210-535 |
| 8 | 114 | 977.0 ± 411.00 | 426.78 ± 60.01 | 28.67 ± 19.81 | 40-2546 | 150-570 |
| 9 | 147 | 1142.0 ± 450.00 | 456.01 ± 54.95 | 34.14 ± 22.94 | 334-2546 | 315-595 |
| 10 | 164 | 1317.0 ± 597.0 | 472.42 ± 72.34 | 39.89 ± 26.11 | 334-3214 | 310-650 |
| 11 | 80 | 1340.0 ± 683.0 | 474.06 ± 77.47 | 37.71 ± 30.03 | 376-3589 | 331-670 |
| 12 | 57 | 1329.0 ± 624.0 | 479.04 ± 73.18 | 50.02 ± 33.89 | 376-2629 | 300-595 |
| 13 | 55 | 1499.0 ± 928.0 | 492.56 ± 71.02 | 48.86 ± 34.65 | 170-6928 | 282-635 |
| 14 | 37 | 1608.0 ± 740.0 | 516.00 ± 73.77 | 58.10 ± 50.83 | 460-3756 | 365-668 |
| 15 | 19 | 1521.0 ± 622.0 | 505.89 74.98 | 19.25 ± 15.09 | 417-2700 | 360-595 |
| 16 | 13 | 1277.50 ± 554.99 | 474.08 ± 69.95 | 52.13 ± 6.47 | 417-2504 | 348-575 |
| 17 | 6 | 1454 ± 432.0 | 510.33 ± 43.14 | 60.23 ± 17.75 | 960-2212 | 436-440 |

Table 11. The weight (g) and length (mm) ranges and mean ± SD of fish weight (MW), length (ML) and weight of stomach contents (MWS) of the age (Years) classes of 2004 samples of Arctic char.

| Age | n | MW ± SD | ML ± SD | MWS ± SD | Weight range | Length range |
|---|---|---|---|---|---|---|
| 5 | 4 | 305 ± 463.9 | 227.5 ± 52.7 | 1.75 ± 0.35 | 50-100 | 192-305 |
| 6 | 27 | 717.5 ± 356 | 361.2 ± 127.3 | 28.25 ± 19.51 | 100-1500 | 271-530 |
| 7 | 64 | 829.7 ± 350.7 | 408.0 ± 56.7 | 18.87 ± 21.13 | 150-1700 | 259-524 |
| 8 | 115 | 1025 ± 446.4 | 433.9 ± 74.5 | 25.81 ± 20.62 | 150-2600 | 264-577 |
| 9 | 119 | 1299.0 ± 596.2 | 474.5 ± 66.5 | 45.83 ± 41.91 | 250-3500 | 310-636 |
| 10 | 127 | 1522.0 ± 765.7 | 498.3 ± 73.4 | 60.72 ± 48.11 | 300-3600 | 320-676 |
| 11 | 110 | 1626.0 ± 727.7 | 505.4 ± 101.8 | 42.36 ± 36.54 | 450-3100 | 346-675 |
| 12 | 73 | 1622.0 ± 729.7 | 514.1 ± 71.2 | 46.01 ± 30.71 | 250-3550 | 316-670 |
| 13 | 47 | 1407.0 ± 636.2 | 489.3 ± 66.1 | 41.76 ± 49.74 | 350-3500 | 346-650 |
| 14 | 34 | 1348.0 ± 715.9 | 488.5 ± 79.9 | 27.24 ± 24.66 | 300-3100 | 346-635 |
| 15 | 22 | 1757.0 ± 811.6 | 523.9 ± 77.3 | 42.31 ± 20.73 | 600-3900 | 412-657 |

Table 12. The weight (g) and length (mm) ranges and mean ± SD of fish weight (MW), length (ML) and weight of stomach contents (MWS) of the age (Years) classes of 2005 samples of Arctic char.

| Age | n | MW ± SD | ML ± SD | MWS ± SD | Weight range | Length range |
|---|---|---|---|---|---|---|
| 5 | 1 | 300 | 310 | 5.9 | 300 | 310 |
| 8 | 8 | 1050 ± 653 | 431.9 ± 87.12 | 17.04 ± 16.99 | 300-2000 | 304-544 |
| 9 | 12 | 1538 ± 570.9 | 509.1 ± 58.1 | 9.62 ± 6.98 | 600-2500 | 370-571 |
| 10 | 24 | 2054 ± 613.2 | 560.7 ± 49.89 | 103.14 ± 101.99 | 1200-3150 | 485-675 |
| 11 | 10 | 2190 ± 572.4 | 568.2 ± 38.48 | 78.34 ± 76.14 | 1300-3200 | 524-654 |
| 12 | 14 | 2625 ± 715.4 | 602.3 ± 52.97 | 163.98 ± 132.58 | 1500-4000 | 523-705 |
| 13 | 12 | 1771 ± 509.7 | 543.1 ± 54.57 | 67.56 ± 76.95 | 1200-2600 | 467-673 |

Table 13. Multivariate analysis of variance (MANOVA) tests of mean weight (MW), length (ML) and weight of stomach contents (MWS) for 2002, 2004 and 2005 samples.

| Test statistics | Value | F-ratio | Hypothesis df | Error df | Sig. (P < 0.05) |
|---|---|---|---|---|---|
| **Intercept** | | | | | |
| Pillai's Trace | 0.954 | 192.607 | 3 | 28.00 | 0.000 |
| Wilk's Lambda | 0.046 | 192.607 | 3 | 28.00 | 0.000 |
| Hotelling's Trace | 20.636 | 192.607 | 3 | 28.00 | 0.000 |
| Roy's Largest Root | 20.636 | 192.607 | 3 | 28.00 | 0.000 |
| **Year** | | | | | |
| Pillai's Trace | 0.493 | 3.163 | 6 | 58.00 | 0.009 |
| Wilk's Lambda | 0.521 | 3.593 | 6 | 56.00 | 0.004 |
| Hotelling's Trace | 0.890 | 4.007 | 6 | 54.00 | 0.002 |
| Roy's Largest Root | 0.858 | 8.296 | 3 | 29.00 | 0.000 |

Table 14. MANOVA results of test of between-subjects (MW, ML and MWS) effects for 2002, 2004 and 2005 samples.

| Source | Dependent variable | Type III Sum of squares | df | Mean square | F-ratio | Sig. (P < 0.05) | Abbrev. |
|---|---|---|---|---|---|---|---|
| Corrected model | MW | 5381645.737 | 2.000 | 2690822.869 | 11.370 | 0.000 | S |
| | ML | 12273.981 | 2.000 | 6136.991 | 0.423 | 0.659 | NS |
| | MWS. | 44999.515 | 2.000 | 22499.757 | 10.383 | 0.000 | S |
| Intercept | MW | 69872132.045 | 1.000 | 69872132.045 | 295.251 | 0.000 | S |
| | ML | 6740992.695 | 1.000 | 6740992.695 | 464.434 | 0.000 | S |
| | MWS | 127686.859 | 1.000 | 127686.859 | 58.926 | 0.000 | S |
| Year | MW | 5381645.737 | 2.000 | 2690822.869 | 11.370 | 0.000 | S |
| | ML | 12273.981 | 2.000 | 6136.991 | 0.423 | 0.659 | NS |
| | MWS | 44999.515 | 2.000 | 22499.757 | 10.383 | 0.000 | S |

Table 15. Summary of regression equations between mean weight of stomach contents and mean fish weight and length and fish age for 2002, 2004 and 2005 samples.

| Regression analysis | Model equation | $r^2$ | Model type | Sampling year |
|---|---|---|---|---|
| MWS vs. MW | $y = 5.4665e^{0.0015x}$ | 0.62 | Exponential | 2002 |
| | $y = 3.0949e^{0.0018x}$ | 0.69 | Exponential | 2004 |
| | $y = 2.0222e^{0.0018x}$ | 0.72 | Exponential | 2005 |
| MWS vs. ML | | | | |
| | $y = 0.7645e^{0.0083x}$ | 0.73 | Exponential | 2002 |
| | $y = 0.3048e^{0.01x}$ | 0.82 | Exponential | 2004 |
| | $y = 0.0089e^{0.0165x}$ | 0.63 | Exponential | 2005 |
| MWS vs. Fish age | | | | |
| | $y = 38.27\ln(x) - 53.38$ | 0.68 | Logarithmic | 2002 |
| | $y = 29.40\ln(x) - 31.44$ | 0.43 | Logarithmic | 2004 |
| | $y = 343.96\ln(x) - 721.02$ | 0.72 | Logarithmic | 2005 |
| General models | | | | |
| MWS vs. MW | $y = 5.1086e^{0.0014x}$ | 0.67 | Exponential | Pooled data |
| MWS vs. ML | $y = 0.503e^{0.009x}$ | 0.75 | Exponential | Pooled data |
| MWS vs. Fish age | $y = 45.437\ln(x) - 61.717$ | 0.23 | Logarithmic | Pooled data |

Table 16. Inter-annual percentage proportion of weight of diets consumed relative to total mean ± SD fish weight for the 3 sampling years.

| Time | *Mean ± SD fish weight (g) | Mean ± SD weight of stomach contents (g) | Prop. of stomach contents to fish weight | % prop. of wt. of stomach contents to fish weight |
|---|---|---|---|---|
| 2002 | 1046.14 ± 531.89 | 35.88 ± 18.15 | 0.034 | 3.4 |
| 2004 | 1223.47 ± 452.06 | 34.62 ± 16.15 | 0.028 | 2.8 |
| 2005 | 1646.86 ± 776.21 | 63.65 ± 58.14 | 0.038 | 3.8 |
| **Mean** | **1305.49 ± 308.64** | **44.72 ± 16.41** | **0.034** | **3.4** |

*Mean of means of fish weight calculated from Tables 12-14

Table 17. Intra-annual fish weight of char by ages (Years) classes (7, 8, 9 and 10) based on 2002 samples

| Statistics | Fish weight | | | |
|---|---|---|---|---|
| | Age 7 (n) | Age 8 (n) | Age 9 (n) | Age 10 |
| Total mean ± SD of fish weight (g) in July | 400.56 ± 305.70 (9) | 690.0 ± 217.0 (18) | 837.86 ± 288 (21) | 1057.0 ± 427.0 (18) |
| Total mean ± SD of fish weight (g) in August | 695.08 ± 08 (56) | 1104.72 ± 326.48 (36) | 1125.25 ± 413.75 (32) | 1171.0 ± 573.83 (34) |
| Percent (%) increase in weight | 74% | 60% | 34% | 11% |

Table 18. Intra-annual percentage proportions of diet consumed relative to total mean ± SD fish weight based on 2002 samples

| Time | Early July (n) | Late August (n) |
|---|---|---|
| Total fish weight (g) | 803.0 ± 517.0 (156) | 995.0 ± 517.73 (375) |
| Total weight of stomach contents (g) | 32.43 ± 26.75 (95) | 33.32 ± 28.82 (77) |
| Percent proportion (%) of diet consumed relative to total fish weight | 4% | 3% |

Table 19. Multiple comparison based on Bonferroni post-hoc tests among effects (Lv, VF and VSI)* for the 3 sampling years.

| Dependable variable | Year (a) | Year (b) | Mean Difference (a-b) | Standard Error | Sig | Abbrev. |
|---|---|---|---|---|---|---|
| Lv | 2002 | 2004 | -5.0191 | 1.55164 | 0.004 | S |
| | | 2005 | -17.6404 | 2.1879 | 0 | S |
| | 2004 | 2002 | 5.0191 | 1.55164 | 0.004 | S |
| | | 2005 | -12.6213 | 2.41221 | 0 | S |
| | 2005 | 2002 | 17.6404 | 2.1879 | 0 | S |
| | | 2004 | 12.6213 | 2.41221 | 0 | S |
| VF | 2002 | 2004 | -6.4026 | 0.85187 | 0 | S |
| | | 2005 | -13.5159 | 1.20118 | 0 | S |
| | 2004 | 2002 | 6.4026 | 0.85187 | 0 | S |
| | | 2005 | -7.1133 | 1.32433 | 0 | S |
| | 2005 | 2002 | 13.5159 | 1.20118 | 0 | S |
| | | 2004 | 7.1133 | 1.32433 | 0 | S |
| VSI | 2002 | 2004 | 0.3294 | 0.04508 | 0 | S |
| | | 2005 | -0.368 | 0.6357 | 0 | S |
| | 2004 | 2002 | 0.3294 | 0.4508 | 0 | S |
| | | 2005 | -0.0386 | 0.07008 | 1 | NS |
| | 2005 | 2002 | 0.368 | 0.06357 | 0 | S |
| | | 2004 | 0.386 | 0.07008 | 1 | NS |

(*): = Lv = Liver weight (g); VF = Visceral fat weight (g) and VSI = Visceralfatsomatic index.

Table 20. Intra-annual changes in fish condition (VSI, LSI and GSI)* based on 2002 and 2004 samples

| Time | Period | Time range (Days) | n | VSI | n | LSI | n | GSI |
|---|---|---|---|---|---|---|---|---|
| 2002 | Early July | 0 - 15 | 50 | 0.61 ± 0.42 | 61 | 1.70 ± 1.23 | 38 | 0.40 ± 0.43 |
| | Late August | 16 - 30 | 78 | 0.90 ± 0.46 | 83 | 1.89 ± 0.70 | 62 | 0.28 ± 0.29 |
| 2004 | Early July | 0 - 15 | 40 | 0.57 ± 0.26 | 38 | 1.57 ± 0.51 | 36 | 0.66 ± 0.50 |
| | Late August | 16 - 30 | 49 | 1.44 ± 0.64 | 52 | 2.10 ± 1.41 | 51 | 0.51 ± 0.57 |

(*): VSI = Visceralfatsomatic index; LSI = Liversomatic index and GSI = Gonadosomatic index

Table 21. Mean ± SD of wet weight (g), length (mm) and ranges of key natural diet species of char. Invertebrate samples were from 2004 and Arctic cod was from 2005 samples.

| Food Species | Mean weight ± STD | Mean length ± STD | Weight range | Length range | n |
|---|---|---|---|---|---|
| *Onesimus littoralis* | 0.0071 ± 0.02 | 9.79 ± 1.68 | 0.0319 - 0.1124 | 7 - 14 | 48 |
| *Mysis* species | 0.1259 ± 0.13 | 26.67 ± 2.66 | 0.0548 - 0.1524 | 20 - 32 | 49 |
| *Themisto libellula* | 0.3212 ± 0.14 | 29.88 ± 5.23 | 0.0576 - 0.7273 | 18 - 37 | 34 |
| *Thysanoessa* species | 0.1929 ± 0.03 | 31.24 ± 2.31 | 0.1281 - 0.2899 | 25 - 36 | 49 |
| *Gammarus* species | 0.1216 ± 0.04 | 13.94 ± 2.16 | 0.0573 - 0.2122 | 11 - 20 | 33 |
| *Calanus* species | 0.0070 ± 0.00 | 6.13 ± 1.25 | 0.0023 - 0.0132 | 4 - 8 | 15 |
| Arctic cod | 29.076 ± 12.62 | 144.90 ± 29.74 | 9 - 64 | 94 - 200 | 49 |

Table 22. Percent frequency occurrence (%O), percent by number (%N) and percent by volume (%V) of each diet category for the 3 sampling years.

| Time (n = no. of stomach analyzed) | Food species | Total no. of diet items | %O | %N | %V |
|---|---|---|---|---|---|
| 2002 (n = 370) | *Mysis* species | 89839 | 76.32 | 64.19 | 98.11 |
| | Sculpin | 2638 | 30.36 | 1.88 | NA |
| | *Themisto libellula* | 27552 | 72.98 | 19.68 | 91.83 |
| | *Onesimus littoralis* | 6188 | 30.08 | 4.42 | 23.42 |
| | *Thysanoessa* species | 8519 | 32.03 | 6.09 | 19.9 |
| | *Calanus* species | 5078 | 22.01 | 3.63 | 1.7 |
| | *Gammarus* species | 42 | 11.70 | 0.03 | 57.75 |
| | Polychaetes | 45 | 12.53 | 0.03 | NA |
| | Arctic cod | 2 | 0.56 | 0.00 | 149.42 |
| | Total | 139968 | | | |
| 2004 (n = 203) | *Mysis* species | 17535 | 43.55 | 52.25 | 17.51 |
| | Sculpin | 268 | 11.29 | 0.80 | NA |
| | *Themisto libellula* | 5590 | 69.89 | 16.66 | 53.78 |
| | *Onesimus littoralis* | 2482 | 15.59 | 7.40 | 17.67 |
| | *Thysanoessa* species | 4945 | 23.66 | 14.73 | 16.98 |
| | *Calanus* species | 1955 | 19.35 | 5.83 | 12.78 |
| | *Gammarus* species | 103 | 7.53 | 0.31 | 5.29 |
| | Polychaetes | 625 | 1.61 | 1.86 | NA |
| | Arctic cod | 8 | 3.23 | 0.02 | 208.10 |
| | Total | 33511 | | | |
| 2005 (n = 68) | *Mysis* species | 1653 | 17.57 | 27.04 | 95.61 |
| | Sculpin | 815 | 14.86 | 13.33 | NA |
| | *Themisto libellula* | 428 | 18.92 | 7.00 | 36.95 |
| | *Onesimus littoralis* | 1019 | 12.16 | 16.67 | 131.63 |
| | *Thysanoessa* species | 10 | 2.70 | 0.16 | 2.61 |
| | *Calanus* species | 71 | 14.86 | 1.16 | 0.47 |
| | *Gammarus* species | 203 | 9.46 | 3.32 | 30 |
| | Polychaetes | 1688 | 4.05 | 27.61 | NA |
| | Arctic cod | 226 | 55.41 | 3.70 | 131.63 |
| | Total | 6113 | | | |

Table 23. The index of relative importance (IRI) and %IRI of diet species for 3 sampling years.

| Time | Diet Species | %O | %N | %V | IRI | %IRI |
|---|---|---|---|---|---|---|
| 2002 | *Mysis* species | 76.32 | 64.19 | 98.11 | 12387 | 53.69 |
| | *Themisto libellula* | 72.98 | 19.68 | 91.83 | 8138 | 35.27 |
| | *Onesimus littoralis* | 30.08 | 4.42 | 23.42 | 838 | 3.63 |
| | *Thysanoessa* species | 32.03 | 6.09 | 19.9 | 832 | 3.61 |
| | *Calanus* species | 22.01 | 3.63 | 1.7 | 117 | 0.51 |
| | *Gammarus* species | 11.7 | 0.03 | 57.75 | 676 | 2.93 |
| | Arctic cod | 0.56 | 0 | 149.42 | 83 | 0.36 |
| | **Total** | | | | **23072** | |
| 2004 | *Mysis* species | 43.55 | 52.25 | 17.51 | 3038 | 29.85 |
| | *Themisto libellula* | 69.89 | 16.66 | 53.78 | 4923 | 48.38 |
| | *Onesimus littoralis* | 15.59 | 7.4 | 17.67 | 391 | 3.84 |
| | *Thysanoessa* species | 23.66 | 14.73 | 16.98 | 750 | 7.37 |
| | *Calanus* species | 19.35 | 5.83 | 12.78 | 360 | 3.54 |
| | *Gammarus* species | 7.53 | 0.31 | 5.29 | 42 | 0.41 |
| | Arctic cod | 3.23 | 0.02 | 208.1 | 671 | 6.6 |
| | **Total** | | | | **10175** | |
| 2005 | *Mysis* species | 17.57 | 27.04 | 95.61 | 2155 | 17.05 |
| | *Themisto libellula* | 18.92 | 7 | 36.95 | 832 | 6.58 |
| | *Onesimus littoralis* | 12.16 | 16.67 | 131.63 | 1804 | 14.28 |
| | *Thysanoessa* species | 2.7 | 0.16 | 2.61 | 7 | 0.06 |
| | *Calanus* species | 14.86 | 1.16 | 0.47 | 24 | 0.19 |
| | *Gammarus* species | 9.46 | 3.32 | 30 | 315 | 2.49 |
| | Arctic cod | 55.41 | 3.7 | 131.63 | 7498 | 59.34 |
| | **Total** | | | | **12635** | |

Table 24. The total energy values of some key diet items of anadromous Arctic char from 2002 samples.

| Food species | n | Mean ± SD of total energy ($KJKg^{-1}$) |
|---|---|---|
| *Mysis mixta* | 12 | 20330 ± 1.45 |
| *Mysis oculata* | 11 | 21330 ± 1.02 |
| Sculpin | 2 | 21480 ± 0.94 |
| *Themisto libellula* | 15 | 22960 ± 0.90 |
| *Onesimus littoralis* | 4 | 17480 ± 0.94 |
| *Thysanoessa inermis* | 3 | 21980 ± 0.41 |
| *Thysanoessa raschii* | 3 | 21520 ± 0.26 |
| Arctic cod* | NA | 24200 ± 00 |

* Source: Weslawski et al. (1994)

Table 25. Proximate compositions (dry matter) analyses of key natural food species of Arctic char in the marine environment from 2004 samples.

| Diet items | *Mysis* species | Sculpin | *Themisto libellula* | *Onesimus littoralis* | *Thysanoessa* species | Arctic cod |
|---|---|---|---|---|---|---|
| n | 4 | 2 | 4 | 2 | 4 | 2 |
| Ash (%) | 12.07 ± 0.69 | 8.64 ± 1.86 | 16.76 ± 1.45 | 26.01 ± 0.05 | 11.49 ± 0.28 | 6.88 ± 0.51 |
| Crude protein (%) | 64.73 ± 2.03 | 55.20 ± 3.54 | 44.68 ± 1.04 | 49.80 ± 2.55 | 72.88 ± 0.57 | 48.85 ± 2.62 |
| Crude fibre (%) | 2.63 ± 0.28 | 0.35 ± 0.07 | 6.75 ± 0.56 | 6.30 ± 0.28 | 2.00 ± 0.20 | 0.60 ± 0.14 |
| Total fat (%) | 16.87 ± 3.11 | 34.72 ± 4.58 | 30.77 ± 1.37 | 12.86 ± 0.93 | 10.48 ± 0.27 | 42.09 ± 1.35 |
| Nitrogen free extract (%) | 3.73 ± 2.49 | 1.10 ± 0.71 | 1.63 ± 0.61 | 5.10 ± 1.84 | 3.18 ± 0.24 | 1.60 ± 0.85 |
| TDN (%) | 93.04 ± 5.96 | 122.76 ± 6.69 | 105.07 ± 2.60 | 71.34 ± 0.14 | 86.52 ± 0.50 | 132.98 ± 0.62 |
| DE crude (Mcal/Kg) | 4.79 ± 0.25 | 5.91 ± 0.23 | 5.02 ± 0.11 | 3.68 ± 0.04 | 4.63 ± 0.03 | 6.25 ± 0.01 |
| GE (Mcal/Kg) | 5.57 ± 0.18 | 6.49 ± 0.27 | 5.86 ± 0.12 | 4.59 ± 0.01 | 5.36 ± 0.02 | 6.87 ± 0.01 |
| ME (Mcal/Kg) | 4.31 ± 0.25 | 5.51 ± 0.26 | 4.70 ± 0.11 | 3.30 ± 0.02 | 4.08 ± 0.03 | 5.90 ± 0.01 |

Calculated digestibility of protein = 88%; calculated digestibility of fat = 95% (Calculations by Norwest Laboratories, Lethbridge, Alberta); Published data on digestibility of fat = 85-95% (range) [Source: NRC (1981)]. Digestibilty of freeze dried *Mysis sp.* = 89.6% [Source: NRC (1981)]. Digestibilty of fish meal (herring) = 93-97% (%fat; range) [Source: NRC (1981)].

Table 26. Prevalence, mean intensity ± SD and abundance of parasite species recovered from Arctic char for the 3 sampling years.

| Year | Parasite species | Prevalence (%) | Mean (± STD) intensity | Abundance |
|---|---|---|---|---|
| 2002 | **Trematoda** | | | |
| | *Brachyphallus crenatus** | 32.43 | 567.90 ± 606.82 | 184.18 |
| | *Derogenes varicus** | 39.19 | 971.06 ± 2506.23 | 380.55 |
| | *Prosorhynchus squamatus** | 6.76 | 2692.8 ± 4427.97 | 181.95 |
| | **Cestoda** | | | |
| | *Diphyllobothrium* sp. | 52.00 | 6.03 ± 32.50 | 3.15 |
| | *Bothrimonus sturionis** | 83.28 | 32.49 ± 27.33 | 27.06 |
| | *Proteocephalus* sp. | 3.50 | 3.58 ± 0.00 | 0.13 |
| | *Eubothrium salvelini* | 58.00 | 0.47 ± 1.42 | 0.28 |
| | **Acanthocephala** | | | |
| | *Corynosoma* sp.* | 77.70 | 4.86 ± 4.90 | 3.78 |
| | *Echinorhynchus gadi** | 2.70 | 3.50 ± 5.00 | 0.10 |
| 2004 | **Trematoda** | | | |
| | *Brachyphallus crenatus** | 4.73 | 895.20 ± 1655.76 | 60.49 |
| | *Derogenes varicus** | 8.11 | 267.17 ± 376.04 | 21.66 |
| | *Prosorhynchus squamatus** | 2.03 | 482.67 ± 784.30 | 9.78 |
| | **Cestoda** | | | |
| | *Diphyllobothrium* sp. | 2.22 | 1.50 ± 0.00 | 0.03 |
| | *Bothrimonus sturionis** | 58.20 | 65.9 ± 62.58 | 38.38 |
| | *Proteocephalus* sp. | 4.40 | 1.80 ± 0.70 | 0.08 |
| | *Eubothrium salvelini* | 4.95 | 1.00 ± 0.00 | 0.05 |
| | **Acanthocephala** | | | |
| | *Corynosoma* sp.* | 6.76 | 1.50 ± 0.71 | 0.10 |
| | *Echinorhynchus gadi* * | 10.81 | 3.20 ± 3.35 | 0.11 |
| 2005 | **Trematoda** | | | |
| | *Brachyphallus crenatus** | 1.35 | 393.50 ± 417.90 | 5.32 |
| | *Derogenes varicus** | 0.00 | 0.00 ± 0.00 | 0.00 |
| | *Prosorhynchus squamatus** | 0.68 | 4882.00 ± 0.00 | 32.99 |
| | **Cestoda** | | | |
| | *Diphyllobothrium* sp. | 2.22 | 1.00 ± 0.00 | 0.02 |
| | *Bothrimonus sturionis** | 14.40 | 7.69 ± 11.59 | 1.11 |
| | *Proteocephalus* sp. | 0.00 | 0.00 ± 0.00 | 0.00 |
| | *Eubothrium salvelini* | 2.22 | 1.00 ± 0.00 | 0.02 |
| | **Acanthocephala** | | | |
| | *Corynosoma* sp.* | 0.67 | 57.00 ± 0.00 | 0.39 |
| | *Echinorhynchus gadi* * | 1.35 | 1.00 ± 0.00 | 0.01 |

* Marine parasite species

Table 27. Mean $\delta^{13}C$ and $\delta^{15}N$ ratios by length classes for the 3 sampling years.

| Length range (mm) | n | Mean $\delta^{13}C$ (‰) | Mean $\delta^{15}N$ (‰) | Mean C:N | Year |
|---|---|---|---|---|---|
| 138-155 | 5 | -19.6 | 12.12 | -0.62 | 2002 |
| 182-295 | 9 | -19.44 | 12.51 | -0.64 | 2002 |
| 313-420 | 23 | -19.69 | 13.79 | -0.70 | 2002 |
| 430-520 | 26 | -19.56 | 13.7 | -0.70 | 2002 |
| 529-585 | 7 | -19.04 | 13.93 | -0.73 | 2002 |
| 185-189 | 2 | -21.99 | 8.7 | -0.40 | 2004 |
| 330-419 | 4 | -20.73 | 11.71 | -0.56 | 2004 |
| 435-522 | 7 | -19.87 | 13.04 | -0.66 | 2004 |
| 528-648 | 17 | -19.87 | 13.58 | -0.68 | 2004 |
| 304-442 | 2 | -20.98 | 10.92 | -0.52 | 2005 |
| 505-522 | 6 | -20.88 | 13.13 | -0.63 | 2005 |
| 538-705 | 7 | -19.87 | 15.11 | -0.76 | 2005 |

Table 28. Mean $\delta^{13}C$ and $\delta^{15}N$ ratios by age (Years) classes for the 3 sampling years.

| Age | n | Mean $\delta^{13}C$ (‰) | Mean $\delta^{15}N$ (‰) | Mean C:N | Year |
|---|---|---|---|---|---|
| 4 | 4 | -19.36 | 13.45 | -0.69 | 2002 |
| 5 | 6 | -20.21 | 9.23 | -0.46 | 2002 |
| 6 | 6 | -18.6 | 14.11 | -0.76 | 2002 |
| 7 | 7 | -19.59 | 15.01 | -0.77 | 2002 |
| 8 | 12 | -19.3 | 13.18 | -0.68 | 2002 |
| 9 | 13 | -19.24 | 13.18 | -0.69 | 2002 |
| 10 | 11 | -20.7 | 13.99 | -0.68 | 2002 |
| 11 | 3 | -19.61 | 13.49 | -0.69 | 2002 |
| 12 | 4 | -19 | 16.34 | -0.86 | 2002 |
| 13 | 1 | -17.92 | 9.2 | -0.51 | 2002 |
| 14 | 1 | -20.4 | 16.22 | -0.80 | 2002 |
| 15 | 1 | -18.26 | 15.71 | -0.86 | 2002 |
| 4 | 1 | -23.15 | 7.29 | -0.31 | 2004 |
| 8 | 4 | -20.21 | 13.5 | -0.67 | 2004 |
| 9 | 1 | -18.18 | 11.36 | -0.62 | 2004 |
| 10 | 9 | -19.98 | 13.12 | -0.66 | 2004 |
| 11 | 6 | -20.29 | 13.48 | -0.66 | 2004 |
| 12 | 4 | -20.22 | 12.85 | -0.64 | 2004 |
| 15 | 2 | -19.22 | 12.8 | -0.67 | 2004 |
| 18 | 1 | -19.2 | 14.08 | -0.73 | 2004 |
| 8 | 2 | -20.98 | 10.92 | -0.52 | 2005 |
| 9 | 2 | -21.26 | 13.04 | -0.61 | 2005 |
| 10 | 4 | -21.09 | 14.37 | -0.68 | 2005 |
| 12 | 3 | -18.78 | 15.04 | -0.80 | 2005 |
| 13 | 1 | -19.43 | 13.35 | -0.69 | 2005 |
| 14 | 1 | -20.25 | 13.13 | -0.65 | 2005 |
| 15 | 1 | -20.53 | 14.21 | -0.69 | 2005 |

Table 29. Multiple comparison of C/N ratio of diet species and Arctic char based on Bonferroni post-hoc between-subjects (invertebrates, Arctic cod and Arctic char) tests based on 2004 and 2005 samples.

| Species (a) | Species (b) | Mean Difference (a-b) | Std. Error | Sig. | 95% Confidence Interval | | Abbrev. |
|---|---|---|---|---|---|---|---|
| | | | | | Lower Bound | Upper Bound | |
| Invertebrates | Polar cod | -0.4254 | 0.16208 | 0.047 | -0.847 | -0.0038 | SS |
| | Arctic char | -0.2963 | 0.21745 | 0.563 | -0.8619 | 0.2694 | NS |
| Polar cod | Invertebrates | 0.4254 | 0.16208 | 0.047 | 0.003 | 0.847 | SS |
| | Arctic char | 0.1292 | 0.20501 | 1.000 | -0.4041 | 0.6625 | NS |
| Arctic char | Invertebrates | 0.2963 | 0.21745 | 0.563 | -0.2694 | 0.8619 | NS |
| | Polar cod | -0.1292 | 0.20501 | 1.000 | -0.6625 | 0.4041 | NS |

Table 30. Daily growth rate constant (k), daily metabolic tissue replacement (m) and half-life (HL) (days) of nitrogen and carbon stable isotopes of Arctic char based on 2002 samples.

| | $\delta^{13}C$ | | $\delta^{15}N$ | |
|---|---|---|---|---|
| k | m ($\%d^{-1}$) | HL (Days) | m ($\%d^{-1}$) | HL (Days) |
| 0.006593 | 0.00142 | 86.50 | 0.00107 | 90.57 |

Figure 7. Model for interpretation of 3-D graphical representation of stomach contents analyses. Legend: D = dominant diet category; R = rare diet category; G = generalized diet; S = specialized diet; See text (p.87) for definitions of *a*, *b*, *c*, *d*, *e*, *f*, *g*, and *h* and the explanation of lines (Cortés 1997).

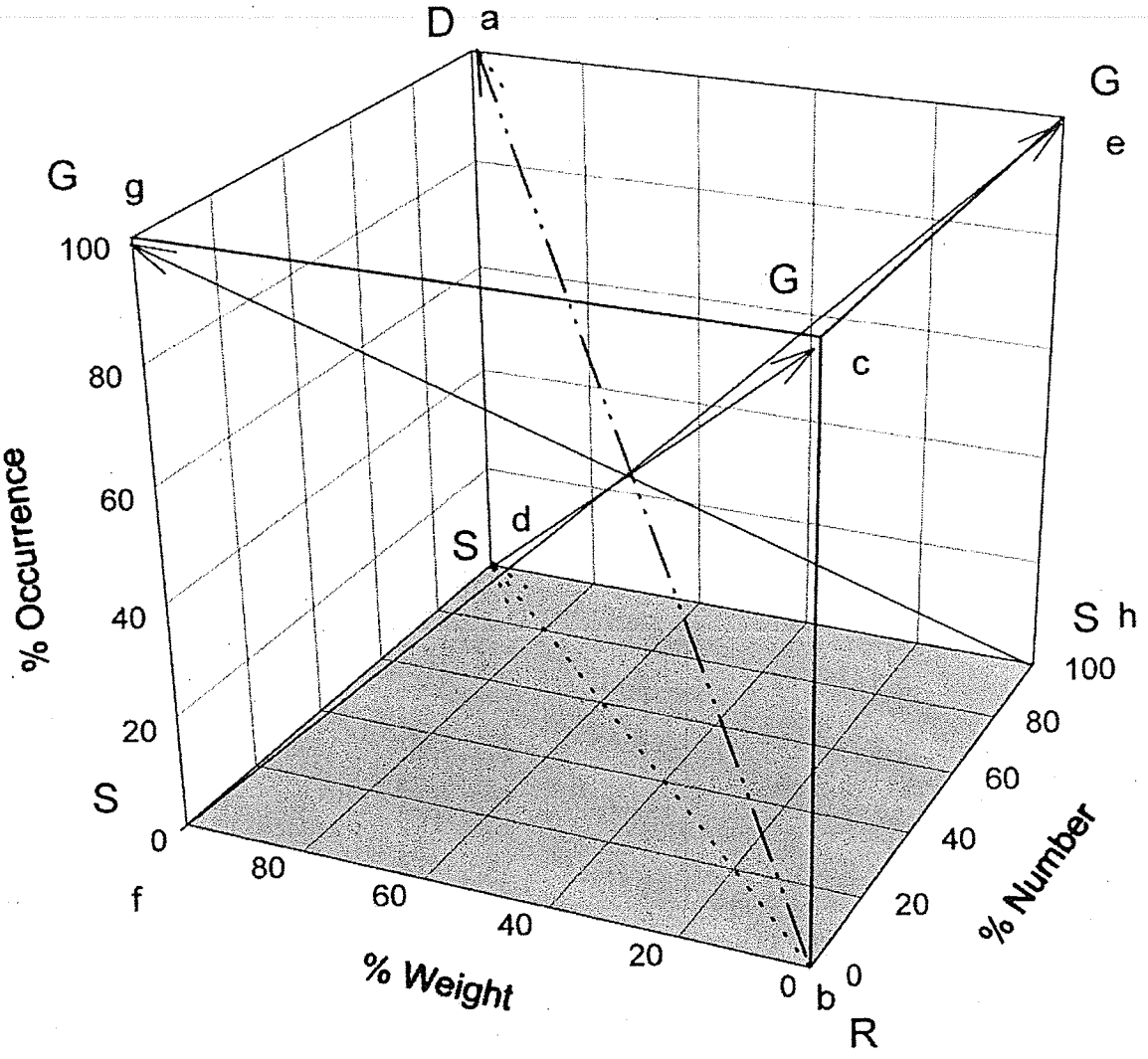
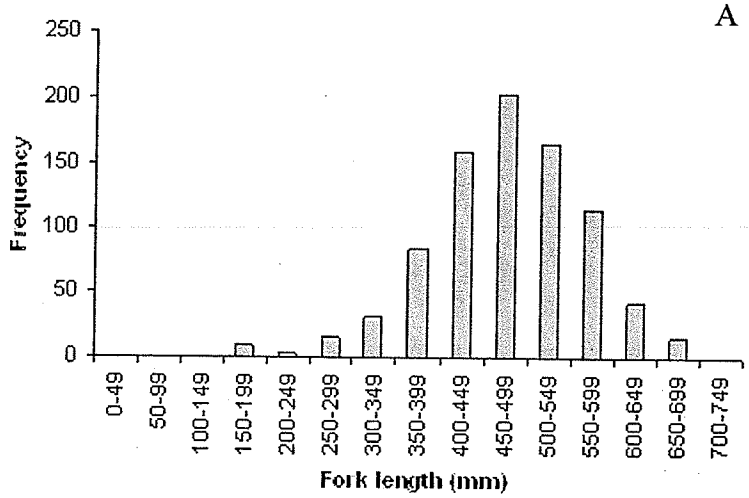
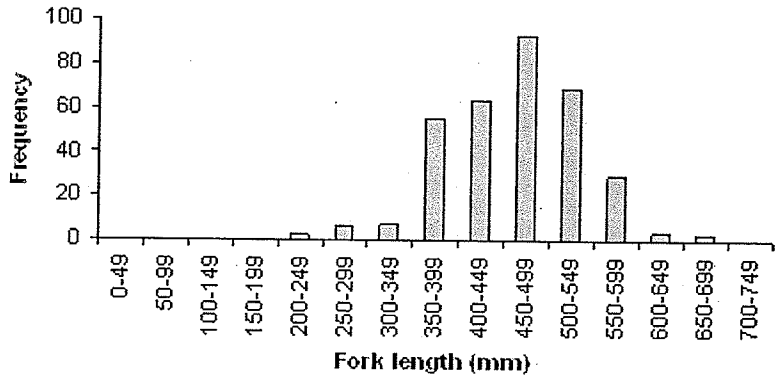

D a
G
e
G g
100
G
c
80
60
% Occurrence
d
S
S h
40
100
20
80
S
60
0
40
f
80
60
40
20
% Number
% Weight
20
0
0
b
R

Figure 8. Frequency distribution of length categories in 2002 (A) (n = 1294), 2004 (B) (n = 894) and 2005 (n = 81) (C) samples of Arctic char

A


Frequency
250
200
150
100
50
0
0-49
50-99
100-149
150-199
200-249
250-299
300-349
350-399
400-449
450-499
500-549
550-599
600-649
650-699
700-749
Fork length (mm)

B


Frequency
100
80
60
40
20
0
0-49
50-99
100-149
150-199
200-249
250-299
300-349
350-399
400-449
450-499
500-549
550-599
600-649
650-699
700-749
Fork length (mm)

C

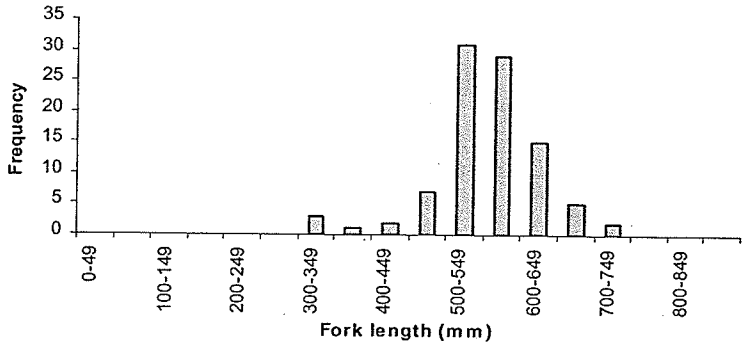
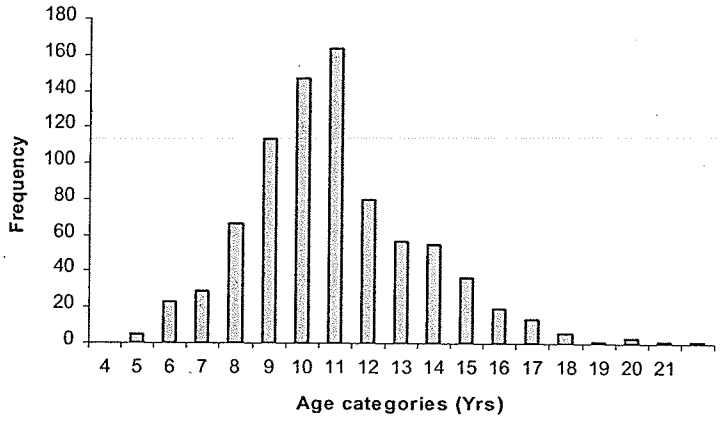
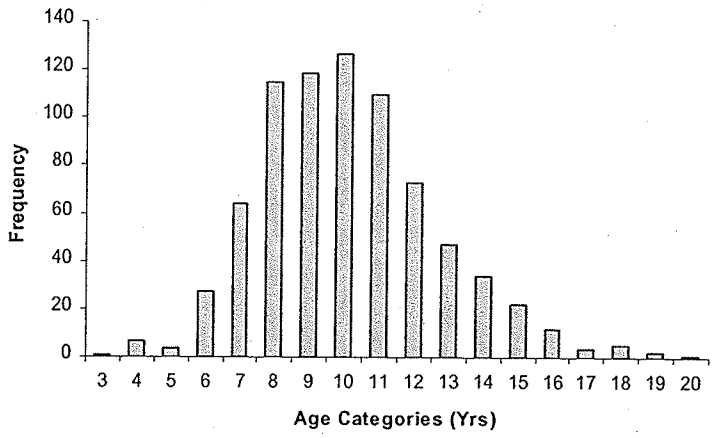

Frequency
35
30
25
20
15
10
5
0
0-49
100-149
200-249
300-349
400-449
500-549
600-649
700-749
800-849
Fork length (mm)

Figure 9. Frequency distribution of age categories of 2002 (A) (n = 1294), (B) 2004 (n = 894) and 2005 (C) (n = 92) samples of Arctic char.

A


Frequency
180
160
140
120
100
80
60
40
20
0
4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21
Age categories (Yrs)

B


Frequency
140
120
100
80
60
40
20
0
3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Age Categories (Yrs)

C

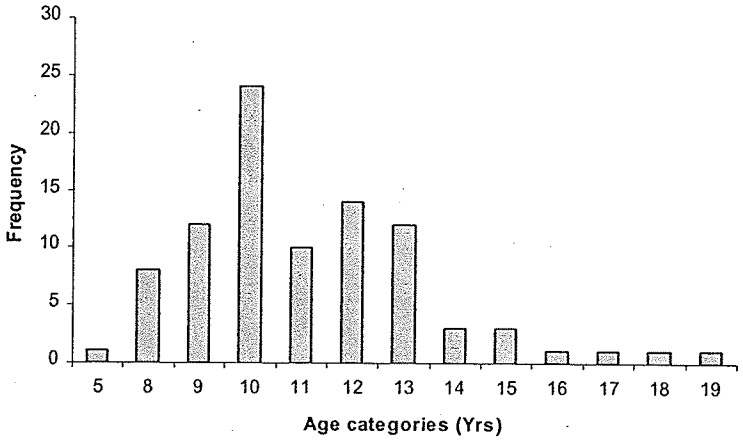

Frequency
30
25
20
15
10
5
0
5 8 9 10 11 12 13 14 15 16 17 18 19
Age categories (Yrs)

Figure 10. von Bertalanffy growth curves of Sylvia Grinnell River Arctic char in different study years. Source: Gallagher and Dick (2007).

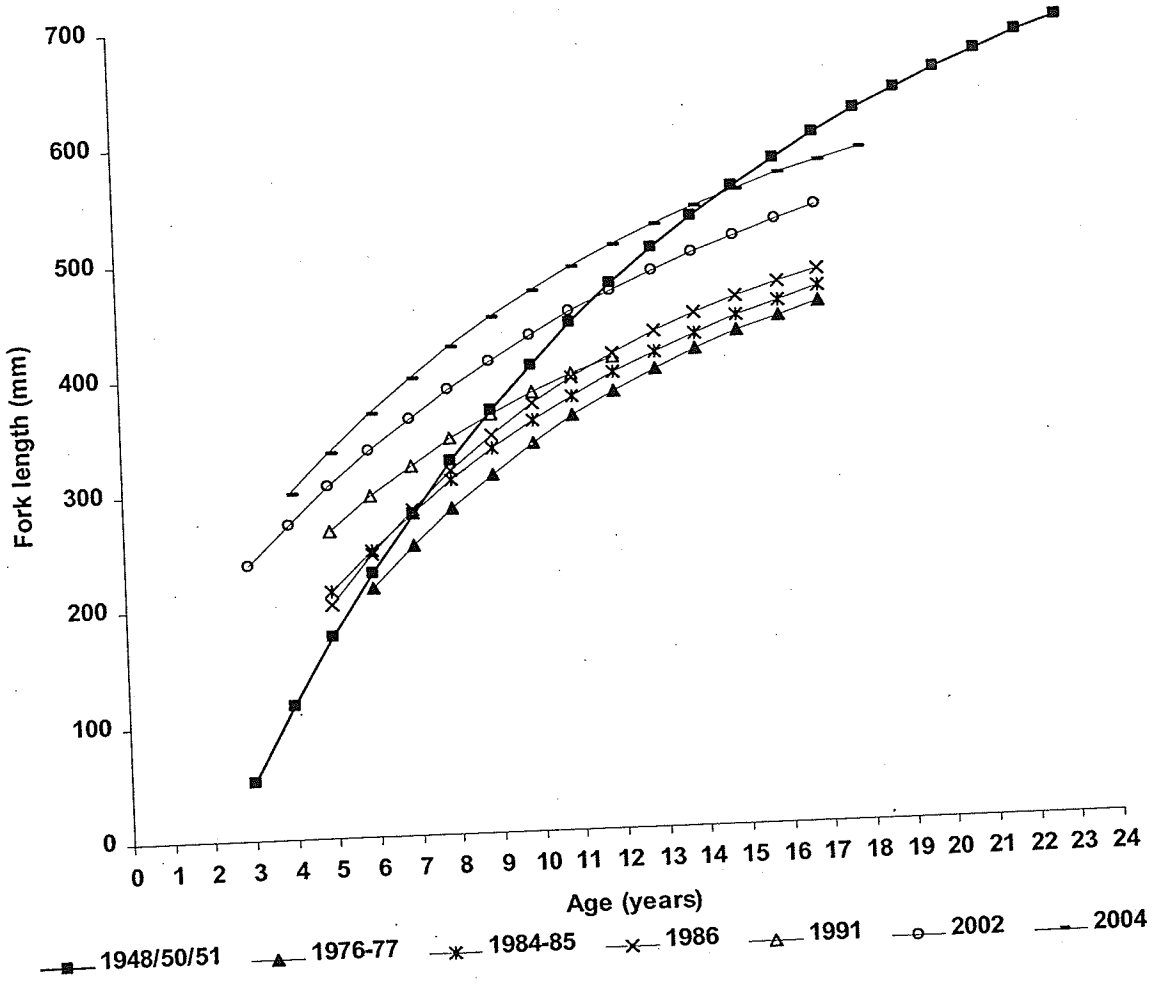
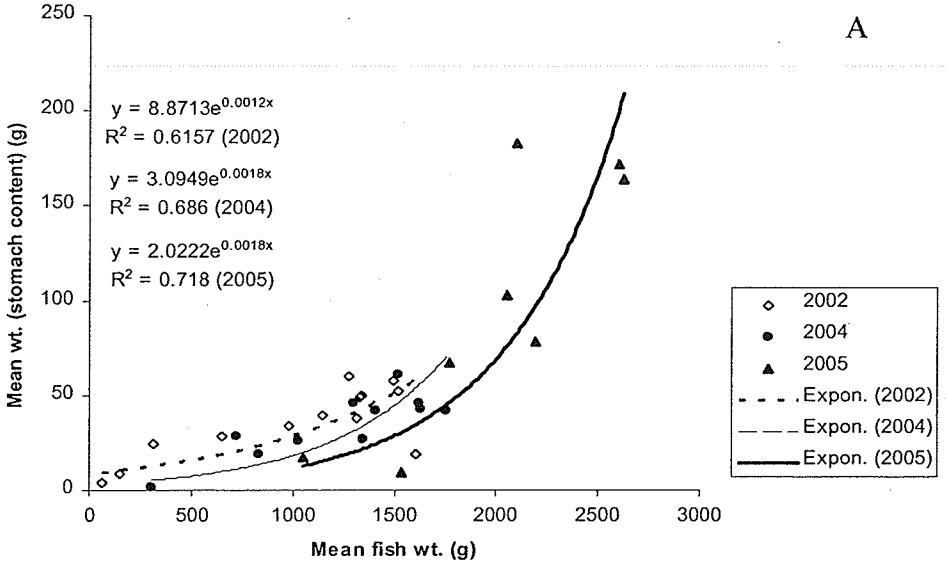

700
600
500
400
300
200
100
0
Fork length (mm)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Age (years)
1948/50/51
1976-77
1984-85
1986
1991
2002
2004

Figure 11. The relationship between mean weight of stomach contents (MWS) and mean fish weight (MW) over time (A) and the general model (B) describing this relationship using pooled data.


A
y = 8.8713e^0.0012x
R² = 0.6157 (2002)
y = 3.0949e^0.0018x
R² = 0.686 (2004)
y = 2.0222e^0.0018x
R² = 0.718 (2005)
Mean wt. (stomach content) (g)
Mean fish wt. (g)
2002
2004
2005
Expon. (2002)
Expon. (2004)
Expon. (2005)

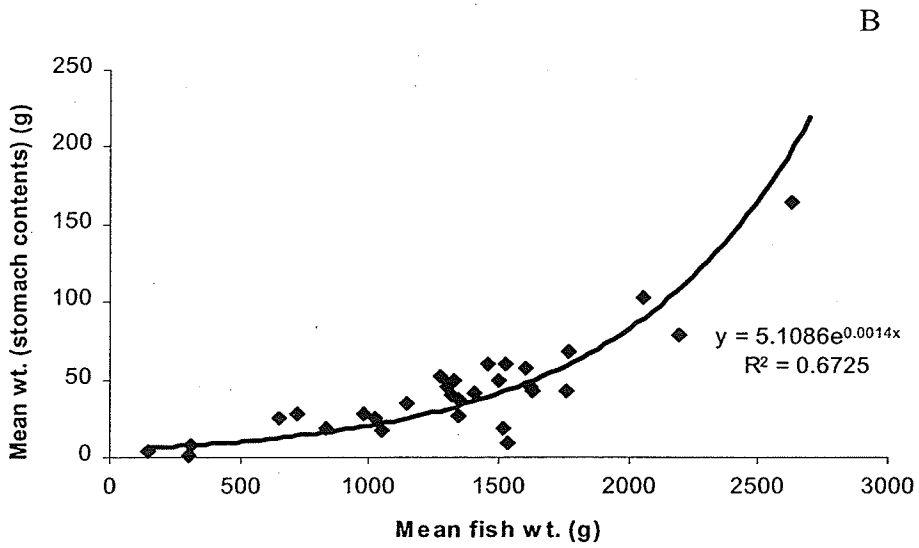
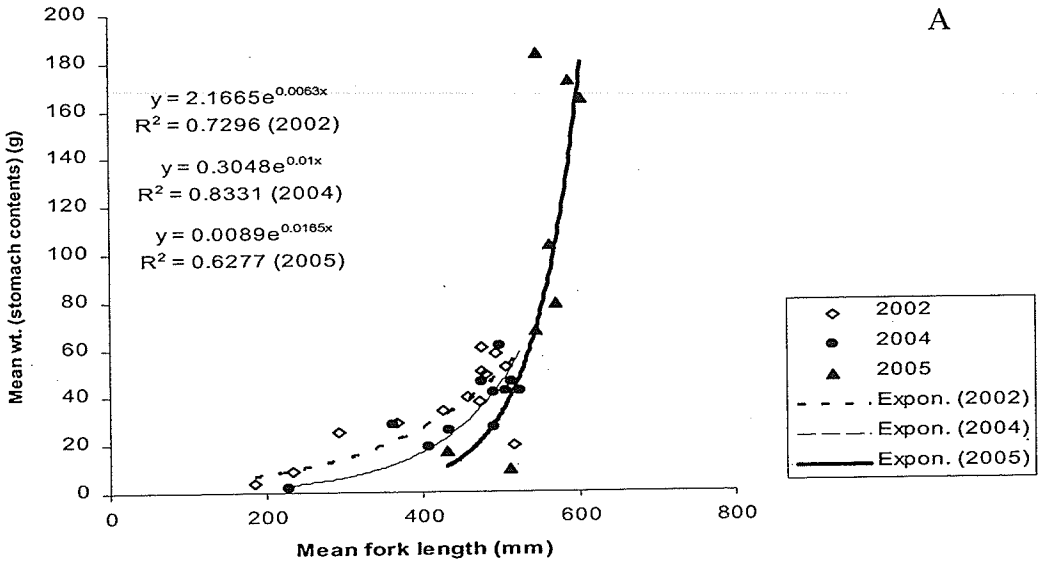

B
y = 5.1086e^0.0014x
R² = 0.6725
Mean wt. (stomach contents) (g)
Mean fish wt. (g)

Figure 12. The relationship between mean weight of stomach contents over time (A) and mean fork length and the general model (B) describing this relationship using pooled data.


A
y = 2.1665e^0.0063x
R² = 0.7296 (2002)
y = 0.3048e^0.01x
R² = 0.8331 (2004)
y = 0.0089e^0.0165x
R² = 0.6277 (2005)
Mean wt. (stomach contents) (g)
Mean fork length (mm)
2002
2004
2005
Expon. (2002)
Expon. (2004)
Expon. (2005)

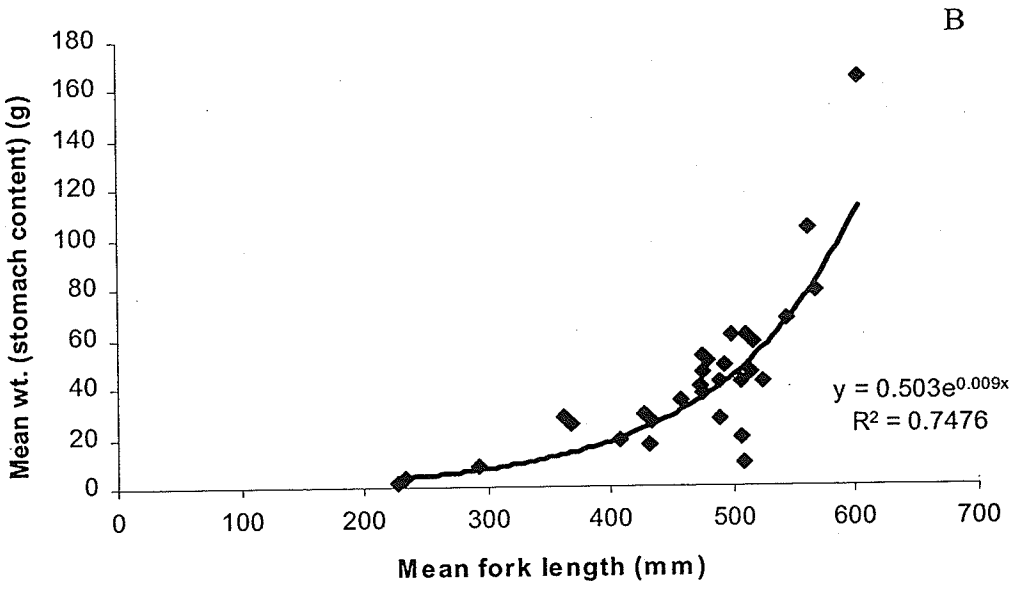
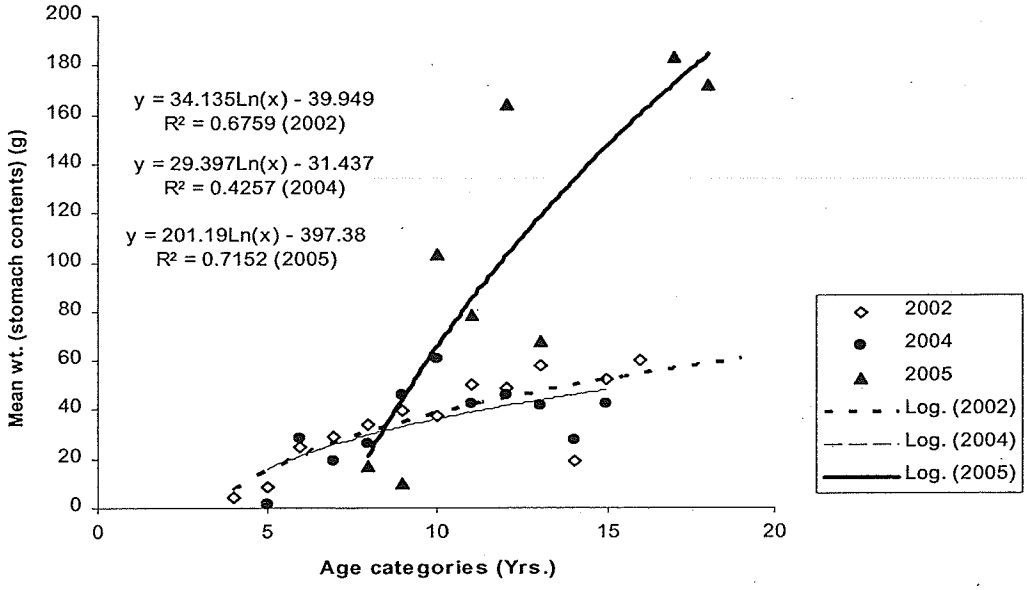

B
y = 0.503e^0.009x
R² = 0.7476
Mean wt. (stomach content) (g)
Mean fork length (mm)

Figure 13. The relationship between mean weight of stomach contents over time and age (A) and the general model (B) describing this relationship using pooled data.

A


y = 34.135Ln(x) - 39.949
R² = 0.6759 (2002)
y = 29.397Ln(x) - 31.437
R² = 0.4257 (2004)
y = 201.19Ln(x) - 397.38
R² = 0.7152 (2005)
Mean wt. (stomach contents) (g)
Age categories (Yrs.)
2002
2004
2005
Log. (2002)
Log. (2004)
Log. (2005)

B

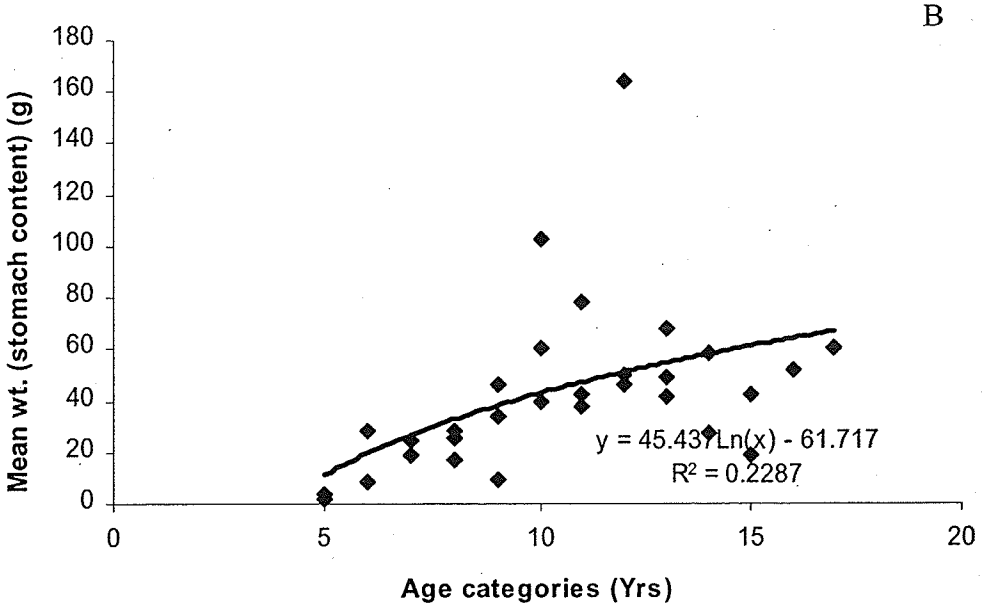
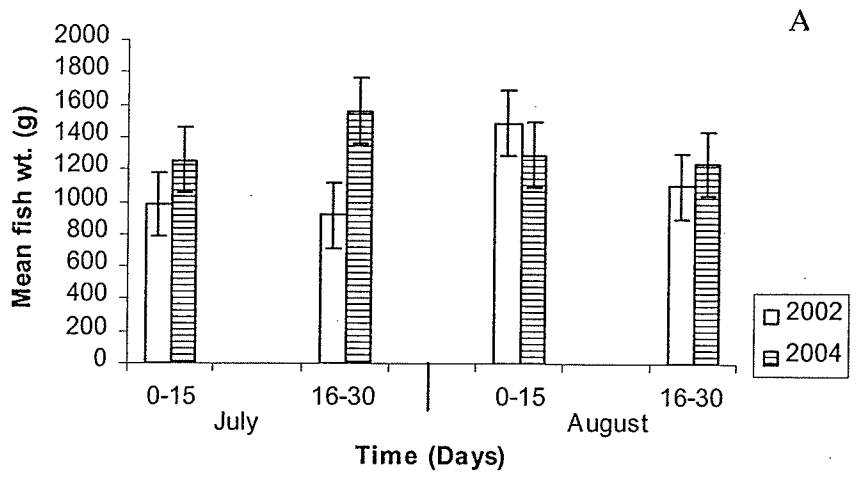

y = 45.437Ln(x) - 61.717
R² = 0.2287
Mean wt. (stomach content) (g)
Age categories (Yrs)

Figure 14. Intra-annual changes in fish growth in 2002 (A) and 2004 (B). Legend: Days; 0-15 = Early; 16-30 = Late. The July data for 0-15 was used as d0 in B.


A
Mean fish wt. (g)
2000
1800
1600
1400
1200
1000
800
600
400
200
0
0-15
16-30
0-15
16-30
July
August
Time (Days)
2002
2004

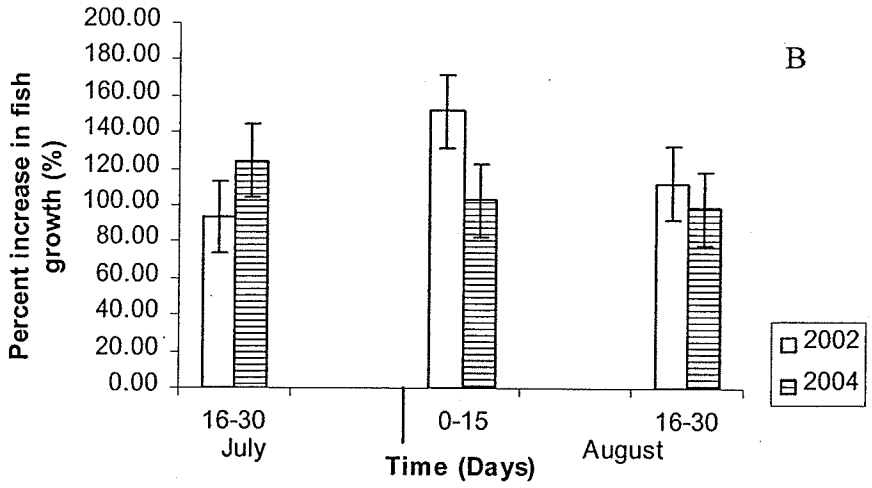
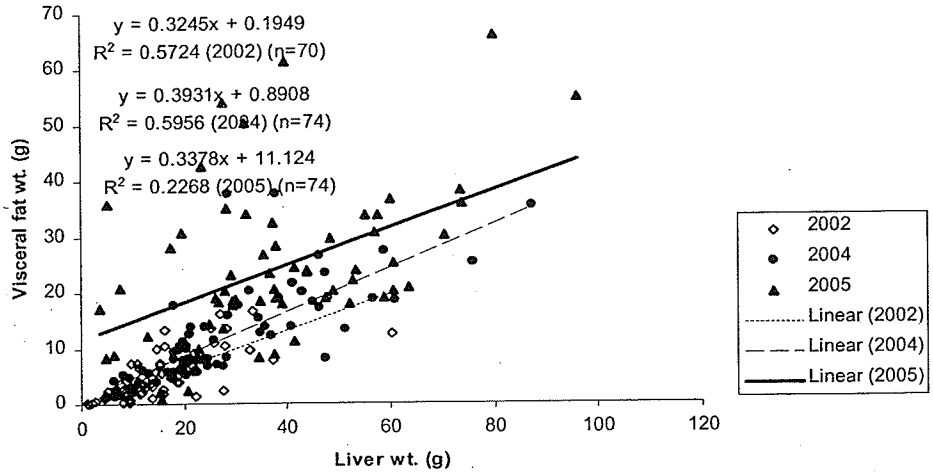

B
Percent increase in fish growth (%)
200.00
180.00
160.00
140.00
120.00
100.00
80.00
60.00
40.00
20.00
0.00
16-30
0-15
16-30
July
August
Time (Days)
2002
2004

Figure 15. The relationship between weight of visceral fat and liver weight over time (A) and the general model (B) (n = 206) describing the relationship in Arctic char.

A


y = 0.3245x + 0.1949
R² = 0.5724 (2002) (n=70)
y = 0.3931x + 0.8908
R² = 0.5956 (2004) (n=74)
y = 0.3378x + 11.124
R² = 0.2268 (2005) (n=74)
Visceral fat wt. (g)
Liver wt. (g)
2002
2004
2005
Linear (2002)
Linear (2004)
Linear (2005)

B

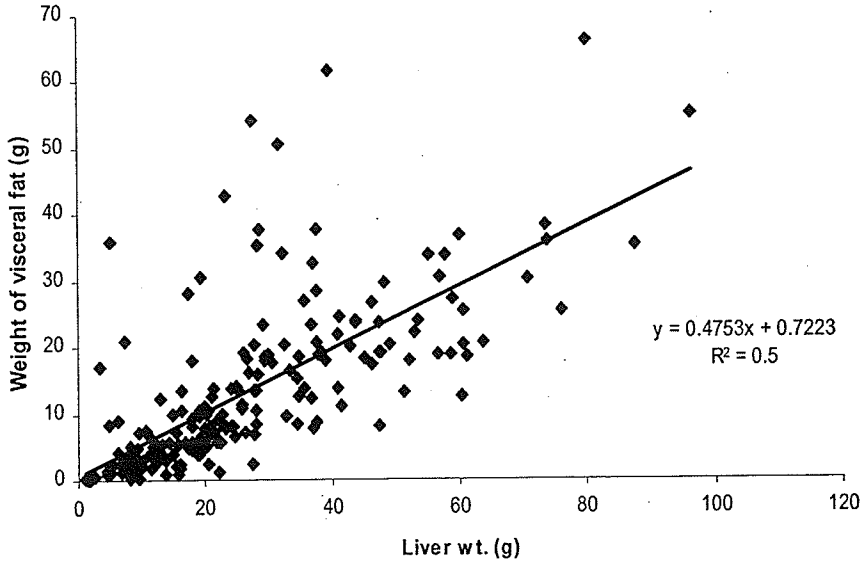

y = 0.4753x + 0.7223
R² = 0.5
Weight of visceral fat (g)
Liver wt. (g)

Figure 16. Inter-annual changes in char condition.

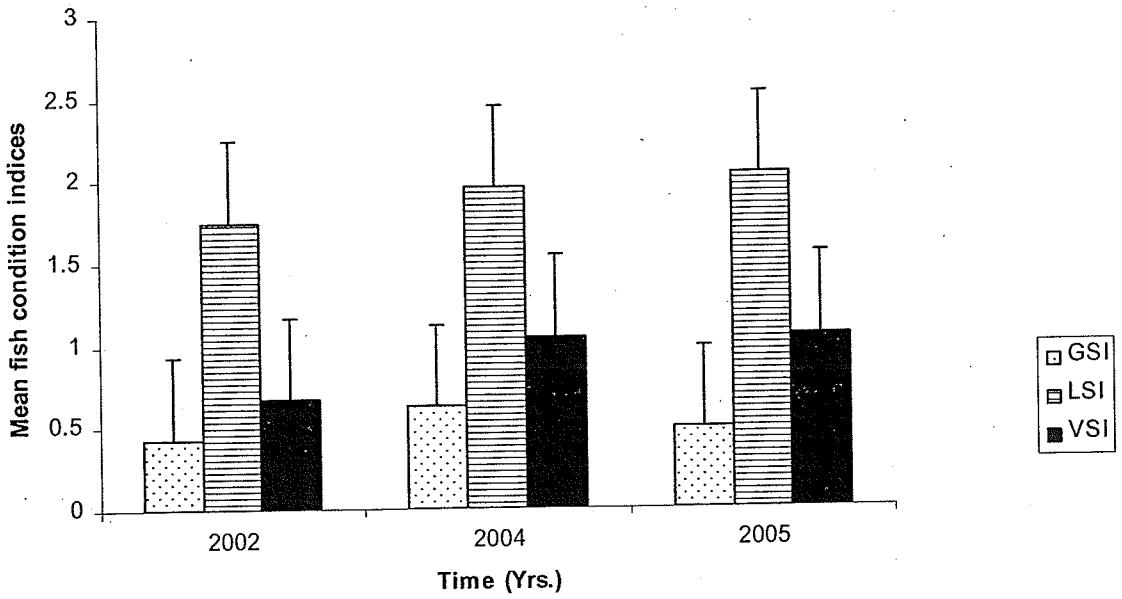
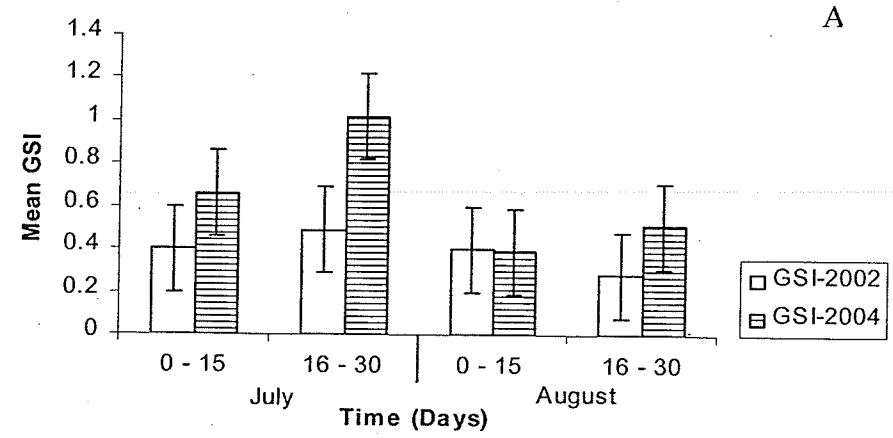
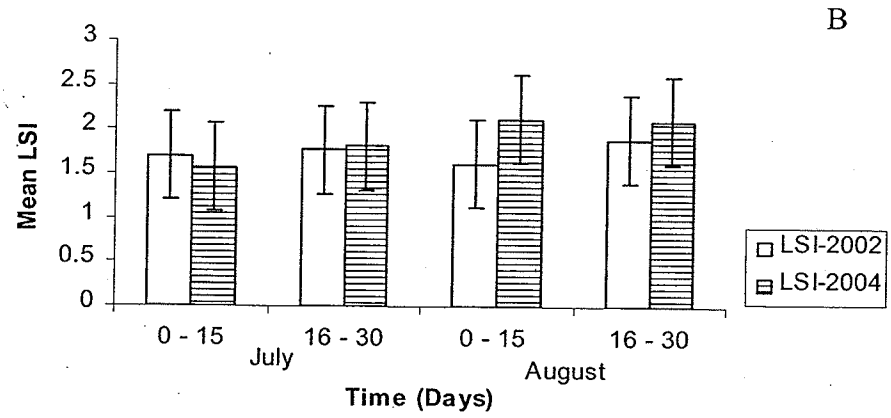

Mean fish condition indices
3
2.5
2
1.5
1
0.5
0
2002
2004
2005
Time (Yrs.)
GSI
LSI
VSI

Figure 17. Intra-annual changes in fish condition indices. Legend: A = GSI; B = LSI and C = VSI. Days: 0 – 15 = Early; 16 – 30 = Late; GSI = Gonadosomatic index; LSI = Liversomatic index and VSI = Visceralfatsomatic index.


A
Mean GSI
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0 - 15
16 - 30
0 - 15
16 - 30
July
August
Time (Days)
GSI-2002
GSI-2004


B
Mean LSI
3
2.5
2
1.5
1
0.5
0
0 - 15
16 - 30
0 - 15
16 - 30
July
August
Time (Days)
LSI-2002
LSI-2004

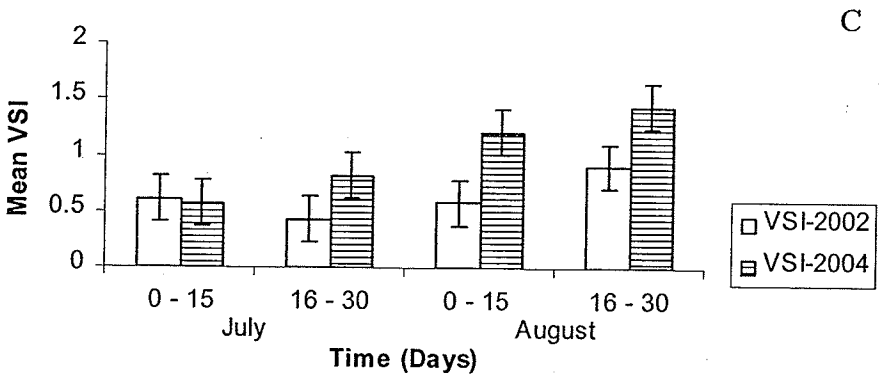
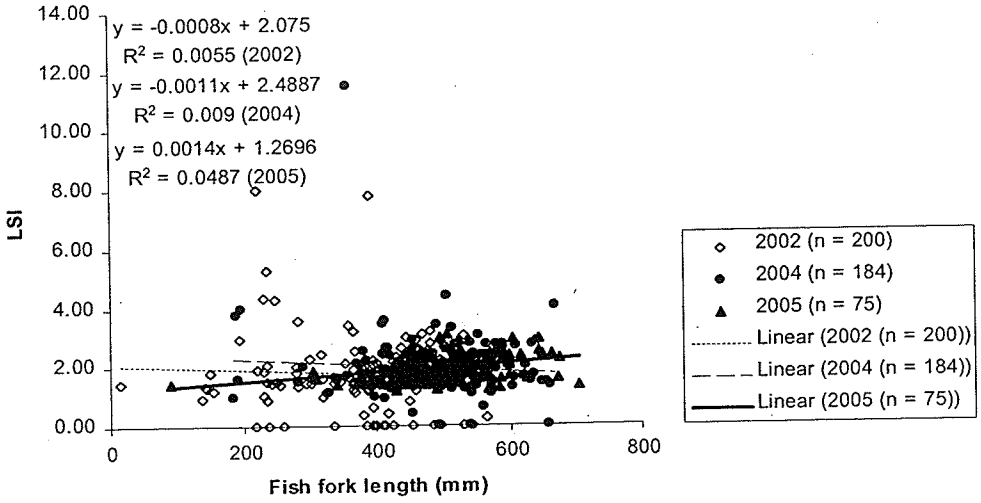

C
Mean VSI
2
1.5
1
0.5
0
0 - 15
16 - 30
0 - 15
16 - 30
July
August
Time (Days)
VSI-2002
VSI-2004

Figure 18. The relationships between liversomatic index (LSI) and fish fork length (A) and between visceralfatsomatic index (VSI) and fish fork length (B) for the 3 sampling years.

A


y = -0.0008x + 2.075
R² = 0.0055 (2002)
y = -0.0011x + 2.4887
R² = 0.009 (2004)
y = 0.0014x + 1.2696
R² = 0.0487 (2005)
LSI
Fish fork length (mm)
2002 (n = 200)
2004 (n = 184)
2005 (n = 75)
Linear (2002 (n = 200))
Linear (2004 (n = 184))
Linear (2005 (n = 75))

B

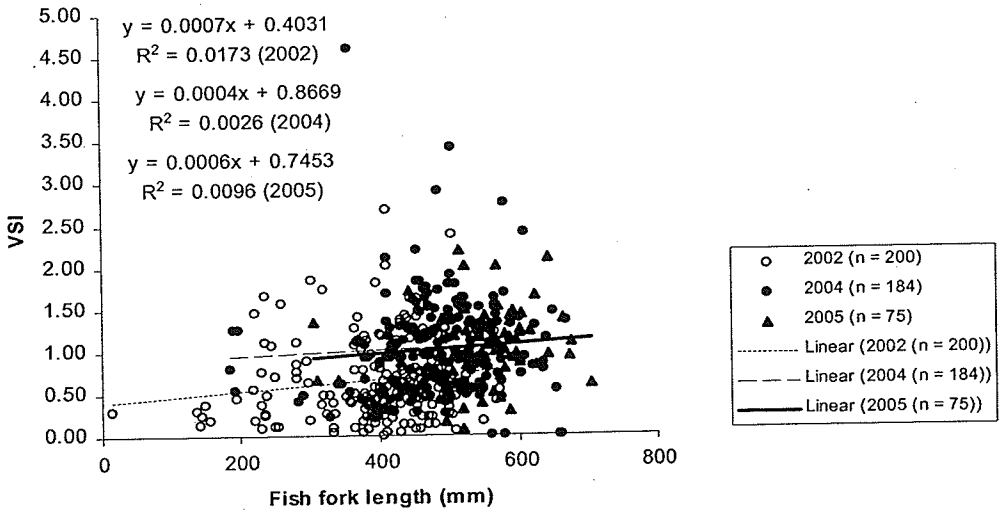
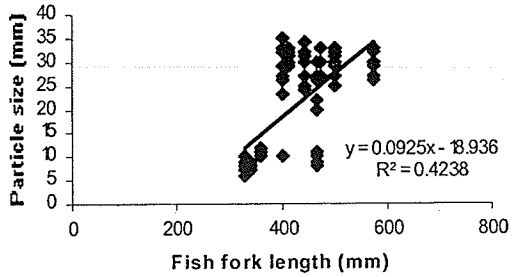
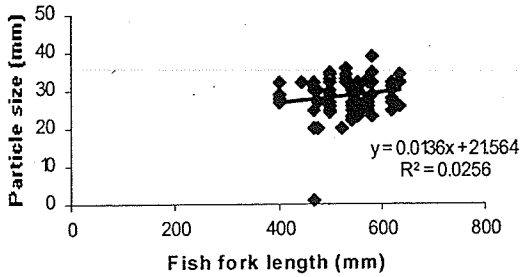

y = 0.0007x + 0.4031
R² = 0.0173 (2002)
y = 0.0004x + 0.8669
R² = 0.0026 (2004)
y = 0.0006x + 0.7453
R² = 0.0096 (2005)
VSI
Fish fork length (mm)
2002 (n = 200)
2004 (n = 184)
2005 (n = 75)
Linear (2002 (n = 200))
Linear (2004 (n = 184))
Linear (2005 (n = 75))

Figure 19. The relationship between char length and particle size of its key diet items: *Mysis* spp. (A; $r^2 = 0.42$; n = 110); *Themisto libellula* (B; $r^2 = 0.026$; n = 95); *Onesimus littoralis* (C; $r^2 = 0.43$; n = 63); *Thysanoessa* spp. (D; $r^2 = 0.004$; n = 101); *Calanus* spp. (E; $r^2 = 0.104$; n = 72) and *Boreogadus saida* Arctic cod (F; $r^2 = 0.022$; n = 77)

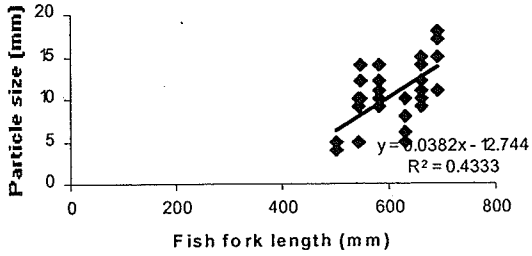
A


Particle size (mm)
Fish fork length (mm)
y = 0.0925x - 18.936
R² = 0.4238

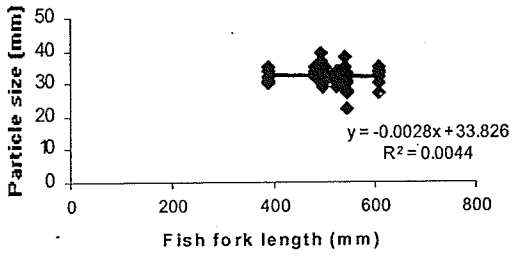
B


Particle size (mm)
Fish fork length (mm)
y = 0.0136x + 21.564
R² = 0.0256

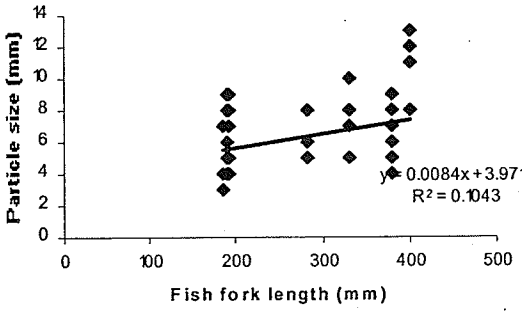
C


Particle size (mm)
Fish fork length (mm)
y = 0.0382x - 12.744
R² = 0.4333

D


Particle size (mm)
Fish fork length (mm)
y = -0.0028x + 33.826
R² = 0.0044

E


Particle size (mm)
Fish fork length (mm)
y = 0.0084x + 3.9711
R² = 0.1043

F

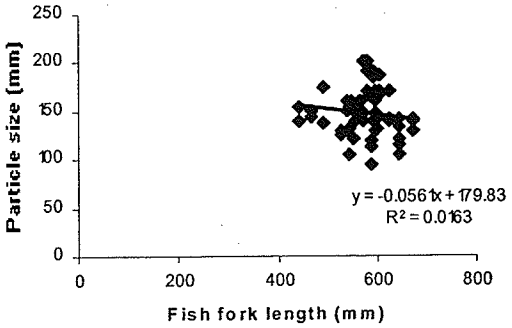
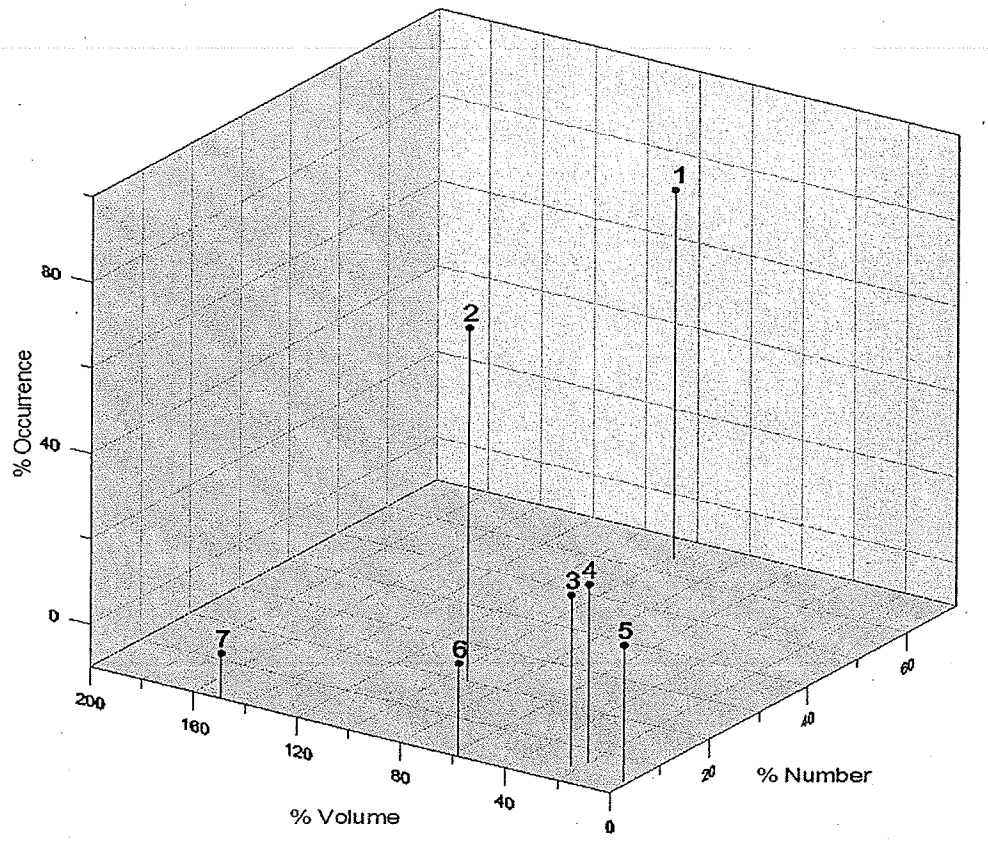
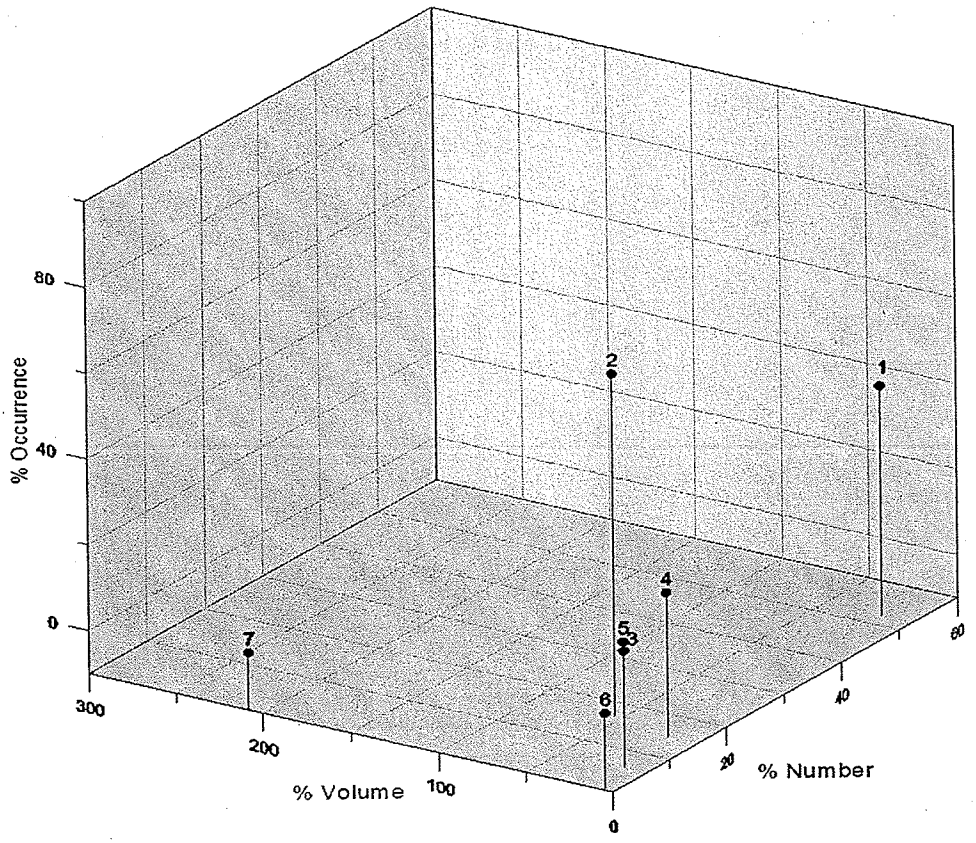

Particle size (mm)
Fish fork length (mm)
y = -0.0561x + 179.83
R² = 0.0163

Figure 20. 3-D graphical representation of stomach content analysis of 2002 (A), 2004 (B) and 2005 (C) samples of Arctic char: Diet items included *Mysis* species = 1; *Themisto libellula* = 2; *Onesimus littoralis* = 3; *Thysanoessa* species = 4; *Calanus* species = 5; *Gammarus* species = 6; Arctic cod = 7. Diet items from Syvial Grinnell River and Kagnitsuatsia sample locations

**A**
**(2002)**



**B**
**(2004)**



**C**
**(2005)**

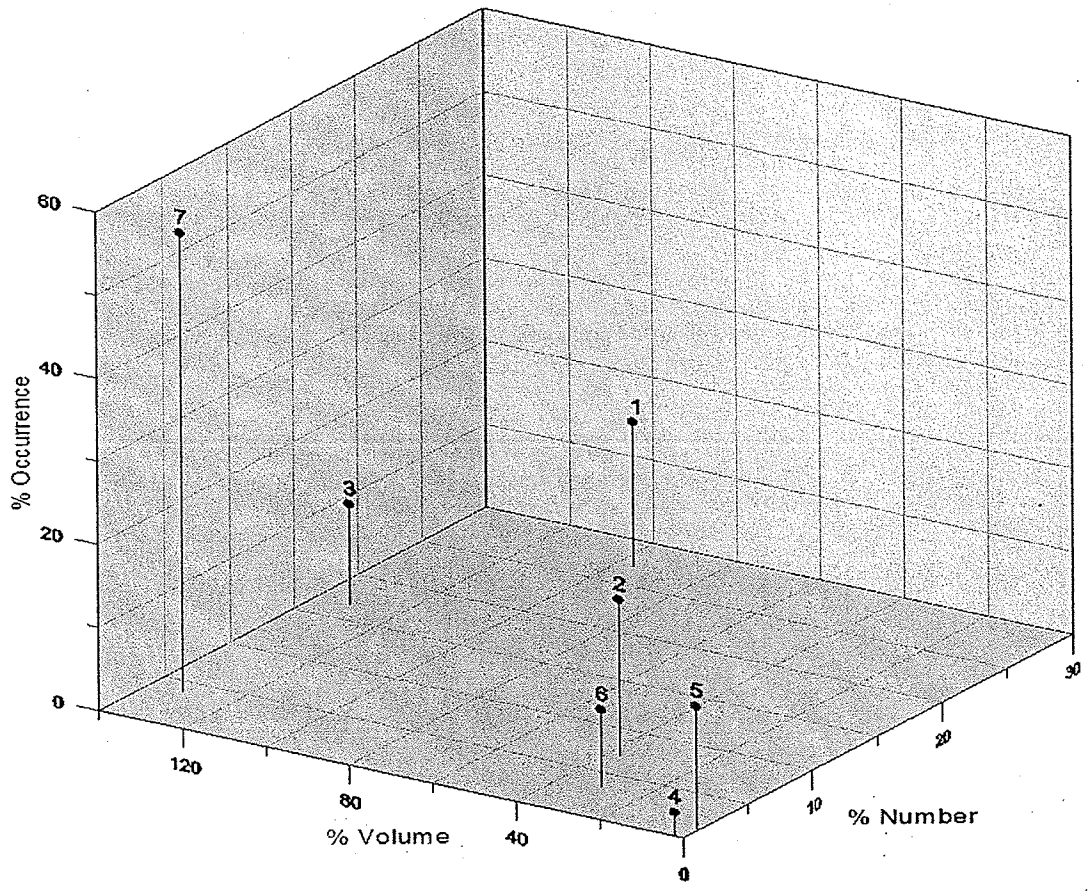
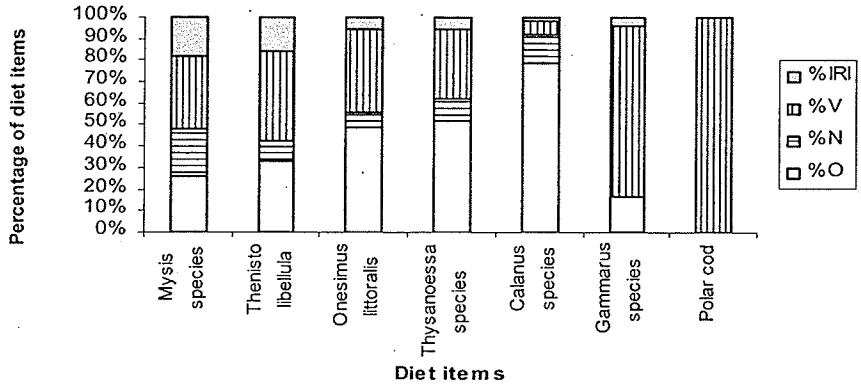
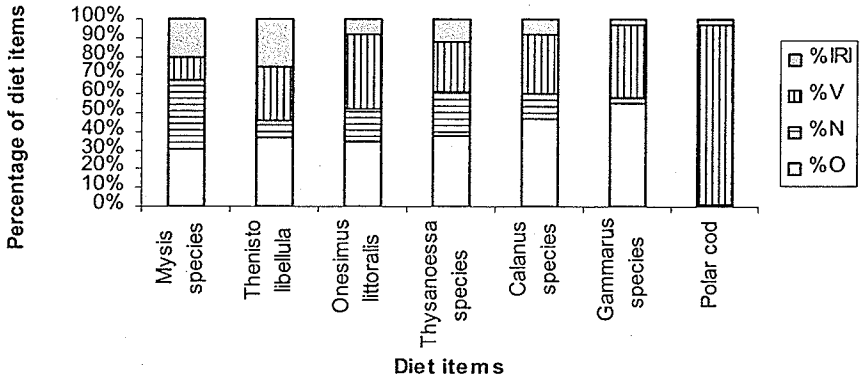

60
40
20
0
% Occurrence
7
3
1
2
6
5
4
120
80
40
0
% Volume
30
20
10
% Number

Figure 21. Bar charts of stomach content analyses showing variations in food habits in 2002 (A), 2004 (B), and 2005 (C) samples of Arctic char. Legend: %IRI = percent index of relative importance; %V = percent by volume; %N = percent by number and %O = percent frequency occurrence of diet items. Diet items from Syvial Grinnell River and Kagnitsuatsia sample locations

A


Percentage of diet items
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Mysis species
Thenisto libellula
Onesimus littoralis
Thysanoessa species
Calanus species
Gammarus species
Polar cod
Diet items
%IRI
%V
%N
%O

B


Percentage of diet items
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Mysis species
Thenisto libellula
Onesimus littoralis
Thysanoessa species
Calanus species
Gammarus species
Polar cod
Diet items
%IRI
%V
%N
%O

C


Percentage of diet items
100%
80%
60%
40%
20%
0%
Mysis species
Thenisto libellula
Onesimus littoralis
Thysanoessa species
Calanus species
Gammarus species
Polar cod
Diet items
%IRI
%V
%N
%O

Figure 22. The mean ± STD $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios of diet items and char. Data for invertebrates (n = 22), char that fed on invertebrates and char that fed on sculpins (n = 13) were from 2002 samples. *Sculpin data (n = 42) was from Chambers et al. (In press). Data for Arctic cod (n = 12) and char that fed on Arctic cod (n = 20) were from 2005 samples. Legend: CI = char that fed on invertebrates; CS = char that fed on sculpins and CA = char that fed on Arctic cod. Fish muscle tissue samples used for analysis were from char from all the sample locations.

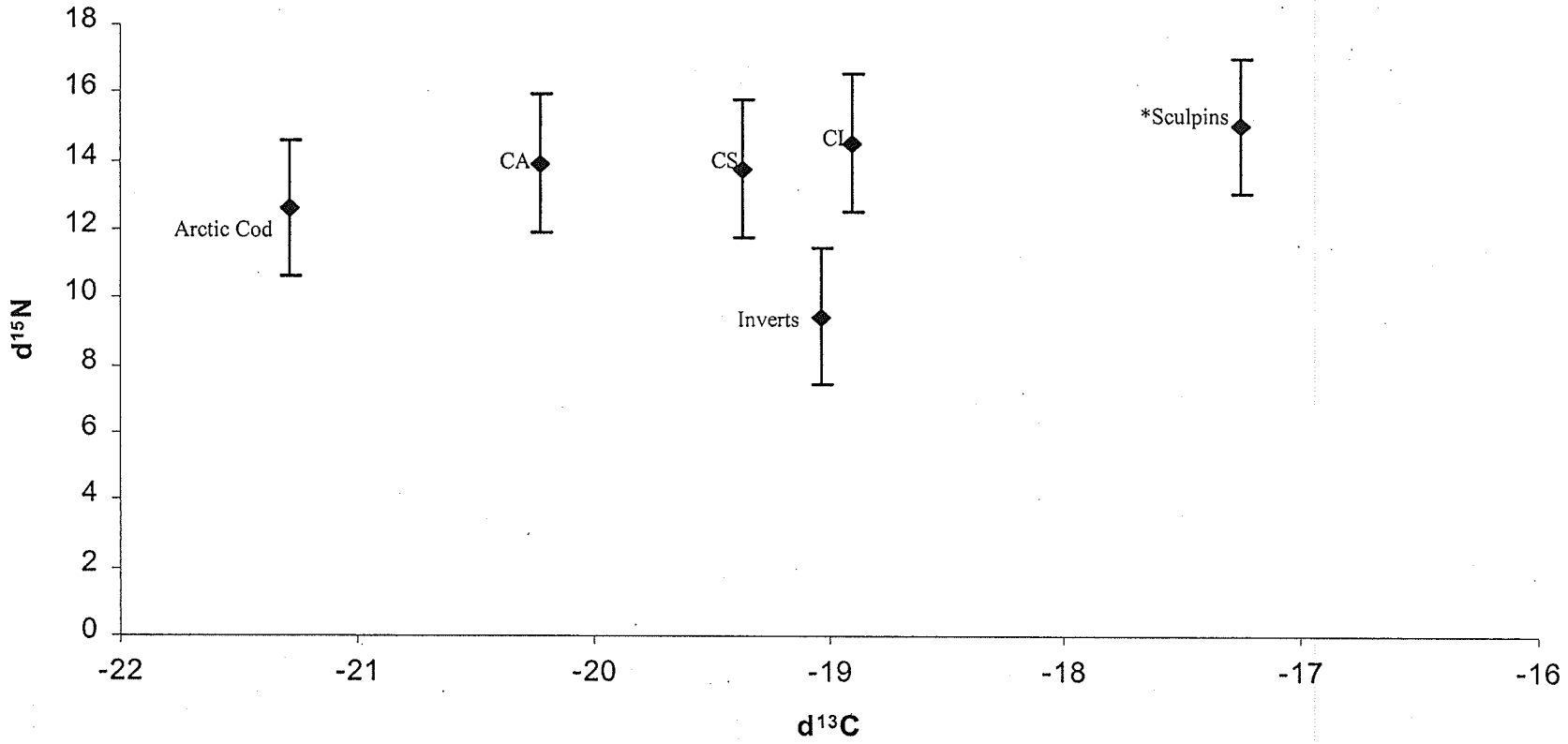
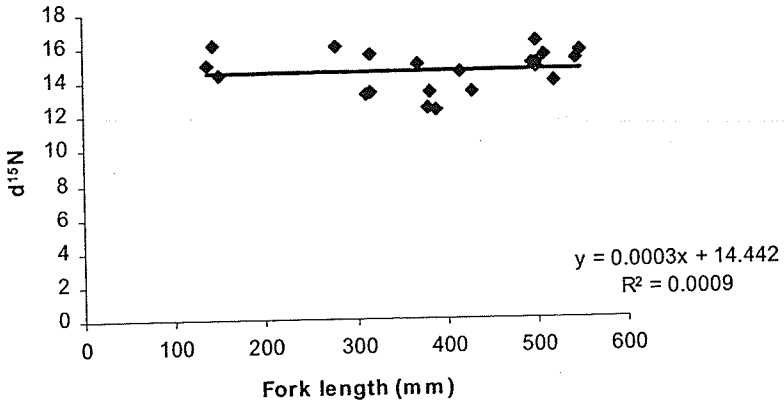
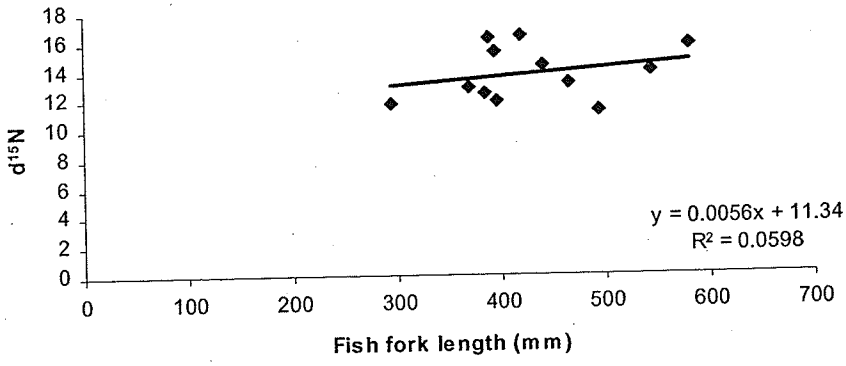

18
16
14
12
10
8
6
4
2
0
d15N
-22
-21
-20
-19
-18
-17
-16
d13C
Arctic Cod
CA
CS
CL
Inverts
*Sculpins

Figure 23. The relationships between $\delta^{15}N$ and char length. A = char that fed on invertebrates (*Mysis* spp., *Themisto libellula*, *Thysanoessa* spp., *Gammarus* spp., and *Onesimus littoralis*; n = 22; 2002 data); B = char that fed on sculpins (n = 13; 2002 data) and C = char that fed on Arctic cod (n = 20; 2005 data). Fish muscle tissue samples used for analysis were from char from all the sample locations. Invertebrates were from Sylvia Grinnell and Kagnitsuatsia locations.

A


18
16
14
12
10
8
6
4
2
0
d15N
0
100
200
300
400
500
600
Fork length (mm)
y = 0.0003x + 14.442
R² = 0.0009

B


18
16
14
12
10
8
6
4
2
0
d15N
0
100
200
300
400
500
600
700
Fish fork length (mm)
y = 0.0056x + 11.34
R² = 0.0598

C

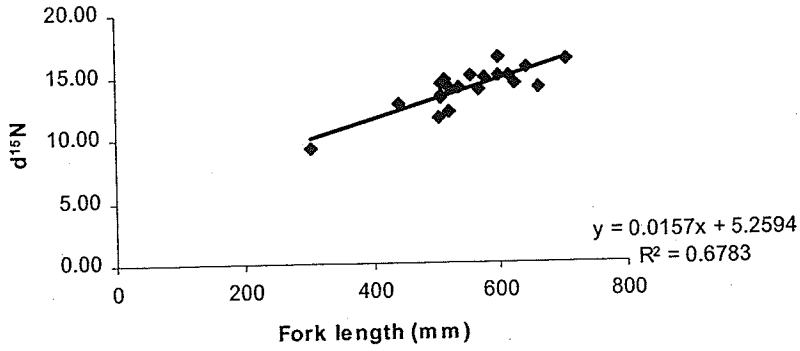
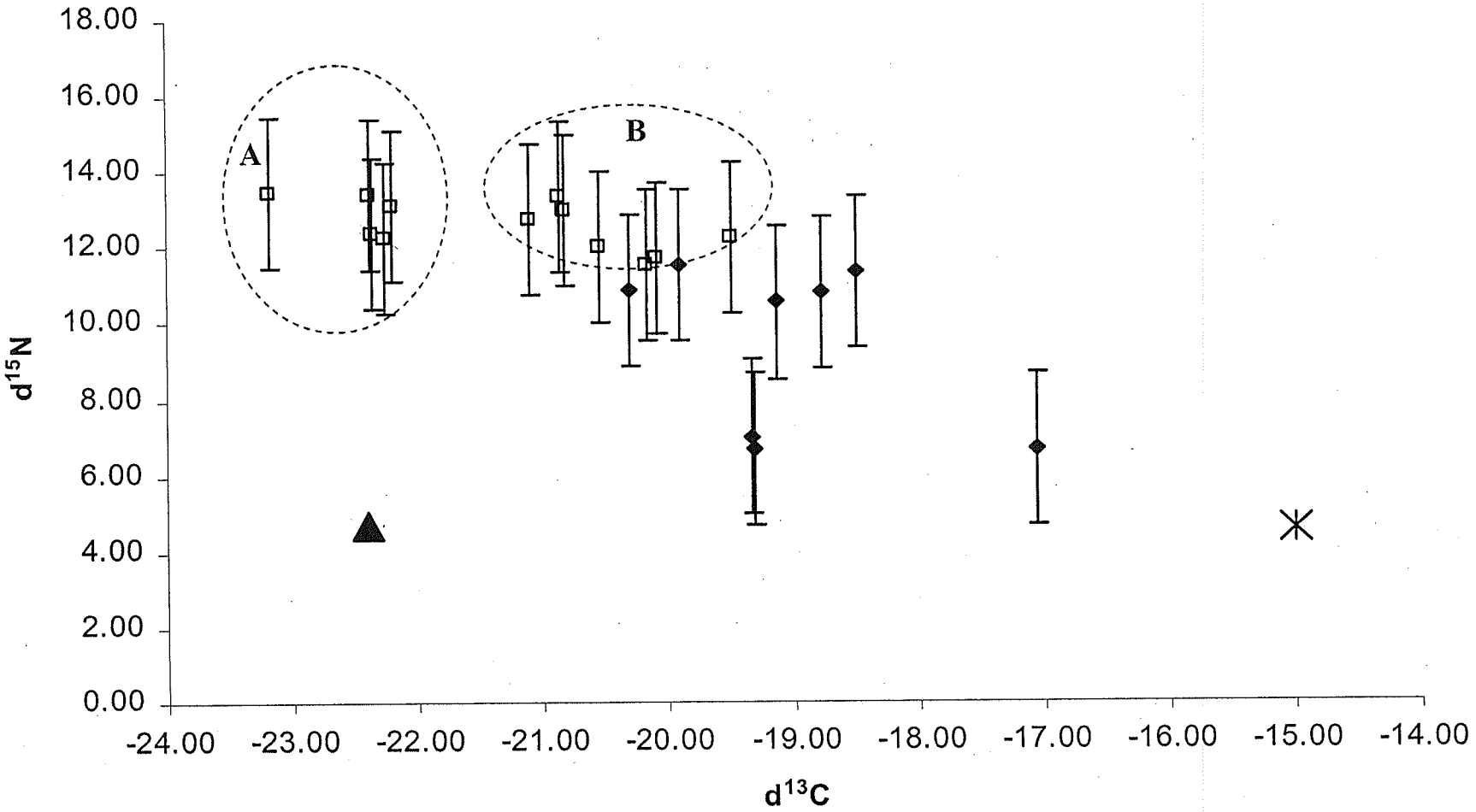

20.00
15.00
10.00
5.00
0.00
d15N
0
200
400
600
800
Fork length (mm)
y = 0.0157x + 5.2594
R² = 0.6783

Figure 24. The relationship between the $\delta^{13}C$ and $\delta^{15}N$ of invertebrates (*Mysis* spp., *Themisto libellula*, *Thysanoessa* spp., *Gammarus* spp., and *Onesimus littoralis*; n = 8) and Arctic cod (n = 12) recovered from char stomach samples. Legend: Open square = Arctic cod; solid diamond = invertebrates, solid triangle = phytoplankton (Source: Grall et al. 2006) and star = microphytes (Source for $\delta^{13}C$ = Moncreiff and Sullivan 2001; [n = 1]; Source for $\delta^{15}N$ = Owens 1987; [n = 1]). Invertebrate samples were from Sylvia Grinnell River and Kagnitsuatsia sample locations while Arctic cod was from 2005 char stomach samples.


18.00
16.00
14.00
12.00
10.00
8.00
6.00
4.00
2.00
0.00
d15N
A
B
-24.00
-23.00
-22.00
-21.00
-20.00
-19.00
-18.00
-17.00
-16.00
-15.00
-14.00
d13C

# CHAPTER FOUR

## Food particle size, growth and stable isotope signatures of young-of-the-year Arctic char under experimental conditions.

## INTRODUCTION

Chapter One examined trophic structuring in the genus *Salvelinus*, based on a review of published data, and the results showed no predictability in food habits of this group. By contrast, diet particle size and nutrient content was correlated with fish size and stomach fullness, based on natural feeding (Chapter Three). Chapter Three established total energy in the food and nutrient content of the main diet items from char in a natural setting and the approximate rates of turnover of stable isotopes based on a calculated SGR and subsequent calculation of the HL for C and N. However, it was difficult to determine the trophic structure of anadromous char using only stable isotopes in a natural setting.

It is generally accepted that small freshwater Arctic char feed predominantly on chironomids, larger invertebrates and fish (Johnson 1980, Hammar 1998). Most of the data from natural populations of Arctic char from small freshwater Arctic lakes indicate that they consume very little zooplankton, even though it comprises *c.* 20% of the biomass of small Arctic lakes (Vanriel and Johnson 1995) and rapidly shift to chironomids and larger invertebrates (Alanärä and Brännäs 1997, Bystrom et al. 2004). A recent study demonstrated that small char feed mainly on benthic near-shore prey (Bystrom et al. 2004). Are small Arctic char unable to consume small food such as zooplankton for any length of time or do they switch to larger food particles to maximize growth? In general, the results of prior studies agree that char feeding habits and growth responses are size-dependent under controlled conditions as well as in natural systems (Tabachek 1988; Power 1980). Total energy and nutrient content of food were the most

important determinants for food intake and growth of char under controlled conditions (Jobling and Wandsvik 1983).

**Stable isotopes**

Numerous factors have been suggested to influence changes in stable isotope ratios following a diet shift. Among these factors were growth rates (Hesslein et al. 1993), feeding rate (Gaye-Siesegger et al. 2004), temperature (Bosley et al. 2002) and biochemical composition of the diets (Focken 2001, Suzuki et al. 2005). My study was designed to be able to calculate the half life of stable isotopes when the diet is comprised of a single food item and when a single diet item is switched. Rarely does a single diet item shift occur in the wild, but experimental diets of a known stable isotope signature should provide information on how rapidly a change in diet through a shift in stable isotope ratios can be detected.

It is difficult to duplicate feeding in a natural setting as diet quantity and quality can change over a short time frame so there is a need for controlled laboratory studies (Gannes et al. 1997). The experiments in this chapter were designed to test the importance of particle size on small Arctic char where growth is rapid and potential shifts in food particle size were most likely to occur in natural setting. A combination of field data from Chapter Three and from the experimental studies in Chapters Four and Five should provide additional insights into the role of food particle size in char diets. Furthermore, I was interested in establishing gut emptying time since it is difficult to calculate from wild char (see Chapter Five). Once total energy and nutrient content of food is known, stomach fullness has been determined, total time to empty a full stomach

and the temperature char are found in, we can begin to develop energetic models for Arctic char (see Chapter Six).

The objectives were to determine: 1) the growth of arctic char fed three natural diets and a commercial feed; 2) the time for young-of-the-year Arctic char reared at 7°C in freshwater fed one diet item to produce a shift in stable isotope signatures that stabilized; and 3) the half life of the isotope signature in char tissue following a diet switch.

# MATERIALS AND METHODS

The Nauyuk strain of Arctic char was donated by the Grand Rapids Manitoba Provincial Fish Hatchery. Char were fed a commercial feed (Silver cup) at swim-up.

**Diets**

*Artemia* nauplii culture: The Artemia hatching medium comprised 35g $L^{-1}$ salt, pH 8.2 and at temperature of 27°C.

Frozen bloodworm and brine shrimp: These diets (and *Artemia* cysts) were obtained from Salt Creek Inc. Salt Lake City, USA) and stored frozen in a deep-freezer at -20 °C.

Commercial feed: The commercial feed, silver cup number 2 granules, comprised 54% protein and 17% fat.

Diet sizes: Particle size range of natural diets were measured while that for ARand CF were obtained from Salt Creek Inc.

**Experiment 1**

Particle size and char growth: The objective of this experiment was to determine if the growth of the young-of-the-year (YOY) Arctic char reared at 7 °C in freshwater under controlled conditions is dependent on food particle size. Char weighed 1.5g at the beginning of experiment. Char were randomly assigned to four different feeding treatments at day 120 post arrival date at the laboratory. Char were assigned to two replicates with 55 fish per 40 $L^{-1}$ tank, at a flow rate of 0.5 L $min^{-1}$. Water temperature was maintained at 7 °C and photoperiod was ambient. The four feeding treatments included char fed freshly hatched *Artemia* nauplii (AR), frozen bloodworm (BW), frozen adult brine shrimp (BS) and commercial feed (CF). The particle sizes of test diets were

measured (Table 31). CF was used as the control. The flow chart of the experimental design is shown in Appendix 32.

Individual fish were weighed and fork length measured at four-week intervals whereas total (i.e. batch) weight measurements were taken biweekly. Fish were also sampled during weighing sessions. Char fed BW and BS were apparently satiated when fed 20% of their total body weight whereas replicates fed AR received about 20,000 – 80,000 *Artemia* nauplii per liter of water. The control (CF) fed to apparent satiation at 3% of their total body weights. Fish were fed three times daily. Total energy and nutrient contents of test diets were determined by bomb calorimetry and proximate analysis. Fish were sampled at day 32, 56, and 114 and experiment 1 was discontinued at day 114 post-initial feed.

**Experiment 2**

Stable isotopes**:** The purpose of the experiment was to determine the time required for isotopic values in muscle tissue to level off following a change in diet. At day 120 post swim-up, char were randomly assigned to a feeding treatment. Treatments were replicated twice with 55 fish $40L^{-1}$ tank, at a flow rate of $0.5L\ min^{-1}$ and a temperature of 7°C. Light was ambient at Winnipeg (N 49° 52', W 97° 08') and was adjusted weekly. The entire experiment extended for about 250 days during which the photoperiod ranged from 18D: 6L at the beginning of the experiment to 12D:12L at the end of the study.

The four treatments comprised Arctic char fed freshly hatched *Artemia* nauplii (AR), frozen bloodworm (BW), frozen adult brine shrimp (BS) and a commercial feed (CF). Reference samples for stable isotopes were collected from char fed CF for 120 days

prior to day 0 of the feeding trial. Char were weighed individually at ~ 4 week intervals (Fig. 25).

Char were fed 4 times daily and each week the diet was adjusted based on *ad libitum* feeding. Total feed for daily feeding was weighed and each tank of char was fed *ad libitum* at the same level for the next 6 days. BS and BW were weighed frozen and placed in the tank while still frozen. Moisture content was determined by freeze drying hatched *Artemia* nauplii which were immediately frozen at -20°C and from BS, BW and CF stored at -20°C. The same batch for each diet was used throughout the study. Nutrient and energy content of each diet was determined by proximate analysis and bomb calorimetry. Char were sacrificed and muscle tissue removed for stable isotope analysis (2-5 individual char) at days 32, 56, 114, 141, 171 and 239 (see Table 33).

The purpose of the experiment was to determine if there were changes in stable isotope ratios after switching the diet and if it was possible to predict the half life of an isotope in the fish muscle. Char from the same diet were combined and randomly selected for the diet switch (Table 34). Mean weight was calculated at the start of the study and char were fed *ad libitum* and weight of diet adjusted weekly based on food consumed by observing feeding. The diets which were switched are listed in Table 32. Some combinations were chosen because, from experiment 1, char fed a specific diet showed significant shifts in stable isotopes values. Examples of why some combinations were selected are outlined below. BW and BS have similar fat content and AR and BS showed similar shifts in stable isotope ratios (experiment 2). BS and AR differed in food particle size and AR was live food while BS was frozen adults. AR and CF were chosen for further assessment because AR is live pelagic food and CF is a commercial crumble

that sinks to the bottom of the tank. Palatability and feeding by char differ for these two diets (char feed on AR in the water column but CF is mostly eaten off the bottom of the tank). Char from experiment 2 continued to be fed BW, CF, AR and these were the controls for experiment 2.

Char were sampled at days 14, 29, 44, 112 from the start of experiment 2. Samples for stable isotope analysis were collected across the size range in each tank. Char were sacrificed in water containing MS-222 and fork length (mm) and weight (g) recorded. Muscle was removed and stored for stable isotope analysis in a -20°C freezer for up to 6 months and then dried to constant weight at 70°C.

**Sample analyses**

Proximate Analysis: Proximate analysis was done for the four diets by Norwest Laboratories, Lethbridge, Alberta using the AOAC official methods. Analyses included moisture content, % protein, % fiber, % total fats (Table 35).

Bomb calorimetry: This is the method used for determination of total energy content of biological samples and was described in Chapter Three.

Stable isotopes: $\delta^{13}$Carbon and $\delta^{15}$nitrogen isotopic analyses on the muscle (protein) were accomplished by continuous flow ion ratio mass spectrometry (CF-IRMS) using a GV-Instruments® IsoPrime attached to a peripheral temperature controlled EuroVector® elemental analyzer (EA) (University of Winnipeg Isotope Laboratory, *UWIL*). 1.0 mg samples of oven-dried fish muscle were loaded into tin capsules and placed in the EA auto-sampler in accompaniment with internally calibrated carbon/nitrogen standards (Pharma casein protein: $\delta^{13}$ C = -22.95 and -26.98 ‰ Vienna PeeDee Belemnite (VPDB); $\delta^{15}$ N = 5.00 and 5.94 ‰ Air, respectively). Batch files were set up as follows: 4

casein, 4 pharma, 10 samples (every 5$^{th}$ sample duplicated and every 15$^{th}$ sample was done in triplicate) and 4 casein.

Carbon and nitrogen isotope results are expressed using standard delta ($\delta$ notation in units of *per mil* (‰). The delta values of carbon ($\delta^{13}C_{cell}$) and nitrogen ($\delta^{15}N_{cell}$) represent deviations from a standard, such that $\delta_{sample} = [(R_{sample}/R_{standard})-1]*10^3$ where R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio in the sample and the standard. The standards used for carbon and nitrogen isotopic analyses are VPDB and IAEA-N-1 (IAEA, Vienna), respectively.

Analytical precision, determined from the analysis of duplicate samples, was ± 0.16 ‰ for $\delta^{13}C$ and ± 0.18 ‰ for $\delta^{15}N$. Accuracy was obtained through the analysis of laboratory standards used for calibration of results.

**Statistical analyses and modeling**

Statistical analyses were done using SPSS (version 11.0.1). Growth was examined by performing an analysis of covariance to determine if there were significant differences among logarithmically transformed weight of fish from each diet treatment over time. An ANOVA was performed on the combined specific growth rates from each sampling period to determine if there were differences among treatments. Coefficients of variation values from the growth experiment were analyzed using a Kruskall Wallace test to determine if there were changes over time. Stable isotopes results were analyzed with multivariate analysis of variance (MANOVA) for each diet treatment at different sampling times and considered significant when P-value < 0.05. Post-hoc tests between subjects were examined using a Bonferroni correction.

The method developed by Hesslein et al. (1993) was used to model the change in carbon and nitrogen stable isotope in muscle:

$$C = C_n + (C_o - C_n) \cdot e^{-(k+m)t} \quad [24]$$

C = the mean isotopic value of a char at any time after a switch, $C_n$ = the mean isotopic value in equilibrium with a new food (experimental diet), $C_o$ = mean isotopic value of a char with the old food (original diet), k = growth rate, m = metabolic turnover constant. The metabolic turnover constant was determined by alternating values in the model and selecting a number based on fitting a least squares regression between observed and expected values. The growth rate (k) of each control/treatment was calculated using the equation:

$$\ln(W/W_o)/t = k \quad [25]$$

W = mean weight of fish at sampling time (g), $W_o$ = mean weight of fish when food was switched (g).

The half life, in days, refers to the decay of a stable isotope in a specific tissue derived from individuals fed a specific diet (Suzuki et al. 2005) and was calculated using the equation:

$$HL = \ln(0.5)/ -(k + m) \quad [26]$$

# RESULTS

## Diets

The particle sizes of the four diets, the amount char were fed and the moisture contents of each diet type are presented in Table 31. The particle size varied among the diets ranging from 160 - 510μm (AR), 5 – 15mm (BW), 3 – 12mm (BS) and 0.7mm for CF (Table 31).

The moisture content was similar for the natural diets, ranging from 89.2 to 92% (Table 31). Total energy values for the four diets ranged from 18,365 to 21,900KJ $kg^{-1}$ (Table 35). The CF had the highest energy content and AR had the lowest energy but the three natural diets were similar (Table 35).

Proximate analyses of the diets also showed a strong similarity among diets (Table 35). Protein varied slightly but all the diets were close to 60% crude protein. Percent fiber was highest for the natural diets ranging from 2.7 to 5.3% and all were higher than CF at 0.2%. Total fat was the most variable of the key nutrients with AR at 10.9%, BW at 5.58, BS at 6.55% and CF at 15.34%.

The required amount of diet for the char, fed *ad libitum* was dependent on the total moisture in the diet. It is apparent from Table 31 that both BW and BS had high moisture levels and the % weight of diet per body mass of char was highly variable for the actual diet (2-25%) but after correcting to dry weight were similar at 1.9- 2.0%. Calculations of the number of AR nauplii $L^{-1}$ ranged from 20,000 nauplii $L^{-1}$ at the beginning of experiment 1 and increased to 80,000 at the end of experiment 2.

Char readily consumed the natural diets in experiment 1 but char fed the natural diets and then shifted to CF in experiment 2 took longer to accept the diet and were only able to maintain the original weight at the time of the diet switch.

**Experiment 1**

Particle size and char growth: At the beginning of experiment 1 char weighed an average of 1.49 ± 0.42 g. Figure **25** illustrates the mean weight and standard error for growth of Arctic char fed four diets over a period of 114 days. Weight of char was similar up to day 114, $F(3, 1768)= 2.22$, $P > 0.05$ (Fig. **25**), but char fed AR weighed less by day 155, $F(3, 1949)= 7.0$, $P < 0.05$. Although food varied in size there was no significant change in the coefficient of variation up to day 114 $H(4)= 4.35$ $P > 0.05$. SGR values of char groups are presented in Appendix **31**.

**Experiment 2**

Stable isotopes: This experiment was not designed as replicated growth trials because random sub-samples of char were taken from each of the treatment tanks for the diet switching study and the remaining char from each of the treatment diets from experiment 1 were the controls for experiment 2. Char were weighed from all treatment tanks at the time samples were randomly selected for stable isotope analysis. All char fed the experimental diets in experiment 2 increased in weight, with the exception of diet switches from natural diets to CF (Table **36**). Char fed the same diets from the beginning of experiment 1 showed an increase in weight over time but char fed BW and BS grew the most. Char fed hatched AR had the lowest mean weight (Fig. **25**). All char where diets were switched from the CF to natural diets showed increased weight (Table **36**). The exception was char fed AR and switched to CF which did not exhibit increased

weight. Those char fed *ad libitum* decreased their food intake as evidenced by feed remaining in the bottom of the tank and weight did not increase.

A MANOVA using stable isotope data from the diets i.e. AR, BW, CF and BS demonstrated significant difference among carbon and nitrogen $F(6,28)= 113.63$ $P< 0.001$, Wilks' lambda= 0.002. Bonferroni corrected post-hoc pair wise comparisons of nitrogen and carbon indicated that the nitrogen signal was similar among AR, BW and CF while the carbon signal was similar between AR and CF (Table 37).

MANOVA results in experiment 1 for char muscle fed the following diets i.e. AR ($F(10, 48)= 5.47$ $P< 0.001$, Wilks' lambda= 0.219), BW ($F(10, 48)= 17.69$ $P< 0.001$, Wilks' lambda= 0.046) and BS ($F(10, 46)= 5.93$ $P< 0.001$, Wilks' lambda= 0.191) demonstrated significant differences in overall stable isotope signals over time. Char fed CF did not show a significant change over time ($F(10, 46)= 1.28$ $P> 0.05$, Wilks' lambda= 0.613). Stable isotope $\delta^{15}N$ values for char fed AR were significantly different by day 141 post first feeding and were different between day 32 and 239, but $\delta^{13}C$ values did not significantly change throughout the experiment. Stable isotope $\delta^{15}N$ ratios for char fed the BW diet were significantly different by day 56 but $\delta^{13}C$ values were significantly different from day 32 onwards. There were no significant differences for either $\delta^{15}N$ or $\delta^{13}C$ ratios for char fed the CF over 239 days. Stable isotope $\delta^{15}N$ ratios for char fed BS, over time, were not significantly different but $\delta^{13}C$ values were significantly different by day 56 post first feed. The $\Delta N$ between the stabilized fish tissue in experiment 2 and their respective diets were 3.14, 5.75, 1.90 and 0.85 for BW, BS, AR and CF, respectively. The $\Delta C$ was -2.32, 1.78, 0.66 and 0.52 for BW, BS, AR and CF, respectively.

Further, experiment 2 was undertaken to determine if stable isotope ratios changed following diet switching. Table 34 lists the $\delta^{15}N$ and $\delta^{13}C$ stable isotope values and reveals a shift in stable isotope ratios over time in some treatments. Significant changes over time were observed for $\delta^{13}C$ values in char switched from AR to BW ($F(6, 52)= 5.824$ $P< 0.001$, Wilks' lambda= 0.358), BW to BS ($F(6, 50)= 4.233$ $P< 0.001$, Wilks' lambda= 0.440), CF to BS in both $\delta^{13}C$ and $\delta^{15}N$ ($F(6, 48)= 7.280$, Wilks' lambda= 0.274), BS to AR in $\delta^{15}N$ ($F(6, 46)= 3.417$ $P< 0.001$, Wilks' lambda= 0.478) and BS to BW in both $\delta^{13}C$ and $\delta^{15}N$ ($F(8, 66)= 19.124$ $P< 0.001$, Wilks' lambda= 0.091). No significant differences in carbon and nitrogen were observed for treatments AR to CF, CF to AR and BW to CF (Table 34).

Isotope values for the controls used in experiment 2 were taken from each diet treatment in experiment 1 after the stable isotope ratios had reached equilibrium. MANOVA performed on the tissues of char fed CF indicated an overall difference $F(6,136) = 116.02$ $P< 0.001$, Wilks' lambda = 0.027, while a post-hoc test demonstrated that the $\delta^{13}C$ values for AR and CF were not significantly different. Data in Table 32 revealed that switching from AR to BW and from BW to BS produced no changes in $\delta^{15}N$ isotope values by day 112, while a switch from CF to BS produced a decrease $\delta^{15}N$ isotope value by day 44 and a switch of diets BS to AR and BS to BW produced an increase in $\delta^{15}N$ isotope values by day 112 and 29, respectively. In the case of $\delta^{13}C$ isotope values there was no change for BS to AR. Increases in the $\delta^{13}C$ isotope values in char muscle were noted when diets were switched from AR to BW and BS to BW and decreases in the $\delta^{13}C$ isotope values were noted when diets were switched from CF to BS and BW to BS. Only a diet switch from CF to BS reached equilibrium by day 112.

Based on the model (Hesslein et al. 1993), the daily growth rate constant (k), daily metabolic tissue replacement (m) and half life (HL) of $\delta^{13}C$ and $\delta^{15}N$ isotopes were calculated (Suzuki et al. 2005). Data from experiment 1 illustrated that k is similar for char fed the three natural diets (Table **38**) and supports growth data presented in Fig. **25**. The HL of the $\delta^{15}N$ isotope in char muscle for CF to AR diet switch was 43.4 days and for the CF to BW diet switch was 32.3 days and for $\delta^{13}C$ were 24.6 and 29.0 days, respectively.

Since k represents the exponential growth rate it is apparent that k differed between experiments 1 and 2 by approximately a factor of 10. Clearly, for experiment 2 the calculated HL for $\delta^{15}N$ is much longer, with some values as long as 726.4 days (diet switch AR to CF) and for $\delta^{13}C$ isotope values as long as 738.5 days (diet switch BW to CF). When char growth was examined from these switched diets, limited or no increase in growth was noted (Table **36**). For example, there was an initial slight decline in growth followed by no growth of char switched from BW to CF and for char where the diet was switched from AR to CF there was initially no growth and then a slight increase at the end of the experiment. By contrast, all other diet switches (Table **38**) resulted in significant increases in char growth (Table **36**) but these diet switches were from natural food to natural food or CF to natural food. It was evident from Table 5 that variation in char growth was high but the HL for $\delta^{15}N$ and $\delta^{13}C$ isotopes differed among the type of diet switched (Table **38**). For example, the diet switched from BS to AR and BS to BW produced different $\delta^{15}N$ and $\delta^{13}C$ ratios and the switch from BW to BS produced different $\delta^{13}C$ (Table **34**). When growth was compared (Table **36**) it was evident that char switched from BS to BW were larger than char switched from BW to BS. The type of

food (palatability and particle size) can also affect growth as diets switched from CF to AR and BS to AR produced different growth rates (Table 36) and this in turn was reflected in the HL of both $\delta^{13}C$ and $\delta^{15}N$ isotopes (Table 38).

# DISCUSSION

## Experiment 1

Particle size and char growth: Arctic char fed diets of different particle size and grown under controlled culture conditions did not have significantly different growth rates up to day 114 ($P \sim 0.05$) () (Fig. 25, Table 32). Char under experimental conditions consumed smaller food particles than char normally do under natural conditions where char of comparable size feed on chironomids. The BW and BS are similar in size to chironomids recovered from the stomachs of similar sized char from Arctic lakes (Dick Pers. Comm.).

The nutrient contents of all test diets in this study were within, or above, minimum requirements (protein; 30-75%: fat; 5-15%: carbohydrates 0-52%) for Arctic char (Dick and Yang 2002, Gurure 1997, NRC 1993). About 10% greater growth was noted for char fed CF four months after the commencement of study. Differences in char growth became more pronounced by day 239 (Fig. 25) and this difference was likely due to the smaller size of AR suggesting there is an upper limit for char size (5-10 g) and diet particle size.

Char fed diets containing ~90% water (BW, BS and AR) required proportionally more food on a wet weight basis than char fed the low moisture nutrient dense CF. In one study, to compensate for lower nutrient content/unit weight of food, Atlantic salmon (*Salmo salar*) fed wet squid showed an improvement in growth and nutrient retention compared to the group fed dried squid (Grove et al. 1985). This advantage was due to faster nutrient release from the stomach and higher digestibility (Grove et al. 1985). In our study, char fed diets BW, BS and AR, maintained similar weights by increasing food

intake, by wet weight. However, these natural foods when corrected to a dry weight basis were similar to the weight of CF fed.

The diets with the highest protein content had less fat while diets with the highest fat content had marginally less protein. Char appear to be able to utilize either protein or fat as energy sources. The amount of CF (2% of body mass) consumed by char had total energy of 21,940 KJ $kg^{-1}$ and weights were slightly higher. The metabolic costs (amount of energy required) for the digestion of diets with high protein may be higher than diets with greater fat. The total energy content of the test diets ranged from 18,000 KJ $Kg^{-1}$ – 22,000 KJ $Kg^{-1}$ (Table 35) and is similar to total energy content of food items consumed by char in the marine environment (Pers. Observation and Dick, Pers. Comm.).

**Experiment 2**

Stable isotopes: A comparison of char, from experiment 1, fed three different natural diets to char originally fed the nutrient rich CF diet, indicated that stable isotope ratios of $\delta^{15}N$ were unchanged over 32 days. Although there was no significant change in $\delta^{15}N$ ratios by day 32 post first feeding, $\delta^{13}C$ ratios started to shift in char fed BW but not for char fed BS. Char fed AR were similar to char fed CF. Char fed BW had a further shift in their $\delta^{13}C$ ratios by day 56.

Data from our study fits Hesslein et al's (1993) growth model and it is clear that stable isotope ratios for both $\delta^{13}C$ and $\delta^{15}N$ were correlated with the growth rate of char. The HL values in our study were variable and were correlated to growth of char. Similarily, published HL values are variable for muscle i.e. 19.3 -25.7 days for $\delta^{13}C$ and $\delta^{15}N$ in *Lateolabrax japonicus,* mean weight 9.87 g, raised at 18-23°C (Suzuki et al. 2005); 50% turnover in 98 days for $\delta^{15}N$ in stingray *(Potamotrygon motoro)*, mean

weight 106 g, raised at 26°C (MacNeil et al. 2006). Our HL values of 43.4 and 32.3 for $\delta^{15}N$ in char muscle fed AR and BW, respectively, indicates that cold water species of fish raised at 7°C had a relatively rapid turnover rate for stable isotopes that is not necessarily tied to temperature. Furthermore, the HL increased as char became older and larger, even though they were still young-of-the-year (Table 38). We predict that char shortly after first feed and even smaller than 1.46 g (the mean weight of char at the start of this study) will have even shorter HLs for both $\delta^{13}C$ and $\delta^{15}N$.

Although previous laboratory studies of trophic fractionation reported little change or slight enrichment in $\delta^{13}C$ from diet to consumer (Fry and Sherr 1984, Peterson and Fry 1987), it is important to note that consumers assimilate dietary components (carbohydrates, proteins and lipids) with varying efficiencies (Vander Zanden and Rasmussen 2001). For instance, lipids are usually depleted in $\delta^{13}C$ due to fractionation that takes place during lipid synthesis (DeNiro and Epstein 1978). Therefore, fish fed diets low in fat/lipid may be more likely to synthesize lipids from dietary carbohydrates or proteins thus, resulting in a more distinctive shift(s) in $\delta^{13}C$ than would be found in fish fed diets with high dietary fat levels. In essence, switching from a high-fat diet to a low-fat diet may show a marked shift in $\delta^{13}C$ and *vice versa.* Perhaps, this is the reason why char fed BW showed a further shift in $\delta^{13}C$ at day 56 in Experiment 1 (Table 31). BW had the least total fat among the 4 test diets and this difference may be sufficient to cause a shift in the long term. It has been indicated that lipid content influenced $\delta^{13}C$ ratios more than feeding level (Gaye-Siesegger et al. 2004). Char fed BW may acquire more of their lipids by biosynthesis rather than absorbing directly from the diet, as suggested for tilapia (Focken 2001), but BW had the lowest $\delta^{13}C$ ratios. The total fat

content in diets AR, BS and CF may be sufficient to meet essential fatty acid requirements directly without additional biosynthesis.

Perhaps type of food in a diet switch influences HL. The BW diet has $\delta^{13}C$ and $\delta^{15}N$ ratios of 11.9 and 10.02 days, respectively, and BS had values for $\delta^{13}C$ and $\delta^{15}N$ of 23.54 and 4.01, respectively (Table 33).

The HL for the BW to BS switch was 217.9 days for $\delta^{15}N$ and 165.8 days for $\delta^{13}C$. By contrast the diet switch from BS to BW had HLs of 63.7 and 64.3 for $\delta^{15}N$ and $\delta^{13}C$, respectively, but the k values for char were similar (Table 38). This suggests that food more enriched for $\delta^{15}N$ and $\delta^{13}C$ will take longer to reach a new HL and equilibrium in the tissues and the corollary is that diets less enriched for $\delta^{13}C$ and $\delta^{15}N$ will have a shorter HL. Similarly, the diet switch of BS to AR had char with $\delta^{13}C$ and $\delta^{15}N$ HL double that of the diet switch BS to BW, but again k values were similar (Table 38). A comparison of diet switches CF to AR had a HL for $\delta^{15}N$ of 105.5 and no change for $\delta^{13}C$. AR and BS have higher fat content (Table 35). Perhaps absolute amount of fat and relative amount of fat to protein may be important in predicting time to shift to new stable isotope equilibrium, especially for cold water species.

Results from this study agree with the published literature that it could take years for slow growing fish to reach a new equilibrium for stable isotope values between fish tissue and diet (Hesslein et al. 1993, Gurure 1997). However, while age of fish is important in interpreting stable isotope turnover rates and time to reach a new equilibrium it is evident from our data that even a maintenance diet i.e. no growth (AR to CF), can have a marked influence on the calculation of the half life of an isotope by extending the time to reach equilibrium in young-of-the-year char (Table 38).

Furthermore, my data showed that new stable isotope equilibria could occur as early as 56 days following a switch in diet (Table 38). These observations suggest that the nutritional state (other than starvation) of the fish, regardless of age, can influence the stable isotope ratios in its tissues.

Recent studies report that different fish tissues give different $\delta^{15}N$ signals and that muscle values may introduce error into estimates in the short term (Gurure 1997, Logan et al. 2006). I agree with this assessment for older, slow growing fish but for young-of-the-year cold water species, such as char, our data suggests that stable isotope HL and a new equilibrium state can be reached quickly and therefore muscle is a valuable reference tissue to interpret short term changes in stable isotope ratios during the exponential growth phase. Moreover, during the first summer for north temperate and Arctic fish species not only is growth rapid, but important shifts in diet can occur in a matter of months in a species such as Arctic char (Johnson 1980). Consequently, while tissues such as liver will undoubtedly contribute valuable information, muscle tissue will continue to have a useful role in interpreting early feeding in young of the year fish.

**Conclusion**

Beyond certain length and age, char feeding and growth are dependent on diet particle size. A shift in stable isotope ratios can occur in char fed one diet item in about 1½ months reflecting both diet quality and high SGR. Mean HL for fast-growing char was *c.* 50 days and this correlated with high SGR. A HL of *c.* 50 days is considerably short in view of the fact that Arctic char is a cold-water fish species. Data from this chapter support the HL approximations of *c.* 90 days calculated for wild marine char (Chapter Three). My results showed that short HL is defined by how fast a fish species

can grow rather than fish size. Overall, the experiments were useful in understanding feeding patterns of wild marine char and can be applied in future ecological studies.

Table 31. Particle size, amount and moisture contents of char test diets.

| Test diets | Size ranges | Feed/day (% body wt.) | % Moisture content | % Dry wt. |
|---|---|---|---|---|
| *Artemia* nauplii (AR) | 160 - 510 µm | 20,000 - 80,000 $L^{-1}$ | 89.2 | 1.95 |
| Frozen Bloodoworm (BW) | 5 - 15 mm | 20% | 93 | 2 |
| Frozen Brine shrimp (BS) | 3 - 12 mm | 20% | 90 | 2 |
| Commercial feed (CF) | 0.7 mm | 2% | 3.6 | 96.4 |

Table 32. Summary of ANOVA results on char growth for char fed AR, BW, BS and CF for a period of 114 days based on total individual weight in experiment 1.

| Day | df | F-ratio | P-value | Sig. Abbrev. |
|---|---|---|---|---|
| 0 | (3, 395) | 0.514 | 0.673 | NS |
| 30 | (3, 386) | 0.956 | 0.414 | NS |
| 56 | (3, 357) | 2.256 | 0.082 | NS |
| 86 | (3, 307) | 3.076 | 0.028* | S |
| 114 | (3, 308) | 2.706 | 0.045 | NS |

* Statistical significance only between AR and CF before AR nauplii count water $L^{-1}$ was increased. Legend: AR = *Artemia* nauplii; BW = frozen Bloodworm; BS = frozen brineshrimp and CF = Commercial feed.

Table 33. Stable isotope ratios (‰) (mean, standard deviation and number) in diets (AR, BW, BS and CF) fed to char and in muscle of char fed the diets over time (days) in Experiment 1*

| | Fish diet | | | Muscle tissue (days) | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 32 | | | 56 | | | 141 | | | 171 | | | 239 | | |
| | $\delta^{13}C$ | $\delta^{15}N$ | n | $\delta^{13}C$ | $\delta^{15}N$ | n | $\delta^{13}C$ | $\delta^{15}N$ | n | $\delta^{13}C$ | $\delta^{15}N$ | n | $\delta^{13}C$ | $\delta^{15}N$ | n | $\delta^{13}C$ | $\delta^{15}N$ | n |
| AR | -20.49 ± 0.22 | 10.14 ± 0.48 | 5 | -19.5 ± 1.2 | 10.2 ± 0.9 | 2 | -19.5 ± 0.4 | 11.5 ± 0.5 | 5 | -20.4 ± 0.5 | 11.9 ± 0.9[a] | 5 | -19.7 ± 0.6 | 12.6 ± 0.2[a] | 4 | -19.6 ± 0.6 | 12.6 ± 0.2[a,b] | 5 |
| BW | -11.94 ± 0.90 | 10.02 ± 0.95 | 5 | -17.7 ± 1.3[a] | 10.9 ± 1.0 | 2 | -15.0 ± 1.0[a,b] | 12.8 ± 0.5[a] | 5 | -13.9 ± 0.4[a,b] | 13.5 ± 0.4[a,b] | 5 | -14.3 ± 0.6[a,b] | 12.9 ± 0.6[a] | 4 | -13.9 ± 0.6[a,b] | 13.4 ± 1.0[a,b] | 5 |
| CF | -19.76 ± 0.46 | 10.28 ± 0.49 | 5 | -19.4 ± 0.4 | 10.9 ± 0.1 | 2 | -19.3 ± 0.2 | 11.4 ± 0.3 | 5 | -19.2 ± 0.3 | 11.2 ± 0.3 | 5 | -19.5 ± 0.2 | 10.6 ± 0.8 | 3 | -19.0 ± 1.1 | 11.1 ± 1.0 | 5 |
| BS | -23.54 ± 1.16 | 4.01 ± 0.47 | 5 | -20.6 ± 0.1 | 10.0 ± 0.7 | 2 | -21.4 ± 0.8[a] | 9.7 ± 0.5 | 5 | -21.4 ± 0.6[a] | 10.0 ± 0.4 | 5 | -21.6 ± 0.7[a] | 9.0 ± 0.6 | 3 | -22.4 ± 0.4[a,b] | 9.8 ± 0.4 | 5 |

*All fish prior to the start of the experiment were fed a control diet (CF). The following values are based on 10 fish samples collected taken at days 90 and 120 pre treatment ( $\delta^{13}C = -19.9 \pm 0.6$ and $\delta^{15}N = 10.5 \pm 1.0$).

Statistically signigficant (Bonferroni corrected) ($P < 0.05$) differences of carbon and/or nitrogen of observed value relative to controls (a) and day 32 (b). All other carbon and nitrogen pairwise values were not significant. Legend: AR = *Artemia* nauplii; BW = frozen Bloodworm; BS = frozen brineshrimp and CF = Commercial feed.

Table 34. Stable isotope ratios (‰) (mean ± SD, and n) among switched diets (AR, BW, BS and CF) over time (days) for Experiment 2*

| Treatment | 29 | | | 44 | | | 112 | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\delta^{13}C$ | $\delta^{15}N$ | n | $\delta^{13}C$ | $\delta^{15}N$ | n | $\delta^{13}C$ | $\delta^{15}N$ | n |
| BW to CF | -14.2 ± 0.1 | 12.4 ± 0.9 | 5 | -13.9 ± 0.5 | 12.4 ± 0.3 | 7 | -13.9 ± 1.2 | 13.1 ± 0.2 | 5 |
| BS to BW | -19.1 ± 0.8[a] | 10.6 ± 0.4[a] | 6 | -19.0 ± 0.6[a] | 10.2 ± 0.8 | 5 | -17.2 ± 0.6[a,b,c] | 12.1 ± 0.6[a,b,c] | 5 |
| CF to AR | -19.2 ± 0.1 | 11.4 ± 0.3 | 5 | -19.4 ± 0.6 | 11.0 ± 0.8 | 5 | -19.9 ± 0.5 | 11.9 ± 1.0 | 5 |
| AR to CF | -19.8 ± 0.5 | 11.6 ± 0.5 | 5 | -19.9 ± 1.2 | 11.4 ± 0.6 | 5 | -18.8 ± 0.7 | 11.5 ± 0.7 | 5 |
| BW to BS | -13.9 ± 0.3 | 13.5 ± 0.2 | 3 | -14.4 ± 0.8 | 12.9 ± 0.6 | 3 | -17.9 ± 3.0[a,b,c] | 12.0 ± 1.3 | 5 |
| AR to BW | -19.8 ± 0.4 | 12.0 ± 0.4 | 3 | -18.6 ± 1.18 | 11.8 ± 0.7 | 4 | -17.5 ± 1.1[a,b] | 12.9 ± 0.9 | 5 |
| CF to BS | -20.3 ± 0.9 | 11.2 ± 0.4 | 3 | -20.4 ± 1.3 | 9.9 ± 0.4[a] | 3 | -21.5 ± 1.0[a] | 9.9 ± 0.5[a] | 5 |
| BS to AR | -22.0 ± 0.6 | 9.8 ± 0.6 | 2 | -20.8 ± 1.0 | 10.7 ± 0.4 | 3 | -20.6 ± 0.8 | 10.8 ± 0.8[a] | 5 |

*AR control: $\delta^{13}C$= -19.8 ± 0.6, $\delta^{15}N$ = 12 ± 0.7 (n= 19), BW control: $\delta^{13}C$ = -14.3 ± 0.8, $\delta^{15}N$ = 13.2 ± 0.7 (n= 19), CF control: $\delta^{13}C$ = -19.2 ± 0.6, $\delta^{15}N$ = 11.1 ± 0.7 (n= 18), BS control: $\delta^{13}C$ = -21.7 ± 0.7, $\delta^{15}N$ = 9.7 ± 0.6 (n= 18).
Statistically signigficant (Bonferroni corrected) ($P < 0.05$) differences of carbon and/or nitrogen of observed value relative to controls (a), day 29 (b) and day 44 (c). All other carbon and nitrogen pairwise values were not significant. Legend: AR = *Artemia* nauplii; BW = frozen Bloodworm; BS = frozen brineshrimp and CF = Commercial feed.

Table 35. Proximate and total energy analyses of the diets* (mean ± SD).

| Diets | AR | BW | BS | CF |
|---|---|---|---|---|
| n | 2 | 2 | 2 | 2 |
| Protein (%) | 60.25 ± 5.87 | 67.15 ± 0.35 | 61.9 ± 1.98 | 56.85 ± 0.35 |
| Fibre (%) | 5.30 ± 0.42 | 3.8 ± 0.28 | 2.7 ± 0.99 | 0.2 ± 0 |
| Total fat (%) | 10.94 ± 0.25 | 5.58 ± 0.33 | 6.55 ± 0.88 | 15.34 ± 0.04 |
| Total Energy (KJ $Kg^{-1}$) | 18,365.0 ± 946.1 | 19,623.5 ± 124.7 | 18,853.5 ± 297.7 | 21,940.0 ± 120.0 |

*AR = *Artemia* nauplii; BW = frozen Bloodworm; BS = frozen brinesrimp and CF = Commercial feed.

Table 36. Mean ± SD and number (in brackets) of char weight (g) over time (day) in diet switching Experiment 2. Days are referenced to Experiment 2. Diets* used were AR, BW, BS and CF

| **Switch** | **Day** | | |
|---|---|---|---|
| | **29** | **59** | **91** |
| BS to BW | 11.6 ± 3.1 (n= 33) | 15.3 ± 5.2 (n= 22) | 21.2 ± 8.0 (n= 22) |
| CF to AR | 9.7 ± 3.4 (n= 25) | 11.9 ± 4.1 (n= 15) | 14.5 ± 5.3 (n= 15) |
| BW to CF | 8.2 ± 1.8 (n= 38) | 7.4 ± 1.4 (n= 26) | 7.4 ± 1.4 (n= 26) |
| AR to CF | 7.5 ± 1.9 (n= 26) | 7.4 ± 1.9 (n= 16) | 8.1 ± 3.5 (n= 16) |
| AR to BW | 10.5 ± 3.9 (n= 19) | 12.9 ± 4.1 (n= 11) | 16.1 ± 5.4 (n= 11) |
| BW to BS | 8.1 ± 2.4 (n= 13) | 9.7 ± 4.5 (n= 7) | 13.7 ± 6.9 (n= 7) |
| CF to BS | 10.6 ± 4.2 (n= 16) | 14.6 ± 6.4 (n= 10) | 20.0 ± 10.1 (n= 10) |
| BS to AR | 9.3 ± 3.6 (n= 19) | 9.1 ± 3.4 (n= 13) | 16.2 ± 21.2 (n= 13) |

*AR = *Artemia* nauplii; BW = frozen Bloodworm; BS = frozen brinesrimp and CF = Commercial feed.

Table 37. Significance values from Bonferroni corrected MANOVA among diets (AR = Artemia nauplii; BW = frozen Bloodworm; BS = frozen brineshrimp; and CF = Commercial feed) NS = not significant and * = $P < 0.05$. Significance values for $\delta^{15}N$ and $\delta^{13}C$ are given in top and bottom diagonals, respectively.

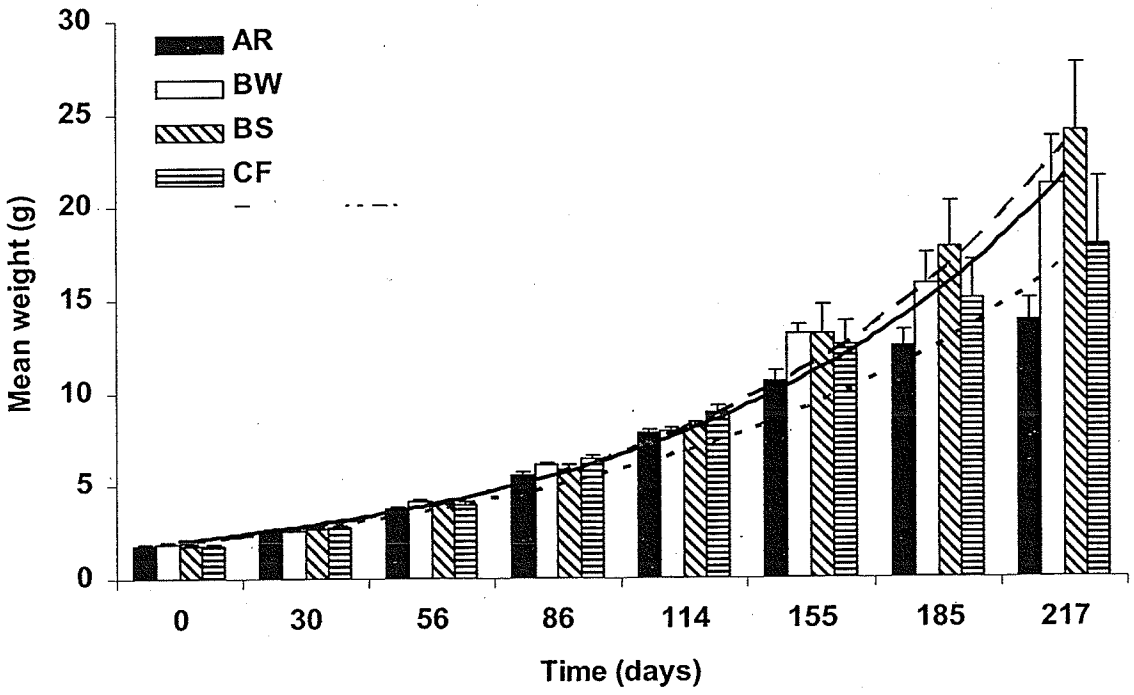
| | AR | BW | CF | BS |
|---|---|---|---|---|
| AR | | NS | NS | * |
| BW | * | | NS | * |
| CF | NS | * | | * |
| BS | * | * | * | |

Table 38. Daily growth rate constant (k), daily metabolic tissue replacement (m) and half life (HL) (days) of Nitrogen and Carbon stable isotopes for Arctic char in Experiments 1 and 2. Slope and $r^2$ of linear regression calculated for observed and modeled values of carbon and nitrogen. * Experiment 1, data for CF (commercial feed) was not given as there were no significant differences. (-) = no significance differences in stable isotope.

| | | $\delta^{15}N$ | | | | $\delta^{13}C$ | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Range of k | m | HL | Slope | $r^2$ | m | HL | Slope | $r^2$ |
| Experiment 1* | | | | | | | | | |
| CF to AR | 0.013-0.01 | 0.0045 | 43.4 | 0.55 | 0.78 | - | - | - | - |
| CF to BW | 0.015-0.012 | 0.0085 | 32.3 | 0.73 | 0.84 | 0.0152 | 24.6 | 0.85 | 0.93 |
| CF to BS | 0.014-0.012 | - | - | - | - | 0.0109 | 29.0 | 0.75 | 0.83 |
| Experiment 2 | | | | | | | | | |
| AR to BW | 0.01-0.009 | 0.00001 | 70.7 | 0.43 | 0.49 | 0.00001 | 70.7 | 1.24 | 0.85 |
| AR to CF$^+$ | 0.001 | 0 | 726.41 | 0.06 | 0.44 | - | - | - | - |
| CF to AR | 0.005-0.006 | 0.0009 | 105.5 | -0.13 | 0.04 | - | - | - | - |
| BW to CF | -0.002 | 0.006 | 168.4 | 0.10 | 0.02 | 0.001 | 738.5 | 0.88 | 0.55 |
| BW to BS | 0.002-0.005 | 0 | 217.9 | 0.88 | 0.86 | 0.001 | 165.8 | 0.77 | 0.90 |
| CF to BS | 0.009 | 0.008 | 40.2 | 0.54 | 0.62 | 0.00001 | 75.0 | 0.74 | 0.97 |
| BS to AR | 0.005-0.006 | 0.0007 | 120.9 | 0.73 | 0.74 | 0.0012 | 111.2 | 0.50 | 0.63 |
| BS to BW | 0.005-0.008 | 0.0037 | 63.7 | 0.82 | 0.80 | 0.0036 | 64.3 | 1.15 | 0.6 |

* char fed CF not shown as there were no changes, $^+$ due to lower feed intake i.e. maintenance diet. Legend:
*AR = *Artemia* nauplii; BW = frozen Bloodworm; BS = frozen brinesrimp and
CF = Commercial feed.

Figure 25. Mean and standard error of weight over time of Arctic char fed diets of *Artemia* (AR), frozen bloodworm (BW), frozen brine shrimp (BS) and commercial feed (CF) in Experiment 1. Exponential regression line for CF ($r^2 = 0.99$) is solid, BW/BS ($r^2 = 0.99$) are long dashed and AR ($r^2 = 0.99$) is short dashed.


AR
BW
BS
CF
Mean weight (g)
30
25
20
15
10
5
0
0
30
56
86
114
155
185
217
Time (days)

# CHAPTER FIVE

## Stomach emptying time of young-of-the-year Arctic char: temperature, rates of gastric evacuation, model and salinity.

# INTRODUCTION

The half-life (HL) of carbon and nitrogen isotopes were determined for char feeding in the marine environment (Chapter Three) and more precise HL were calculated from controlled feeding experiments in Chapter Four. Knowledge of the stomach emptying time and the rate of gastric evacuation of the young-of-the-year Arctic char under controlled conditions is important in estimating how much food char can consume at a given temperature and time in freshwater and marine environments. Stomach emptying time is the time (hours) it will take char to empty its stomach (Elliot 1972) while rate of gastric evacuation is the change of weight of stomach contents over time (Elliot and Persson 1978, Amundsen and Klemetsen 1988). Estimates of food consumption are also required to quantify predation and feeding interactions among and within fish species (Koed 2001). The common objective of most studies on gastric evacuation under controlled conditions had usually been to correlate results of such studies to field estimates since there are no direct methods for measuring food consumption in the field (Andersen 1999).

Studies on gastric evacuation have been carried out for whiting *Melangius merlangus* (Andersen 1999), whiting, *M. merlangus*, saithe *Pollachius virens* and cod *Gadus morhua* (Andersen 2001), burbot *Lota lota* (Pääkkönen and Marjomäki 1997), pikeperch *Stizostedion lucioperca* (Koed 2001), horse mackerel *Trachurus trachurus* (Temming and Hermann 2001), Atlantic mackerel *Scomber scombrus* (Temming et al. 2002), bream *Abramis brama*, silver bream *Blicca bjoerkna*, roach *Rutilus rutilus*, gibel *Carassius gibelio* and carp *Cyprinus carpio* (Specziár 2002), bluegill sunfish *Lepomis*

*machrochirus* (Windell 1966), juvenile Pacific halibut *Hippoglossus stenolepis* (Hurst 2004), and plaice *Pleuronectes platesssa* (Jobling 1980). Although there is generally little information on salmonids, rates of gastric evacuation have been studied in brown trout *Salmo trutta* (Elliot 1972, 1976), brook char *Salvelinus fontinalis* Mitchell (Hess and Rainwater 1939), rainbow trout *Onchorhynchus mykiss* (Reimers 1957, Windell and Norris 1969, Brett and Higgs 1970). Amundsen and Klemetsen (1988) investigated the gastric evacuation rates of wild char fed natural diets under controlled conditions.

**Fish size**

The effect of fish size on the rate of gastric evacuation has been controversial. Windell (1966) observed no significant differences in the stomach emptying time among bluegill sunfish *L. machrochirus* of different ages and body weights fed single- or multi-unit meals. Similarly, Andersen (1999, 2001), reported no significant effect of sizes of whiting, saithe and cod on gastric evacuation for meal sizes expressed relative to body size of these predators. Further, dos Santos and Jobling (1991, 1995) and Hurst (2004) did not report an effect of meal size expressed relative to body size on gastric evacuation rates in cod and juvenile Pacific halibut, respectively. By contrast, Elliot (1976) and Pääkkönen and Marjomäki (1997) reported that body weight affected gastric evacuation in brown trout and burbot, respectively.

**Temperature and time**

Studies that have reported a direct relationship between temperature and stomach emptying time in fish species included Pääkkönen and Marjomäki (1997) (burbort *L. lota*), Elliot (1976) (brown trout *S. trutta)*, Andersen (1999, 2001) (whiting *M. merlangus*, cod *G. morhua*), Koed (2001) (pikeperch *S. lucioperca*), Specziár (2002)

(bream *A. brama*, silver bream *B. bjoerkna*, roach *R. rutilus*, gibel *C. gibelio*, carp *C. carpio*), Vinni et al. (2005) (bluefish *O. eperlanus*), and Temming et al. (2002) (Atlantic mackerel *Scomber scombrus*). By contrast, Cui and Wootton (1988) noted that at a given restricted ration level, food conversion efficiencies generally decreased with increased temperature whereas at maximum rations, conversion efficiencies were insensitive to temperature in the minnow *Phoxinus phoxinus*. Further, Andersen and Riis-Vestergaard (2003) did not find a direct effect of temperature on net conversion efficiency in saithe *Pollachius virens* and whiting *Merlangus merlangus*.

The effects of temperature on char growth were investigated by Larsson and Berglund (1998) and Jobling (1983) but only Amundsen and Klemetsen (1988) examined the effect of temperature on the rate of gastric evacuation on anadromous Arctic char.

Elliot and Persson (1978) stated that the relationship between the cumulative quantity of diet consumed and time appears to be asymptotic in larger fish, especially at abundant food resources, but often tends towards linearity with decreasing fish size and food availability since larger fish rarely feed to satiation. This information is lacking for YOY char at different temperatures in freshwater.

**Models for rates of gastric evacuation**

Several models for rates of gastric evacuation include: 1) exponential for brown trout *S. trutta* and perch *P. fluviatilis* (Elliot and Persson 1978), burbot (Pääkkönen and Marjomäki 1997), five cyprinids (bream *A. bramas*, silver bream *B. bjoerkna*, roach *R. rutilus*, gibel *C.gibelio* and carp *C. carpio*) (Specziár 2002), square root for three gadoids (whiting, *M. merlangus*, saithe *P. virens* and cod *G. morhua*) (Andersen 2001); 2) power for whiting *M. merlangus* (Andersen 1999, 1998); and 3) generic (a product of square

root model) (Andersen and Beyer 2005) have been used to describe gastric evacuation rates in fish species. Andersen (2001) and Specziár (2002) attempted to use one model to describe gastric evacuation rates of more than one fish species while Nelson and Ross (1995) noted that a single equation may not describe the evacuation process for all food types. Temming and Hermann (2001) have reported a general consumption model that may be applicable to a variety of prey types that have not yet been tested in experiments provided the energy content of such prey organisms are known. Once stomach fullness has been determined, total time to empty a full stomach under the temperature char frequent, then we can begin to develop energetic models for Arctic char (see Chapter Six).

The objectives of this chapter were to: a) determine stomach emptying time of the YOY Arctic char reared under controlled conditions at different temperatures; b) determine gastric evacuation rates and model of YOY Arctic char at different temperatures and c); speculate on the effect of salinity on char growth based on data from literature and exploratory results.

# MATERIALS AND METHODS

## Experiment

Freshwater: This experiment was done at the end of experiments 1 and 2 discussed in Chapter Four, hence the differences in fish weight. Young-of-the-year char of average weight 21.97 ± 6.07 g (mean ± SD) were held in a 40 $L^{-1}$ flow-through tank at a flow rate of 0.5 L $min^{-1}$. Char had parr marks indicating that they were ready to go to the sea (Reist et al. 2006).

For conditioning purposes, char were maintained at temperatures of 4, 7 and 10 °C and fed bloodworm (BW) 3 times daily for one week. For the actual experiment, char were starved for 24 hours and then fed with BW to satiation.

Bloodworm was considered appropriate for this experiment because physical observations in previous experiments revealed that char readily accepted the diet. Pilot studies showed that char stomachs were not empty at 8 hours postfeed and that there were no digesta in char gut 1-4 hours after initial feeding. Hence, char were sampled at 2 and 4 hourly intervals from 8 hours postfeed (i.e. 8, 12, 14, 16, 18, 20, 22, and 24 post-feeding). Char were terminated using 1 g of MS 222 (Tricaine methanesulfonate) per liter of water (Canadian Council on Animal Care 2005). Immediately after sampling, char weight, and length were taken and then, char were eviscerated and the fresh stomach contents weighed and counted. Observations were also made on food remains in the foregut, midgut and hindgut.

The ratio of weight of full stomach to char weight was evaluated to determine if char weight affected the amount of diet char consumed. This was done using stomach

content data of 1-4 hours post-initial feeding. Although the *n* values were small, the ratio of weight of full stomach to fish weight of small and large char was the same (see Appendix 33).

Salt water: Salinity level of 23‰ was chosen for comparative purposes since sea salinity for anadromous char (Chapter Three) is about 23‰. Salinity was calculated from conductivity values recorded in the field. Char was acclimated in 23‰ salinity for 1 week. Feeding was observed in salinity levels up to 35‰ for 1 hour. Opercula movements in both salinities were physically observed and compared to that in freshwater.

**Statistical analyses**

Statistical analyses were done using SPSS (version 11.0.1), and Microsoft Excel® packages.

Stomach emptying time: Weight of stomach contents was corrected to a percent ratio of the fish weight with the following formula:

$$\%WS = (WS/FW)*100 \qquad [27]$$

where $WS$ = weight of stomach content and $FW$ = fish weight in grams (g). Simple regression analyses were carried out to determine the relationship between $\%WS$ and time at given temperatures (Fig. 26).

Temperature: An ANOVA was done to determine the significance of temperature on $\%WS$.

Models of rates of gastric evacuation: Although the focus of this chapter was to determine the stomach emptying time of YOY char under conditioned environment, rates of gastric evacuation were also estimated because the results were used in discussions presented in Chapter Six. Rates of gastric evacuation were calculated from slopes of the percent (%) ratios of weight of stomach contents/fish weight over time. This method was considered appropriate since it involved ratios of weights of stomach contents to fish weight. The slopes represented the rate of decrease in the weight of stomach contents (relative to fish weight) with time (Amundsen and Klemetsen 1988). The unit of gastric evacuation rates is gram per hour ($gh^{-1}$)

# RESULTS

## Experiment

**Freshwater:** Stomach emptying time: The stomach emptying time of YOY char at different temperatures are presented in Fig. 26. Char stomachs were empty at *c.* 22, 18 and 16 hours at 4, 7 and 10 °C, respectively (Fig. 26).

Temperature: ANOVA results showed that temperature had significant effects on *WS* [$F(2, 0.342) = 17.817$, $P < 0.05$).

Saltwater: The stomach emptying time of YOY char fed bloodworm in saltwater at 7 °C was *c.* 17 hours post-initial feeding. Char feeding efficiency was greatly reduced in 35‰ saltwater. Char swimming activity and opercula movements in 35‰ saltwater were much higher than in 23‰ salinity while these movements in freshwater were comparable to that of 23‰ salinity. The rate of gastric evacuation of char in saltwater was *c.* $0.17gh^{-1}$ (Fig. 27).

## Model of rates of gastric evacuation

Gastric evacuation of YOY char was best described by a linear model. The linear equations at different temperatures are as follow: 4 °C ($Y = -0.12x + 2.5923$; $r^2 = 0.5984$); 7 °C ($Y = -0.2229x + 4.2052$; $r^2 = 0.5434$) and 10 °C ($Y = -0.3618x + 5.748$; $r^2 = 0.8058$) where Y = %ratio of *WS/FW* and $x$ = time $t$ postfeed. Rates of gastric evacuation at 4 °C, 7 °C and 10 °C were $0.12gh^{-1}$, $0.22gh^{-1}$ and $0.36gh^{-1}$ respectively (Fig. 26, Table 39).

The general linear equations and model constants describing the relationships between *WS*, temperature and time are presented in Table 40. The general linear equation when one predictor was involved is expressed as $Y = a + bx$ where Y = *WS* (the ratio of

weight of stomach content/fish weight = dependent variable), $a$ = intercept at Y, $b$ = constant and $x$ = predictor. But when two predictors were combined to predict *WS* (Table **40**) the linear equation is expressed as:

$$Y = a + b_1x_1 + b_2 x_2 \quad [28]$$

where $b_1$ and $b_2$ = constants for the two predictors and $x_1$ and $x_2$ = the two predictors.

The general linear model describing the relationship between gastric evacuation and temperature over time in char is given by:

$$Y = 0.953 + (-0.0405*t) + (-0.02591*T) \quad [29]$$

where Y = weight of stomach content (% body weight), $t$ = time and $T$ = temperature (Table **40**).

# DISCUSSION

## Freshwater

### Temperature

Stomach emptying time (hours): The stomach emptying times of char were influenced by temperature (Fig. 26), because diet intake and digestion vary with changes in temperature (Jobling 1994). Stomach emptying time is positively correlated with temperature (Fig. 26). Results showed that slight increases in temperature may lead to significant effects in stomach emptying times among char (Fig. 26, Table 39). Similar findings have been reported for wild char fed euphausiids (Amundsen and Klemetsen 1988) and brown trout fed *Gammarus pulex* (Elliot 1972) under controlled conditions.

Rates of gastric evacuation ($gh^{-1}$): Temperature significantly affected rates of gastric evacuation in char (Table 39). Calculated rates of gastric evacuation were $0.12gh^{-1}$, $0.22gh^{-1}$ and $0.36gh^{-1}$ for 4, 7 and 10 °C and these results supported the hypothesis that rate of gastric evacuation increases with increasing temperature. Similar results have been reported for plaice *P. platessa* (Jobling 1980), char (Amundsen and Klemetsen 1988) and brown trout (Elliot 1972, 1976; Elliot and Persson 1978) under controlled conditions.

## Saltwater

### Stomach emptying time

The stomach emptying time (*c.* 17 hours) of YOY char in 23‰ salt water were comparable to that from freshwater (*c.* 18 hours) at 7 °C. Since there are no published data on stomach emptying time of char in saltwater, this study is particularly important because char used in this experiment had parr marks. The presence of parr marks is

indicative that char were ready for sea migration (Reist et al. 2006). Further, the results are suggestive that 23‰ salinity may not influence diet intake, stomach emptying time and growth of post-smolts in the sea. Arnesen et al. (1994) reported non-significant differences in feed intake and specific growth rates between char reared at 20‰ saltwater and in freshwater at temperature 8 °C. My results are comparable to that of Arnesen et al. (1994) on the basis of similarities in temperature and salinity levels. By contrast, Arnesen et al. (1994) noted that char reared at 35‰ salinity grew at lower rate than char reared in freshwater at the same temperature. Similar observations were noted by Jobling (1983) although Jobling (1983) did not state the range of salinities in which the experiment was conducted.

Since SGR of wild marine char and YOY char are similar (Chapters Three and Four) and growth is dependent on stomach emptying time (Elliot 1972, 1976), I conclude that salinity of 23‰ will not affect char diet consumption, gastric evacuation rates and growth.

**Model rates for gastric evacuation**

This study recorded faster gastric evacuation rates of $0.22gh^{-1}$ and $0.36gh^{-1}$ at temperatures of 7 and 10 °C compared to gastric evacuation rates of 0.07 and 0.11 at temperatures of 6 and 10 °C reported by Amundsen and Kletmetsen (1988). Reasons for these differences are not fully known since results from my study suggest that gastric evacuation rates of YOY char at 7 °C in freshwater and char in the marine environment are comparable (Chapters Three and Six). Amundsen and Klemetsen (1988) used char at age 5+ of mean weight of 70 g. Since age/weight differences did not affect the SGR and rates of gastric evacuation of both wild marine and YOY char in my study, Amundsen

and Klemetsen's (1988) model appears to be valid (see Chapter Six). Perhaps the char used by Amundsen and Klemetsen (1988) were stressed since these char were from the wild instead of laboratory-reared char. By contrast, there were no possibilities of influence of stress factor in my data since char used in this thesis were natural feeding and laboratory-reared YOY char.

Anadromous char (Chapter Three) fed at temperature ~ 4-7 °C (Johnson 1980) and their daily diet consumption, digestion and assimilation rates (see Chapter Six), were similar to YOY char at 7 °C in freshwater regardless of diet item. Although Jobling (1994) reported that smaller rainbow trout under experimental conditions had lower digestion rates than large rainbow trout, the optimum temperature of these was ~ 17 °C (Jobling 1994) whereas the optimum temperature for char is a mean of 11.4 °C (see Larsson 2005).

**Conclusions**

The stomach emptying time and rate of gastric evacuation of the YOY char reared under controlled conditions increase with increasing temperature. Gastric evacuation rate of YOY char at 10 °C was 38% higher than that at 7 °C and 67% higher than that at 4 °C. Similarly gastric evacuation rate at 7 °C was 45% higher than that at 4 °C. These findings are indicative that char will consume more food in a day as temperature increases since the stomach emptying time will be shorter and rate of gastric evacuation will be faster.

Considering the fact that SGR and rates of gastric evacuation of wild marine char and YOY char are comparable in my study, perhaps the data presented by Amundsen and Klemetsen (1988) were compromised. My data has revealed that short stomach emptying time and fast rate of gastric evacuation, are among the factors that enhance rapid growth

of anadromous char feeding in the marine environment and YOY char reared in freshwater, under controlled conditions and abundant supplies of food resources.

Table 39. Linear regression equations/constants, stomach emptying time and rates of gastric evacuation of YOY char at different temperatures.

| Temperature | n | *a* | *b* | Linear equation (Y = *a* + *bx*) | $r^2$ values | $S_T$ (Approx.) (Hours) | *R* ($gh^{-1}$) |
|---|---|---|---|---|---|---|---|
| 4 °C | 10 | 2.5923 | -0.12 | Y = 2.5923 + (-0.12*t*) | 0.5984 | 22 | 0.1200 |
| 7 °C | 9 | 4.2052 | -0.2229 | Y = 4.2052 + (-0.2229*t*) | 0.5434 | 18 | 0.2200 |
| 10 °C | 7 | 5.748 | -0.3618 | Y = 5.748 + (-0.3618*t*) | 0.8058 | 16 | 0.3600 |

Legend: Y = ratio of weight of stomach content/fish weight; t = time; a and b = coefficient constants; $S_T$ = stomach emptying time and *R* = rate of gastric evacuation calculated from the slope of standardized weight of stomach content.

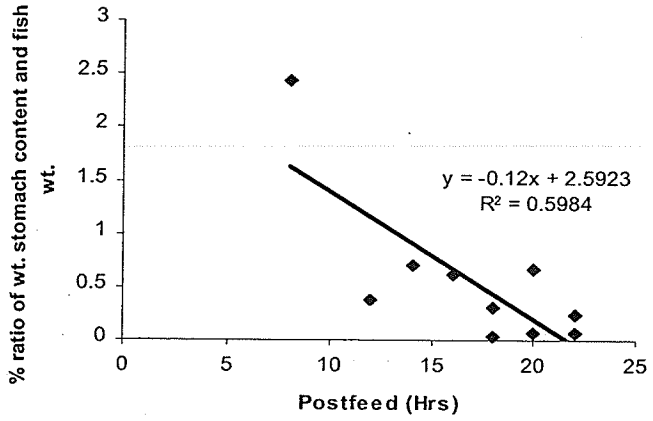
Table 40. General linear equations and model constants describing the relationships between gastric evacuation, temperature and time.

| Dependent variable | Predictor(s) | n | *a* | $b_1$ | $b_2$ | $SE_1$ | $SE_2$ | $SE_3$ | Linear equation |
|---|---|---|---|---|---|---|---|---|---|
| *WS* | *T* and *t* | 38 | 1 | -0.041 | -0.03 | 0.155 | 0.007 | 0.01 | Y = 0.953 + (-0.04051*time) + (-0.02591*temp) |
| *WS* | *T* | 38 | 0.2 | -0.002 | | 0.111 | 0.016 | | Y = 0.162 + (-0.002404*temp.) |

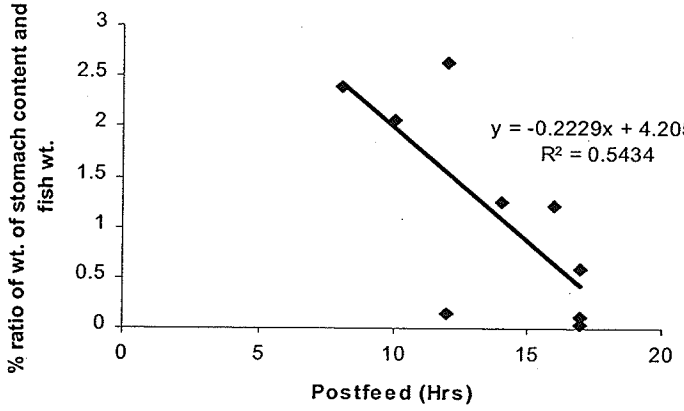
*WS* = ratio of weight of stomach content/fish weight; *T* = temperature; t = time; SE (1-3) for a, b1 and b2

Figure 26. Stomach emptying time of the YOY char at 4 (A), 7 (B) and 10 °C (C) in freshwater

**A** (4 °C)


% ratio of wt. stomach content and fish wt.
y = -0.12x + 2.5923
R² = 0.5984
Postfeed (Hrs)

**B** (7 °C)


% ratio of wt. of stomach content and fish wt.
y = -0.2229x + 4.2052
R² = 0.5434
Postfeed (Hrs)

**C** (10 °C)

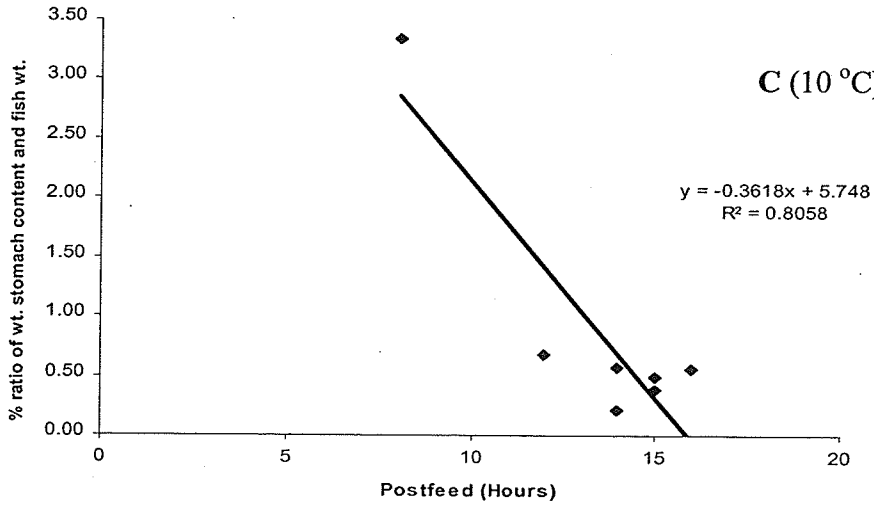
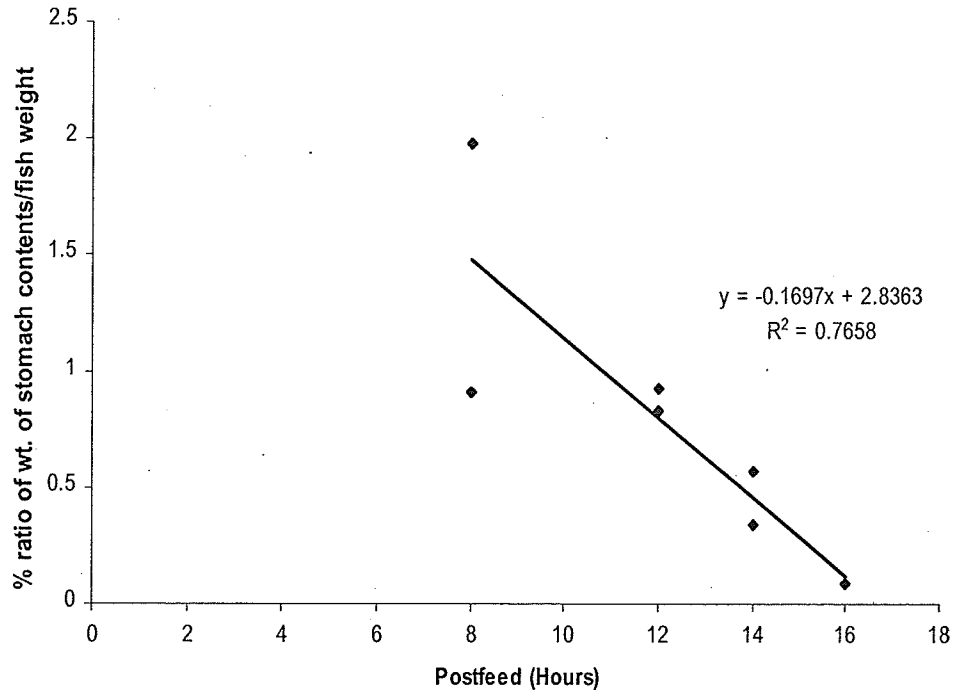

% ratio of wt. stomach content and fish wt.
y = -0.3618x + 5.748
R² = 0.8058
Postfeed (Hours)

Figure 27. Stomach emptying time of YOY char in 23‰ salinity at 7 °C


% ratio of wt. of stomach contents/fish weight
2.5
2
1.5
1
0.5
0
0
2
4
6
8
10
12
14
16
18
Postfeed (Hours)
y = -0.1697x + 2.8363
R2 = 0.7658

# CHAPTER SIX

Hypothetical estimations of energy requirements of anadromous and experimental Arctic char: daily rates of diet consumption, gastric evacuation rates and testing of Amundsen and Klemetsen's model.

# INTRODUCTION

Chapter Three discussed total energy and nutrient contents of natural diet items of wild marine char and their SGR relative to calculated half-life (HL) of C and N stable isotopes in the marine environment. Chapter Five established stomach fullness, stomach emptying time and gastric evacuation of YOY char in freshwater under controlled conditions. All of these factors are important in understanding trophic structuring. Diet composition and nutrient density plus gastric evacuation provided additional information to feeding patterns of char in the marine environment. But rates of daily diet consumption are needed to develop energy budgets. Once rates of daily diet consumption and gastric evacuation are estimated, then a model of the energy budget of char can be developed.

**Daily food consumption rates: anadromous char**

Estimates of daily food consumption by wild fish was pioneered by Bajkov (1935) and reviewed by Eggers (1979). The Bajkov-Eggers method (Eggers 1979) estimates daily food consumption over a 24-h period and uses field measurements of stomach contents and estimates of instantaneous rate of gastric evacuation. This method has been used to estimate daily rates of food consumption for Arctic char (Amundsen and Klemetsen 1988, Rikardsen et al. 2000), 6 northern hemisphere freshwater fishes (Finstad 2005) and sand goby *Gobius minutus* (Healey 1972).

**Gastric evacuation rates: anadromous char**

The rate of gastric evacuation in the young-of-the-year (YOY) char at different temperatures under laboratory conditions was discussed in Chapter Five and the experimental results corroborated results calculated for naturallly feeding char. Little is

known about the gastric evacuation rates of anadromous char. The work by Amundsen and Kletmetsen (1988) appears to be the only reference on gastric evacuation rates of char.

**Energy requirements**

Energy requirements in fishes were reported by Ivlev (1939) and Winberg (1956) and reviewed by Beamish et al. (1975). Fish energetic pathways were described by Elliot (1976) and appear to be the same for all vertebrates (e.g. Leeson and Summers 2001). Figure 30 illustrates a typical energetic pathway. A bioenergetic equation was described by Ricker (1971) as:

$$C = F + U + \Delta B + R \qquad [30]$$

where $C$ is the total energy content of the diet consumed by fish, $F$ is the energy value of the feces, $U$ is the energy value of the excretory products (i.e. urine and other ammonia waste), $\Delta B$ is the total change in the energy value of body materials (growth or loss in energy content) while $R$ is the energy of metabolism.

Healey (1972) and Jobling (1994) simplified the energy budget equation to:

$$E(\text{In}) = E(\text{Out}) + E(\text{P}) \qquad [31]$$

where $E$(In) represent energy ingested as diet, $E$(Out) is the energy lost and $E$(P) is energy retained and utilized for production and growth. Ingested energy is commonly described as gross energy, while energy lost through feces and urine and other excretory products are generally referred to as fecal/urinary energy and energy retained for production, growth and maintenance is called metabolizable energy. In other words, metabolizable energy is the energy remaining after digestible energy had been corrected

for energy losses through feces and urine (Fig. 30, Leeson and Summers 2001, Nyachoti Pers. Comm.).

Winberg (1956) reported that about 20% of gross energy is lost by fish in feces and other excretory products. This has been confirmed for brown trout (Elliot 1976), sand goby (Healey 1972) and Arctic char (Amundsen and Klemetsen 1988).

The objectives of this chapter were to use stomach contents data of anadromous Arctic char (Chapter Three) to estimate: 1) daily rate of diet consumption 2); rates of gastric evacuation at different temperatures; 3) annual energy budgets of anadromous char; 4) to compare results to energy requirements of the YOY char fed a single diet item in freshwater; and 5) to predict, annual changes in available diet and/or energetics of anadromous char in the event of changes in proportional diet intake due to warming trends in the Arctic.

# MATERIALS AND METHODS

## Anadromous char

Fish weight: The fish weight data was obtained from Chapter Three by calculating mean annual weight of anadromous char. Mean ± SD of fish weight were 1046.14 ± 531.9g, 1223.50 ± 452.1g and 1646.9 ± 776.21g for 2002, 2004 and 2005 samples, respectively. The mean of means of annual fish weight was 1305.50 ± 308.64g.

Mean weight of stomach contents: The mean ± SD of stomach contents of anadromous char were 35.90 ± 18.20g, 34.62 ± 16.20g and 63.70 ± 28.14g for 2002, 2004 and 2005 sampling periods (see Chapter Three; Tables **10-12**) . The mean of means of stomach contents was 44.72 ± 20.67g. Dry weight of diet items of anadromous char were determined by bulk freeze-drying the stomach contents by diet species. The mean moisture content (%) of marine diet items in bulk was 77.65 ± 8.40% and the dry weight was ~ 22.35%.

Total energy of diet items: Char stomach contents data for all the sampling years (i.e. 2002, 2004 and 2005) were used. Diet items included *Mysis* spp., *Themisto libellula*, *Onesimus littoralis*, *Thysanoessa* spp., *Gammarus* spp., *Calanus* spp. and *Boreogadus saida* (Arctic cod). Total energy values of all diet items were obtained from bomb calorimetry analysis of dry matter and are presented in Chapter Three (see Table **24**). The total energy values of *Gammarus* spp., *Calanus* spp. and Arctic cod were obtained from Weslawski et al. (1994).

**Experimental char diet**

Total energy: The total energy content of commercial feed (21,900 $KJKg^{-1}$) was determined by bomb calorimetry. Methods involved in bomb calorimetry were discussed in Chapter Three.

**Statistical analyses**

**Daily diet consumption rates: anadromous char**

Daily rate of diet consumption ($C_{24}$): Data from all sampling years were used since char shifted diets in each sampling year. Daily rate of diet consumption was estimated for anadromous char using Bajkov-Eggers method (Eggers 1979) and is expressed by:

$$C_{24} = 24SR \qquad [32]$$

where $S$ is the mean weight of stomach contents for the whole 24-h period while $R$ is the instantaneous gastric evacuation rate. The unit for $C_{24}$ is gram per day ($gd^{-1}$).

Simple regression analysis was performed to examine the relationship between daily rate of food consumption and temperature and also to develop an equation for prediction of mean $C_{24}$ of anadromous char for any given temperature. This model was tested by computer-generated temperature values to estimate how much food char will consume for rise or decline in temperature.

**Gastric evacuation rates: anadromous char**

Gastric evacuation rate ($R$): Data from all sampling years were used given changes in food habits among years. Rate of gastric evacuation was estimated using Amundsen and Klemetsen's (1988) model given by:

$$R = 0.034e^{0.12T} \qquad [33]$$

where $e = 2.718$ is the base of natural logarithms and T is the temperature value. By using the general model describing the relationship between the mean weight of stomach contents and fish weight (Chapter Three), the rate of gastric evacuation was determined and compared with the estimated values obtained from Amundsen and Klemetsen's (1988) model. This provides the temperature at which char were feeding (Chapter Three). The unit of gastric evacuation rate is gram per hour ($gh^{-1}$) (Salvanes et al. 1995).

**Energy requirements: anadromous and experimental char**

Data used for anadromous char were from all samples. This is because the 3 important diet items for 2002 (*Mysis* sp.), 2004 (*T. libellula*) and 2005 (Arctic cod) had different nutrient and total energy contents.

Gross energy (GE): Calculated after Elliot (1975, 1976) by converting diet dry weight to energy units using the total energy value of the diet. GE is given by the equation:

$$GE = TE \times Dm \qquad [34]$$

where TE is the total energy content and D*m* is the dry weight of diet. TE was determined by bomb calorimetry (see Table 24, Chapter Three).

Fecal/urinary energy (FU) (i.e. of feces/urine): It is important to note that fish feces contain urine, unlike some vertebrates that excrete separately. About 20% of GE obtained from diet items is lost through feces/urine and other excretory wastes (Winberg 1956, Elliot 1976, Healey 1972, Amundsen and Klemetsen 1988). Therefore, FU is calculated by:

$$FU = 20/100 \times GE \qquad [35]$$

Metabolizable energy (ME): The energy budget equation by Healey (1972) and Jobling (1994) is written as:

$$GE = FU + ME \quad [36]$$

Therefore, transposing the formula;

$$ME = GE - FU \quad [37]$$

Energy budget in both anadromous and experimental char were estimated using equations 28-31 and all energy values are expressed in $KJKg^{-1}$.

Calculations of energy budgets of anadromous char: Since the discussion was based on GE only, FU and ME were not calculated. One char sample was selected in order to estimate (i.e. hypothetically) the amount of GE each diet item contributed to char. The GE of each diet item was calculated based on the dry weight of each diet item in char stomach. Since 2 classes of diet items [most important (*Mysis* spp., *Themisto libellula* and Arctic cod) and rare (*Onesimus littoralis*, *Thysanoessa* spp., *Calanus* spp. and *Gammarus* spp.)] were observed from stomach content analyses (see Fig. 30, Tables 22, 23- Chapter Three), mean ± SD of the proportion (wet weight) and GE of these 2 classes were calculated.

Three different char samples that fed 100% percent on a single diet item were selected as examples for hypothetical estimation of GE (potential energy) that each of these diet items contributed on individual char. The 3 most important diet items in 2002 (*Mysis* spp.), 2004 (*T. libellula*) and 2005 (Arctic cod) were used in this calculation (see Fig. 30, Chapter Three).

Since *Mysis* spp. and *T. libellula* were predominantly consumed by char (Chapter Three), the GE was calculated for each of these diet items. Four char samples that fed exclusively on these diet items in varying proportions were selected to examine the how varying proportions of key diet items affect the GE they contribute to char.

Estimated total GE of diet items that char recieved in the absence of Arctic cod was calculated using 2002 and 2004 samples. These data were used because Arctic cod was apparently absent in char stomachs in both years. The 2005 data was used to calculate mean GE available to char that fed 100% on Arctic cod. This estimation was based on the observation that char fed predominantly on Arctic cod in 2005. Rare diet items were combined because analysis showed that total proportion of these diet species were < 1% of the total proportion of diet items in char stomachs. Ratio of wet weight of stomach contents were corrected for fish weight. The purpose of this calculation was to compare the GE that char will receive from Arctic cod when they feed on 100% of this diet item to that they will receive from the combination of *Mysis* spp. and *T. libellula*.

# RESULTS

## Daily diet consumption rates ($C_{24}$): anadromous char

Estimates of daily diet consumption of anadromous char at different temperatures over time are presented in Table **41**. Estimated consumption varied among years even when the temperature was the same. It is estimated in 2002, and at temperatures of 4, 7 and 10 °C, char consumption were $132gd^{-1}$, $231gd^{-1}$ and $330gd^{-1}$, respectively. The $C_{24}$ values for 2004 char samples were $127gd^{-1}$, $223gd^{-1}$ and $318gd^{-1}$ for 4, 7 and 10 °C, respectively. By contrast, higher rates of daily food consumption were observed in 2005 samples and these included $234gd^{-1}$, $409gd^{-1}$ and $585gd^{-1}$ at temperatures 4, 7 and 10 °C, respectively. Estimation of $C_{24}$ using the mean of mean values were $164gd^{-1}$, $288gd^{-1}$ and $411gd^{-1}$ at 4, 7 and 10 °C temperatures, respectively (Table **41**).

Simple regression analysis showed a linear relationship between daily rate of food consumption and temperature. The linear equation describing this relationship is:

$$Y = 41.111x + -0.11 \ (r^2 = 0.55) \qquad [38]$$

where Y = daily rate of food consumption and $x$ = temperature (Fig. **31**). For an increase or decrease in temperature, char were estimated to consume 41g/24 hours (mean wet weight) more or less at an increase or decrease in temperature, respectively.

## Gastric evacuation rates ($R$): anadromous char

Rate of gastric evacuation given by an exponential equation (Amundsen and Klemetsen 1988) is a function of temperature but not time. The $R$ values for anadromous char at 4, 7 and 10 °C were $0.153gh^{-1}$, $0.268gh^{-1}$ and $0.383gh^{-1}$ (Table **41**). An estimated $R$ value of $0.14gh^{-1}$ was calculated for anadromous char from the general model

describing the relationship between mean weight of stomach contents and mean fish weight (Chapter Three) while gastric evacuation rates of YOY char at 4, 7 and 10 °C under controlled conditions in freshwater (i.e. experimental data) were $0.12gh^{-1}$, $0.22gh^{-1}$ and $0.36gh^{-1}$ respectively (Chapter Five).

**Energy requirements**

Anadromous char: Estimates of gross energy (see equation 29, p.249) values of diet items available to a single char when it consumed all 6 key diet items (namely: *Mysis* spp, *T. libellula*, *O. littoralis*, *Thysanoessa* spp., *Calanus* spp., *Gammarus* spp., and polar cod) are presented in Table 42. Total GE of diet items available to a single char was 434.50 KJ (Table 42). The highest amount of GE was contributed by Arctic cod (314.53 KJ) followed by *T. libellula* (65.93 KJ) and *Mysis* spp. (48.65 KJ) (Table 42).

Hypothetical estimation of GE available to char that fed 100% on *Mysis* spp. was 299.35 KJ, char that fed 100% on *T. libellula* received a GE of 569.6 KJ and char that fed 100% on Arctic cod received a GE of 879.45 KJ (Table 43).

Figure 32 shows mean (± SD) GE of char that fed predominantly on *Mysis* spp. and *T. libellula* at varying proportions. Char that fed on 69% *Mysis* spp. and 8% *T. libellula* had 66.23 ± 38.96 KJ from *Mysis* spp. and 9.07 ± 5.83 KJ from *T. libellula*. Char that fed on 66% *T. libellula* and 3% *Mysis* spp. had 140.93 ± 4.56 KJ from *T. libellula* and 4.98 ± 4.60 KJ from *Mysis* spp.

Estimated mean GE that char received from their diet items in 2002, 2004 and 2005 are presented in Fig. 33. 2002: The total mean (± SD) GE was 248.53 ± 73.68 KJ. Out of this, char obtained 90.3 KJ from *Mysis* spp, 152.53 KJ from *T. libellula* and 5.74 KJ from other diet items. 2004: The total mean (± SD) GE was 130.07 ± 25.51 KJ. *T.*

*libellula* (70.88 KJ) contributed the highest GE followed by *Mysis* spp. (38.68 KJ) and other diet items (20.51 KJ) contributed the lowest. 2005: Char that fed 100% on Arctic cod had a GE of 629 KJ (Fig. 33).

Experimental char: I assumed that YOY char fed 100% commercial feed (CF) will consume all the food. Based on this assumption, YOY char will receive a GE of *c.* 140.2 KJ. This value was calculated by using the average weight of 21.97g (see Chapter Five). Young-of-the-year char fed to apparent satiation at 3% of their total body weight (i.e. 3/100 x 21.97 = 0.66g) (see Chapter Four). Since the percent dry weight of CF is 97%, the actual amount (i.e. dry matter) of diet consumed by YOY char is 0.64g (i.e. 0.97 x 0.66 g = 0.64g). The GE of CF (i.e. 140.2 KJ) was calculated by multiplying 0.64 g and 21.9 $KJg^{-1}$ (TE of CF) (see eq. 34 p. 243).

# DISCUSSION

**Daily diet consumption rates** ($C_{24}$): anadromous char

Annual variations in daily rates of diet consumption at the same temperature are indicative of differences in feeding efficiencies due to changes in diet quality and quantity while variations in $C_{24}$ at different temperatures reflect differences in rates of digestion and absorption due to changes in temperature (Fig. 31, Table 41). My results are in agreement with the reports of Jobling (1980) and Amundsen and Klemetsen (1988). Jobling (1980) observed increased feeding efficiency in plaice, *Pleuronectes platessa* fed a low quality food and attributed this to increased gastric evacuation rates. Similarly, Amundsen and Klemetsen (1988) noted that the amount of food in char stomachs at any point is a function of the consumption rate and gastric evacuation. Since a preferred diet item will be consumed more than a less preferred diet item (Rikardsen et al. 2000), data from this chapter suggests that char diet quality influences daily consumption rate. This observation is supported by the findings in Chapter Three which showed that Arctic cod, the most important diet in 2005, is likely a preferred diet when available (Table 42).

The Bajkov-Eggers method (Eggers 1979) was applied to long-term stomach contents data of anadromous char population (Chapter Three) and eq. 33 was developed where $C_{24}$ is the rate of daily diet consumption and $x$ is temperature (Fig. 31). This is a simple equation for predicting the mean rate of daily food consumption of char in the marine environment at any given temperature. Based on this model, char will consume *c.*

41 g (wet weight) more per 24 hour for each rise in temperature, or *c.* 41 g (wet weight) per 24 hour less for each decline in temperature (Appendix 34).

**Gastric evacuation rates (*R*): anadromous char**

Predicted gastric evacuation rates are correlated with temperature changes. This prediction is in agreement with the results of gastric emptying of YOY char fed single diet item (Chapter Five) and falls within the values reported by Amundsen and Kletmetsen (1988). It is expected that gastric evacuation of anadromous char will increase with temperature. Similar findings had been reported for brown trout (Elliot 1976), burbot, *Lota lota* (Pääkkönen and Marjomäki 1997), whiting *Merlangus merlangus*, (Andersen 1999, 2001) and Atlantic mackerel *Scomber scombrus* (Temming et al. 2002). Further, predicted gastric evacuation rates of anadromous char corresponded to proportional increases in the rate of daily food consumption over time (Table 41).

Estimated rates of gastric evacuation of anadromous char in my study at all temperatures were consistently higher than those reported by Amundsen and Kletmetsen (1988) for freshwater char at similar temperatures (Table 41). Amundsen and Kletmetsen (1988) reported an *R* value of $0.11 gh^{-1}$ for char fed euphausiids at 10 °C in freshwater. I estimated the *R* value of $0.383 gh^{-1}$ for anadromous char at 10 °C and $0.360 gh^{-1}$ for YOY char in freshwater. Results were comparable (*R*) for anadromous char and YOY char at 10 °C. These values are supported by the SGR of anadromous char and YOY char in freshwater (see Chapters Three and Four).

**Energy requirements**

Anadromous char: Gross energy available to anadromous char is dependent on the energy contents and proportional weights of preferred diet items. Results based on a single char showed that, among the important diet items (i.e. *Mysis* spp., *T. libellula* and Arctic cod, Fig. 30, p. 173- Chapter Three), Arctic cod had *c.* 18% more GE than *Mysis* spp. and 25% more GE than *T. libellula* (Table 42). Diet proportion influenced estimates of GE. Highest proportional weight of Arctic cod is reflective of its corresponding higher nutrient and energy densities (see Tables 24, 25, p.138, 139 Chapter Three, Cortés 1997). These variables determine GE (Grove et al. 2001).

Based on estimates of GE of diet items and the correlation of these to char growth and condition data (Chapter Three), I conclude that char growth is dependent on nutrient and total energy contents of diet items (Tables 42). The implication is that char that feed more on Arctic cod will grow more than char that feed exclusively on invertebrates. But if invertebrates are not available, char will feed more on Arctic cod. Char feeding more on *T. libellula* than *Mysis* spp. received *c.* 70% more GE than char that fed predominatly more on *Mysis* spp. (Fig. 32). This 70% difference corresponds to about 747 $KJKg^{-1}$ differences between TE of *Mysis* spp and that of *T. libellula* and if sustained over a period of time, will affect inter-annual growth of char (see Fig. 33, Tables 42).

Inter-annual weight data (not based on age classes) presented in Chapter Three showed that, 2004 char weighed 17% more than 2002 char and, 2005 char weighed 57% and 34% more than 2002 and 2004 char, respectively (Table 16, p.130). It is worth noting that *T. libellula* had *c.* 50% and *c.* 80% GE higher than *Mysis* spp. in 2002 and 2004, respectively (Fig. 33). Since the proportions of *Calanus* spp. and Arctic cod (i.e. the 2

diet items with TE higher than that of *T. libellula*) were negligible in both 2002 and 2004, I conclude that growth difference between 2002 and 2004 char were due to proportional differences in wet weight of *T. libellula* and *Mysis* spp. in char stomachs. Perhaps this is the reason why; a) the GE which char that fed 100% on Arctic cod received from this diet item was much higher than estimated GE which char received from *Mysis* spp. and *T. libellula* in 2002 and 2004, respectively; b) the mean weight of char in 2005 was higher than that of 2002 and 2004 samples, respectively [Fig. **33**, Tables **16** (p. 132), **43**].

This data correlated with results obtained from 3-D graphing (Fig. **20**, pp.173-176) and agree with the report of Jobling and Wandsvik (1983) that char growth under controlled conditions was dependent on nutrient and total energy contents. Perhaps higher digestibility of Arctic cod played a role (see Jobling 1994).

Jobling (1994) reported that salmonids absorb between 80-98% of dietary protein and 70-97% of dietary GE intake. These findings also agree with the reports of Brugger (1993) for digestibilities of three fish species (bluegill *Lepomis machrochirus*, channel catfish *Ictalurus puntactus* and gizzard shad *Dorosoma cependianum*).

Estimates of GE available to char in the absence of Arctic cod (Fig. **33**) provided more insights on the importance of *Mysis* spp. and *T. libellula* and the very small contribution of rare diet species (namely: *O. littoralis*, *Thysanoessa* spp., *Calanus* spp. and *Gammarus* spp.) to char growth/total energy budgets. It is worth noting that out of a mean total of 248.53 KJ available to char as GE in 2002, *Mysis* spp. and *T. libellula* contributed *c.* 242.83 KJ. This is > 97.1% of total GE consumed by char in 2002. By contrast, other diet species contributed only 5.74 KJ corresponding to < 1 % of the total energy available to char in 2002 (Fig. **33A**). Since Fig. **33** revealed that *T. libellula* had

about 50% more GE than *Mysis*, I predict that a 50% increase in GE in *T. libellula*, contributed to 17% growth difference between 2002 and 2004 char samples (see Table 16 p.130- Chapter Three). This further highlights the importance of *Mysis* spp. and *T. libellula* as important diet items to char. The importance of these diet species to marine salmonids and seal have been reported by Dunbar (1942, 1946) and Grainger (1953). But this may change when Arctic cod occurs in abundant numbers in the marine environment.

Estmated mean GE of 100% Arctic cod in char stomachs in 2005 was *c.* 66% more than GE of *Mysis* spp. and *c.* 57% more than GE of *T. libellula* char in 2002 and 2004 char samples, respectively (Fig. 33). Therefore, based on dietary GE, the ranking of diet importance is Arctic cod > *T. libellula* > *Mysis* spp. > other diet items (see Fig 33, Tables 42, 43).Digestibility of invertebrates is a possible factor influencing their total GE.

Although the digestibility of crustaceans was not assessed, there is evidence that it is lower than for fish (NRC, 1981; Bitterlich and Gnaiger 1984). Grove et al. (2001) observed that Atlantic salmon (*Salmo salar*) fed wet squid grew better than the group fed dry squid. Grove et al. (2001) attributed this advantage to faster nutrient release from the stomach and higher digestibility. Although char fed on wet amphipods, char may lose some energy due to the entire exoskeleton of these diet items. Bitterlich and Gnaiger (1984) observed that 30% of zooplankton were found undigested in the alimentary tract of silvercarp *Hypophthalmichthys molitrix* (Val.) under laboratory conditions. Thus, suggesting about 70% invertebrates are digested. These observations were similar to those of wild older char. The digesta of char that fed 100% on Arctic cod were finer in texture than that from char that fed predominantly on invertebrates (e.g. *Mysis* spp. or *T. libellula*). The latter did not completely digest the carapace of the invertebrates (Pers.

Observation). Lower GE and digestibility, and higher energy cost of searching and foraging (see Beamish et al. 1975) on invertebrates may also have influenced growth differences between char that fed more on Arctic cod and char that fed more on invertebrates.

Gross energy available to YOY char that fed 100% on a single diet item (CF) under controlled conditions in freshwater is smaller than that of older wild char that fed 100% on single diets (Table 43). However, the estimated GE of the diet (CF) available to YOY char is within the range of GE of natural diet items of older wild char (Fig. 33, Table 43). Although older wild char will have a higher diet GE because of the higher quality of their marine diet items, body size, age and metabolic costs, comparable SGR of older wild char (0.71% $d^{-1}$) and YOY char (1.23% $d^{-1}$) suggests that both size classes invest comparable amounts of energy into growth. Excess energy acquired by older wild char are stored as fat reserves and utilized for body building, maintenance and reproduction during harsh winter period in freshwater systems (Johnson 1980, Hammar 1998, Dick Pers. Comm.).

The rates of gastric evacuation between older wild char and YOY char at different temperatures revealed similar values. Therefore, I predict that the stomach emptying time of older wild char will be similar to that of YOY char since their SGR and $R$ are comparable (see Chapter Five, Table 41).

**Conclusions**

Based on the model [$C_{24} = 41.1*T - 0.11$] where $C_{24}$ is the daily rate of food consumption and $T$ is the temperature of the water body, char will consume *c.* 41 g (wet

weight) more per 24 hour for each rise in temperature, or *c.* 41 g (wet weight) less per 24 hour for each decline in temperature.

Gastric evacuation rate value 0.14 $gh^{-1}$ calculated for anadromous char by using data obtained from Chapter Three was similar to predicted gastric evacuation rate at 4 °C (0.153 $gh^{-1}$) and comparable to that (0.12 $gh^{-1}$) calculated for YOY char at the same temperature under controlled conditions (Chapter Five). This validates Amundsen and Klemetsen's (1988) model as well as the value of the general model describing the relationship between the mean weight of stomach contents and mean fish weight (Chapter Three). High rates of gastric evacuation corresponded to higher temperatures and daily rates of food consumption in anadromous char. The estimated rate of gastric evacuation rate of anadromous char at 10 °C is *c.*72% higher than what is reported for adult char fed natural diets at the same temperature in freshwater (Amundsen and Klemetsen 1988). Although differences exist between my values and Amundsen and Klemetsen's (1988) data, my results showed that Amundsen and Klemetsen's (1988) model is useful, especially since rates are similar for wild and experimental char.

Estimates of GE of diet items showed that char growth is dependent on nutrient and total energy contents (i.e. diet quality) and proportions of important diet items.

This is the first study that: 1) had estimated char energy requirements based on long-term stomach contents data; and 2) compared stomach emptying time of older wild char in the marine environment and YOY char under laboratory conditions based on estimated rates of gastric evacuation.

My results have shown that proportional changes in char food habits may be related to diet shifts corresponding to nutrient and total energy contents of key diet items.

All of these factors affect total gross energy available to char and its growth in the marine environment. Undoubtedly, changes in water temperature will have an effect on char growth but we need to factor in the influence of high quality diet on char growth.

Table 41. Estimated rates of daily diet consumption in anadromous char at different temperatures using mean weight of stomach contents data for the 3 sampling years.

| Time | n | Mean ± STD of fish weight (g) | $S^*$ ± STD (g) | $C_{24}$ at 4 °C ($gd^{-1}$) | $C_{24}$ at 7 °C (gd-1) | $C_{24}$ at 10 °C (gd-1) | $R$ at 4 °C ($gh^{-1}$) | $R$ at 7 °C ($gh^{-1}$) | R at 10 °C ($gh^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|
| 2002 | 370 | 1046.14 ± 531.89 | 35.88 ± 18.15 | 132 | 231 | 330 | 0.153 | 0.268 | 0.383 |
| 2004 | 203 | 1223.47 ± 452.06 | 34.62 ± 16.15 | 127 | 223 | 318 | 0.153 | 0.268 | 0.383 |
| 2005 | 68 | 1646.86 ± 776.21 | 63.65 ± 28.14 | 234 | 409 | 585 | 0.153 | 0.268 | 0.383 |
| Mean of means | | 1305.49 ± 308.64 | 44.72 ± 20.67 | 164 | 288 | 411 | 0.153 | 0.268 | 0.383 |

*$S$ = mean weight of stomach contents; $R$ = instantaneous gastric evacuation rate.

Table 42. Hypothetical estimation of gross energy of diet items recovered from a single anadromous char in 2002. (Char data: Wt. = 1540 g, age = 8, sex = male, wet wt. of stomach contents = 82.66 g).

| Diet items | Wet wt. of diet items in char stomach (g) [A] | Dry wt. of diet items (g) [B] (= A*22.35%) | §TE ($KJg^{-1}$) | †GE (KJ) |
|---|---|---|---|---|
| *Mysis* spp. | 10.4497 | 2.336 | 20.83 | 48.65 |
| *Themisto libellula* | 12.848 | 2.872 | 22.96 | 65.93 |
| *Onesimus littoralis* | 0.0568 | 0.013 | 17.48 | 0.22 |
| *Thysanoessa* spp. | 0.7716 | 0.172 | 21.75 | 3.75 |
| *Calanus* spp. | 0.021 | 0.005 | 26.00 | 0.12 |
| *Gammarus* spp. | 0.3648 | 0.082 | 16.00 | 1.30 |
| Arctic cod | 58.152 | 12.997 | 24.20 | 314.53 |
| **Total** | | | | **434.50** |

Wt. = weight

§TE = total energy of diet items calculated from bomb calorimetry analysis of dry matter of diet species.

†GE: Gross energy available to char calculated by multiplying TE and [B]

Mean (± SD) moisture content of diet items = 77.65 ± 8.40%

Mean percent dry weight of diet items = 22.35%

Table 43. Hypothetical estimation of gross energy of the 3 most important diet items of char when these diet species occur exclusively in char stomachs.

| Diet items[a] | Char wt. (g) | Age | Sex | Wet wt. of stomach contents (g) [A] | Dry wt. of diet items (g) [B] (= A*22.35%) | §TE ($KJg^{-1}$) | †GE (KJ) |
|---|---|---|---|---|---|---|---|
| *Mysis* spp. | 860 | 10 | Male | 64.30 | 14.37 | 20.83 | 299.35 |
| *Themisto libellula* | 1753 | 13 | Female | 111.00 | 24.81 | 22.96 | 569.60 |
| Arctic cod | 1750 | 13 | Male | 162.60 | 36.34 | 24.2 | 879.45 |

([a]): The most common diet items in 2002, 2004 and 2005, respectively (see Fig. 20 A-C; pp. 173-176 Chapter Three).
Wt. = weight
§TE = total energy of diet items calculated from bomb calorimetry analysis of dry matter of diet species.
†GE: Gross energy available to char calculated by multiplying TE and [B]
Mean (± SD) moisture content of diet items = 77.65 ± 8.40%

Figure 30. General vertebrate bioenergetic pathway: Redrawn from Beamish et al. (1975), Elliot (1976) and Leeson and Summers (2001).

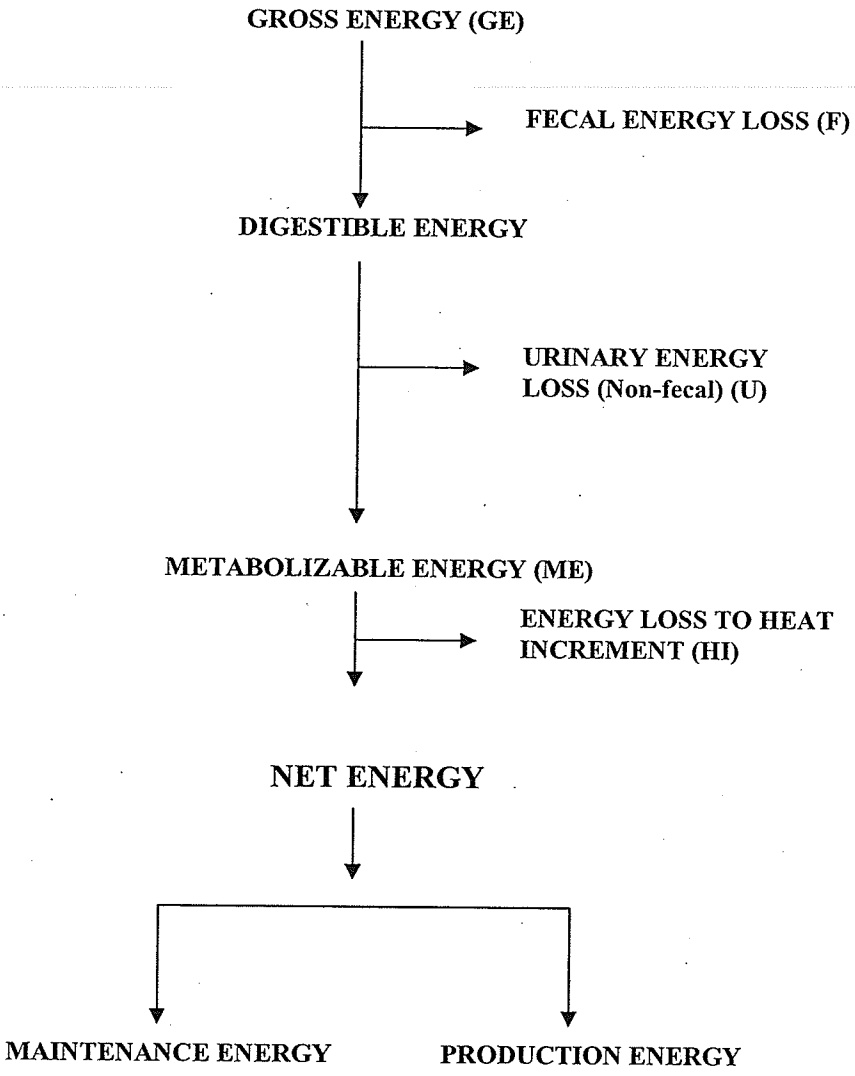

GROSS ENERGY (GE)
FECAL ENERGY LOSS (F)
DIGESTIBLE ENERGY
URINARY ENERGY
LOSS (Non-fecal) (U)
METABOLIZABLE ENERGY (ME)
ENERGY LOSS TO HEAT
INCREMENT (HI)
NET ENERGY
MAINTENANCE ENERGY
PRODUCTION ENERGY

Figure 31. The relationship between daily rate of food consumption and temperature

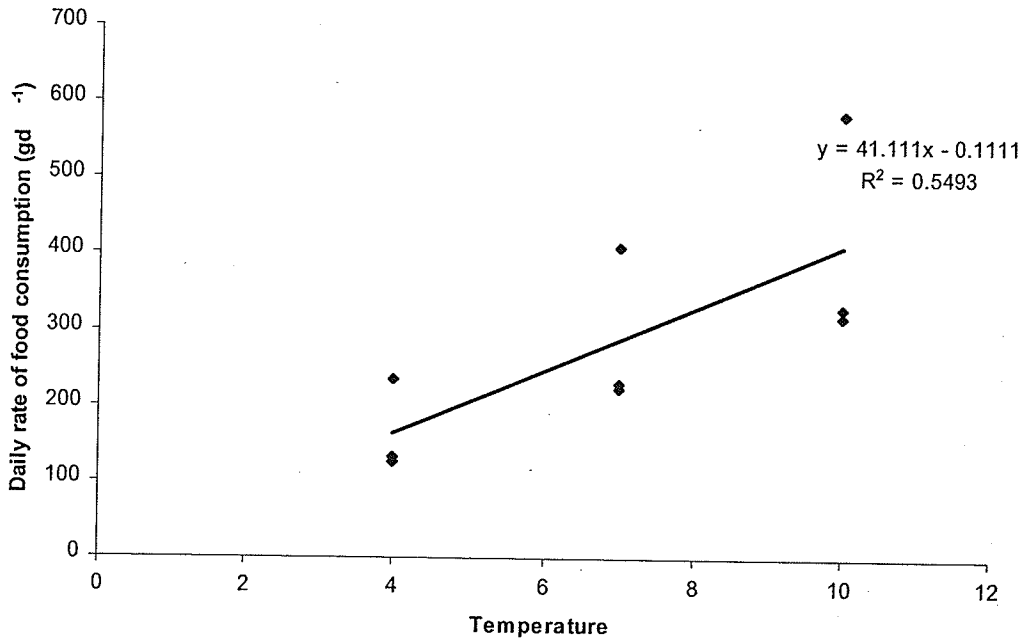

Daily rate of food consumption (gd -1)
700
600
500
400
300
200
100
0
0
2
4
6
8
10
12
Temperature
y = 41.111x - 0.1111
R2 = 0.5493

Figure 32. The gross energy of char when *Mysis* spp. and *Themisto libellula* are consumed in varying (%) proportions. Legend: My = *Mysis* spp. and TL = *Themisto libellula*.

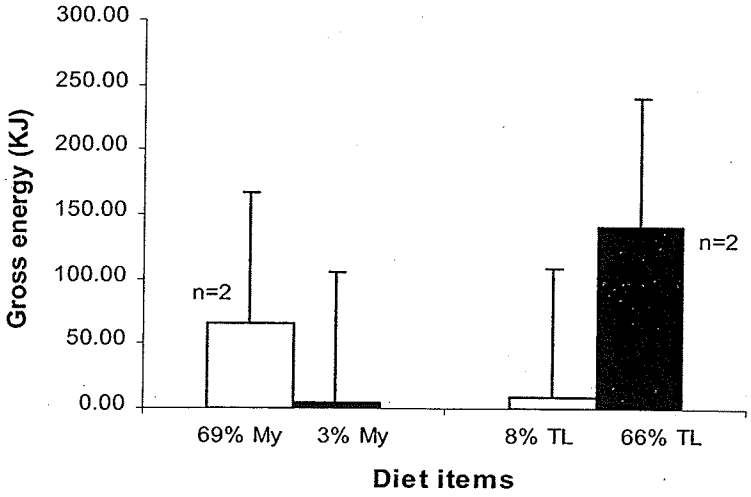
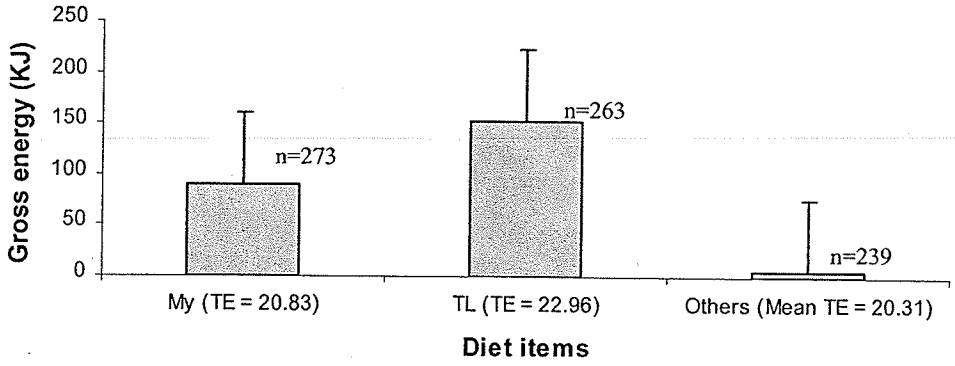
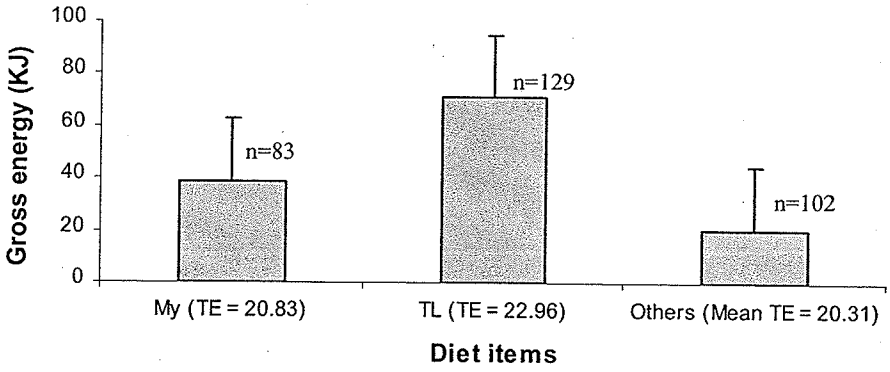

300.00
250.00
200.00
150.00
100.00
50.00
0.00
Gross energy (KJ)
n=2
n=2
69% My
3% My
8% TL
66% TL
Diet items

Figure 33. A): Estimates of gross energy (KJ) that char received from on all diet items in 2002 excluding char (n = 1) that had *Boreogadus saida* Arctic cod, B): The gross energy of char that fed on all diet items in 2004 excluding char (n = 6) that had Arctic cod and C): The gross energy of char that fed 100% on Arctic cod in 2005 excluding char (n = 22) that fed exclusively on invertebrates. Legend: My = *Mysis* spp (Total energy, TE = 20.83 $KJg^{-1}$); TL = *Themisto libellula* (TE = 22.96 $KJg^{-1}$); others include: *Onesimus littoralis*, *Thysanoessa* spp., *Calanus* spp., and *Gammarus* spp (mean TE = 20.31 $KJg^{-1}$).

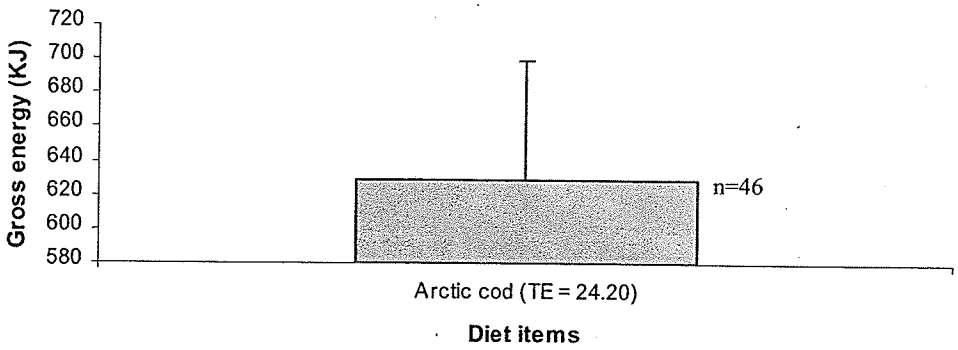
A
(2002)




B
(2004)




C
(2005)



## General Summary

The primary objective of my thesis was to determine if there is trophic structuring among char that feed in the marine environment. Trophic structuring among freshwater char populations is well documented and is due to scarcity of food resources. But little was known about trophic structuring in the marine environment where diet items are diverse and occur in abundant numbers. I reviewed published data in search of evidence to support the existence of trophic structuring among marine Arctic char. My findings revealed that similar to the Salmoniformes as a group, anadromous Arctic char feeding in the ocean are infected by a non-host specific community of parasites. Consequently, I determined that endohelminth communities in Arctic char and diet will not likely reflect a trophic structuring of char in the marine environment, even if there is a change in diet size. However, it was unknown if factors other than diet size affect char food habits upon their arrival in the marine environment.

Assessment of the effect of location, diet, sex and age on char feeding was done since char were sampled from closely and geographically associated populations within Frobisher Bay. I found that location of char foraging in the marine environment does not affect this condition although the relative abundance of diet species may differ from location to location. This is because char are exposed to abundant marine food species of similar overall energy and nutrient contents. Male and female char consume comparable amounts of diet items. This corresponded to their comparable length and weight values and is understandable since they receive comparable amounts of nutrients from diet items that meet the minimum nutrient requirements of char. Although char migrate to the

marine environment at different age classes, there is no sex related differences in fish length, weight, and condition when they return to freshwater in late August. Using multivariate analysis, I was able to establish that the relative abundance of diet items from char collected from several locations in Frobisher Bay in Baffin Island were predictable. However, the predictability of diet items within sample locations did not imply predictability of trophic structuring among local population of char.

Stomach contents analysed based on particle size suggested a potential for trophic structuring but the correlation was dependent on a specific diet species and its size range during its life stages. Further, char growth and condition were dependent on diet quality (i.e. nutrients and total energy content) of key diet items. This suggests the possibility of trophic structuring in the marine environment if char are exposed to quality diet items with a broader size range. Overall, char diet and parasite species were unable to show trophic structuring as char were infected by a non-host specific parasite community. These parasite species were in turn a reflection of char diet. Since parasite species provided strong prediction of diet shift, quality and quantity, parasite species can predict diet shifts even if there is not a trophic shift.

The SGR of older anadromous char is comparable to YOY char reared under controlled conditions and this corresponded to the HL of their $\delta^{13}C$ and $\delta^{15}N$ ratios. Although recent publications had reported that liver tissues are better alternatives to muscle tissues in stable isotopes studies, my calculations using data obtained from char muscle tissues revealed relatively short HLs of $\delta^{13}C$ and $\delta^{15}N$ (86.50 and 90.57 days) for larger and older marine char. This discovery strongly supports the argument that short HL is dependent on how fast fish can grow and not on the fish size.

I was able to establish that in the absence of abundant quality diet items, char may consume diet items that are more abundant while still retaining their innate instinct to feed preferentially on high quality larger diet items when these occur in great quantity.

This is the first study that combined diet, parasites and stable isotope data to examine trophic relationships among anadromous char feeding in the marine environment.

My study is the first to use char from both the natural environment and char reared under laboratory conditions to examine rate of gastric evacuation in anadromous char. Amundsen and Klemetsen (1988) were the first to develop an equation for rate of gastric evacuation for char, and while their results are comparable, there were some differences. Using Amundsen and Klemetsen's (1988) model, I found that wild anadromous char and YOY char have comparable rates of gastric evacuation under similar temperatures. Based on my results, I established that the relationship describing rate of gastric evacuation in YOY char in freshwater system is best described by linear equations but exponential in wild char in the marine envrionment. The Bajkov-Eggers method (Eggers 1979) was applied to long-term data on stomach contents of anadromous char population and the following equation [$C_{24} = 41.111*T - 0.1111$] was developed. This is a simple equation for predicting the mean rate of daily food consumption of char in the marine environment at any given temperature. Based on this model, I predicted that char will consume *c.* 41g (wet weight) more per 24 hour for each rise in temperature, or *c.* 41g per 24 hour less for each decline in temperature.

Estimates of GE to char weight relevant to char growth revealed it is dependent on nutrient and total energy contents of diet items. The implication is that char that feed more on Arctic cod will grow more than char that feed exclusively on amphipods. Mean GE of char that fed 100% on Arctic cod in 2005 was *c.* 66% more than GE of char that fed predominantly on *Mysis* spp. in 2002 and *c.* 57% more than GE of char that fed chiefly on *T. libellula* char in 2004. This corresponded to weight differences across these samples. Based on dietary GE, the ranking of diet importance is Arctic cod > *T. libellula* > *Mysis* spp. > other diet items. Estimates of GE available to char in the absence of Arctic cod provided more insights on the importance of *Mysis* spp. and *T. libellula* and the very small contribution of rare diet species (namely: *O. littoralis*, *Thysanoessa* spp., *Calanus* spp. and *Gammarus* spp.) to char growth/total energy budgets. Considering the fact that 1), smaller and larger char consume proportionally equal amounts of food, 2), SGR and rates of gastric evacuation of older wild and YOY char are the same at different temperatures and, 3) direct proportionality between rate of gastric evacuation and stomach emptying time, I conclude that the stomach emptying time of older wild char is comparable to YOY char.

Although GE available to older wild char were relatively higher than that of YOY char (reflecting differences in size, age and marine diet quality), comparable SGR between YOY and older wild char showed that both groups invest comparable amount of energy into growth.

Grainger (1953) reported that a total of 60,200 diet items which represented *c.* 30 diet species from this char population in 1948, 1950, and 1951. Of this number, 49,166 (*c.* 82% of the total number) were *O. littoralis* (formerly: *Pseudalibrotus littoralis*

Kröyer). *Mysis* spp had 3712 and *T. libellula* had 3715 and no Arctic cod was recorded. By contrast, my data presented a total of 179,592 diet items from 2002, 2004 and 2005 char stomach samples represnting *c.* 11 diet species. This is about 66% increase in total number of diet items compared to Grianger's (1953) data. Out 179,592 *O. littoralis* had 9,689; *Mysis* spp. had 108,947; *T. libellula* had 34,570 and Arctic cod had 236.

It is worth noting that the most important diet items in my study were *Mysis* spp in 2002, *T. libellula* in 2004 and Arctic cod in 2005 but was *O. littoralis* in Grainger (1953). *O. littoralis* was among the least occurring and also among the least in terms of GE in my study. The differences between my data and Grainger's (1953) explain the differences in growth curves calculated by Dick and Gallgher (2007) (see Fig 10, p.153) since energy available to char for growth is positively correlated to proportional weight of diet items.

Total thermal increase leading to early fast ice disappearance and early migration of char to the sea may result in longer periods of time at higher water temperatures, and this will influence diet proportions in char stomachs. I have used long-term stomach contents data to establish that char diet shifts are related to diet nutrient and total energy contents of key diet items. And, all of these factors affect total gross energy available to char and its growth in the marine environment.

To conclude, 1a) although parasite species were unable to show trophic structuring among char in the marine environment, they have the potential do so if char fed exclusively on single diet items since 1b) parasite species were good predictors of diet quality and quantity e.g. *B. crenatus*, *D. varicus* and *B. sturionis*, 1c) parasite species were able to detect diet shifts since they are able to provide recent feeding history of char,

2) stable isotope ratios were able to show trophic structuring but this was for char feeding on *Mysis* spp., and *O. littoralis*, 3) $\delta^{13}C$ ratios of diet items can be used to predict spatial and temporal variations in char carbon sources, 4) short HL of C and N isotopes is indicative of fast-growing and not dependent on fish size, 5) SGR, stomach emptying time, and rate of gastric evacuation of older wild char and YOY char reared under controlled conditions in freshwater are comparable 6), nutrient and total energy contents of diet species were the reasons why a long-term diet shift occurred [i.e. from less nutrient/energy dense *Onesimus littoralis* (Grainger (1953) to high nutrient and energy dense Arctic cod (my study)], 7) Changes in nutrient and total energy content of diet species resulted to inter-annual shift [i.e. from *Mysis* spp. (a fairly quality diet) in 2002 to *T. libellula* in 2004 and to Arctic cod in 2005], 8) char feeding patterns in the marine environment is predictable based on diet quality, 9) modeling of energy budgets of anadromous char feeding in the marine environment is possible since char feeding patterns can be predicted from diet quality and, 10) the experiments were useful in understanding the feeding patterns of wild marine char and can be applied in future ecological studies.

## LITERATURE CITED

Adams, CE., and Huntingford, FA. 1997. Growth, maturation and reproductive investment in Arctic char. *J. Fish Biol.* **51**:750-759.

Adams, CE., and Huntingford, FA. 2002. The functional significance of inherited differences in feeding morphology in a sympatric polymorphic population of Arctic charr. *Evolutionary Ecology*. **16**: 15-25.

Adams, CE., Fraser, D., McCarthy, ID., Shields, S., Waldron, S. and Alexander, G. 2003. Stable isotope analysis reveals ecological segregation in a bimodal size polymorphism in Arctic charr from Loch Tay, Scotland. *J. Fish. Biol.* **62**:474-481.

Adams, N., Power, G and Barton, DR. 1989. Diet and daily ration of anadromous Arctic charr in Ungava Bay. *Physiol. Ecol. Japan*. Special Volume **1**:253-264.

Alanärä A., Brännäs E. 1997. Diurnal and nocturnal feeding activity in Arctic char (*Salvelinus alpinus*) and rainbow trout (Onchorhynchus mykiss). *Can. J. Fish. Aquat. Sci.* **54**: 2894-2900.

Alanärä, A., and Kiessling, A. 1996. Changes in demand feeding behaviour in Arctic charr Salvelinus alpinus L., caused by differences in dietary energy content and reward level. *Aquaculture Research* **27**:479-486.

Allan, JD. 1981. Determination of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. *Can. J. Fish. Aquat. Sci.* **38**:184-192.

Amundsen PA, Damsgård B, Arnesen AM, Jobling M, Jørgensen EH 1995. Experimental evidence of cannibalism and prey specialization in Arctic char *Salvelinus alpinus. Env. Biol. Fish.* **43**:285-293.

Amundsen PA, Kristoffersen R 1990. Infection of whitefish (*Coregonus lavaretus* L. *s.l.*) by *Triaenophorus crassus* Forel (Cestoda: Pseudophyllidea): a case study in parasite control. *Can. J. Zool.* **68**: 1187-1192.

Amundsen, PA., and Klemetsen, A. 1988. Diet, gastric evacuation rates and food consumption in a stunted population of Arctic charr, Salvelinus alpinus L., in Takvatn, northern Norway. *J. Fish Biol.* **33**:697-709.

Anderson DM 1993. Occurrence of *Salmincola siscowet* (Copepoda: Lernaeopodidae) on lake trout (*Salvelinus namaycush*) and lake trout backcross (*S. namaycush* x *S. fontinalis*) in Lake Huron. *Can. J. Zool.* **71**:2330-2333.

Andersen, NG. 1998. The effect of meal size on gastric evacuation in whiting. *J. Fish Biol.* **52**:743-755

Andersen, NG. 1999. The effects of predator size, temperature, and prey characteristics on gastric evacuation in whiting. *J. Fish Biol.* **54**:287-301.

Andersen, NG. 2001. A gastric evacuation model for three predatory gadoids and implications of using pooled field data of stomach contents to estimate food rations. *J. Fish Biol.* **59**:1198-1217.

Andersen, NG., and Riis-Vestergaard, J. 2003. The effects of consumption rate, body size and temperature on net food conversion efficiency in saithe and whiting. *J. Fish Biol.* **62**:395-412.

Andersen, NG., and Beyer, JE. 2005. Mechanistic modeling of gastric evacuation in predatory gadoids applying the square root model to describe surface-dependent evacuation. *J. Fish Biol.* **67**:1392-1412.

Andrievskaya, LD. 1957. Summer migrations of the Pacifc salmon and their nutrition during the marine period of their life. Izvestiya Tikhookeanskogo Nauchno-Issledovatel skogo Instituta Rybnogo Khozyaistva i Okeanografii (TINRO) **44**:75-96.

AOAC (Association of Official Analytical Chemists). 1990. Official methods of analysis. AOAC, Inc., Washington, DC, 1298 pp.

Arai HP, Mudry DR. 1983. Protozoan and metazoan parasites of fishes from the headwaters of the parsnip and McGregor Rivers, British Columbia: a study of possible transfuanations. *Can. J. Fish. Aquat. Sci.* **40**:1676-1684.

Arnesen, AM., Jørgensen, EH., and Jobling, M. 1994. Feed-growth relationships of Arctic char transferred from freshwater to saltwater at different seasons. *Aquaculture International*, **2**:114-122.

Arthur, JR., and Albert, E. 1994. A survey of the parasites of Greenland halibut (*Reinhardtius hippoglossoides*) caught off Atlantic Canada, with notes on their zoogeography in this fish. *Can J. Zool.* **72**:765-778.

ASTM (International Standards D5865-03a). 2004. Standard test method for gross calorific values of coal and coke.

Bajkov, AD. 1935. How to estimate the daily food consumption of fish under natural conditions. *Trans. Amer. Fish Soc.* **65**:288-289.

Bangham, RV. 1955. Studies of fish parasites of Lake Huron and Manitoulin Island. *American Midland Naturalist* **53**:184-194.

Bangham, RV., and Adams, JR. 1954. A survey of the parasites of freshwater fishes from the mainland of British Columbia. *J. Fish. Res. Board Can.* **11**:673-708.

Beacham, TD. 1986. Type, quantity, and size of food of Pacific salmon (*Onchorhynchus*) in the Strait of Juan de Fuca, British Columbia. *Fish. Bull.* **84**:77-89.

Beamish, FWH., Niimi, AJ and Lett, PFKP. 1975. Bioenergetics of teleost fishes: environmental influences. Comparative Physiology- Functional Aspects of Structural Materials eds L. Bolis. HP Maddrell and K. Schmidt-Nielsen, pp. 187-209. North-Holland, Amsterdam.

Beasley, G., and Kneale, PE. 2003. Investigating the influence of heavy metals on macroinvertebrate assemblages using Partial Canonical Correspondence Analysis (pCCA). *Hydrology and Earth System Sciences* 7(2): 221-233.

Behnke, RJ. 1984. Organizing the diversity of the Arctic charr complex. *In* Johnson and Burn *eds.* International symposium on Arctic charr. Univ of Manitoba Press, Winnipeg Canada Pp. 3-21.

Behnke, RJ. 1980. A systematic review of the genus *Salvelinus*. *In* EK Balon *ed.* Charrs: salmonid fishes of the genus *Salvelinus*. Dr W. Junk. The Hague Pp. 441-480.

Behnke, RJ. 1972. The systematics of salmonid fishes of recently glaciated lakes. *J. Fish Res. Board Can.* **29**:639-671.

Bernard D., and Holmstrom, C. 1978. Growth and food habits of rainbow trout (formerly: *Salmo gaidneri* Richardson- *Onchorhynchus mykiss*) in winterkill lakes of western Manitoba. FMS MS Rep. 1477: iv + 20pp.

Ben-David, M., and Schell, DM. 2001. Mixing models in analyses of diet using multiple stable isotopes: a response. *Oecologia* **127**:180-184.

Berg, OK., and Berg, M. 1989. Sea growth and time of migration of anadromous Arctic char (Salvelinus alpinus) from the Vardines River, in northern Norway. *Can. J. Fish. Aquat. Sci.* **46**:955-960.

Beverly-Burton M. 1978. Metazoan parasites of Arctic charr (*Salvelinus alpinus* L) in a high arctic landlocked lake in Canada. *Can J. Zool.* **56**:365-368.

Bitterlich, G., and Gnaiger, E. 1984. Phytoplanktovorous or omnivorous fish? Digestibility of zooplankton by silvercarp, Hypophthalmichthys molitrix (Val.), *Aquaculture* **40**(1):261-263.

Black, GA. 1981. Metazoan parasites as indicators of movements of anadromous brook charr (*Salvelinus fontinalis*) to sea. *Can. J. Zool.* **59**:1892-1896.

Black, GA. 1983. Origin, distribution, and postglacial dispersal of a swimbladder nematode, *Cystidicola stigmatura*. *Can. J. Aquat. Sci.* **40**:1244-1253.

Black, GA., and Lankester, MW. 1984. Distribution and biology of swimbladder nematodes, Cystidicola spp. (Habronematoidea), in char, *Salvelinus* spp. *In* Johnson and Burns [eds] International symposium on Arctic char. Pp. 413-429. University of Manitoba Press, Winnipeg Canada.

Bosley, KL., Witting, DA., Chambers, RC, Wainright, SC. 2002. Estimating turnover rates of carbon and nitrogen in recently metamorphosed winter flounder Pseudopleuronectes americanus with stable isotopes. *Mar. Ecol. Prog. Ser.* **236**:233-240.

Bradstreet, MSW., and Cross, WE. 1982. Trophic relationships at high arctic ice edges. *Arctic* **35**:1-12.

Brett, JR., and Higgs, DA. 1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Onchorhynchus nerka*. *J. Fish Res Bd. Can.* **27**:1767-1779.

Brett, JR., and Shellbourn, JE. 1975. Growth rate of young sockeye salmon, *Onchorhynchus nerka*, in relation to fish size and ration level. *J. Fish. Res. Bd. Can.* **32**:2103-2110.

Brodeur, RD. 1990. A synthesis of the food habits and feeding ecology of salmonids in marine waters of the North Pacific. (INPFC) Doc.) FRI-UW-9016. Fish Res. Inst. Univ. Washington, Seattle. 38pp.

Brody, S. 1945. Bioenergetics and growth. Reinhold Publishing Co., New York.

Brugger, KE. 1993. Digestibility of three fish species by double-crested cormorants. *The Condor* **95**:25-32.

Brunner RJ, Douglas MR, Osinov A, Wilson CC and Bernatchez L 2001. Holarctic phylogeography of Arctic charr (*Salvelinus alpinus*) inferred from mitochondria sequences. *Evol.* **55**(3). Pp. 573-586.

Bystrom, P., Andersen, J., Persson, L., De Roos, AM. 2004. Size-dependent resources limitation and foraging predation risk trade-offs: growth and habitat use in young Arctic char. *Oikos* **104**:109-121.

Canadian Council on Animal Care. 2005. Ottawa, Canada.

Carney JP, Dick TA. 2000. Parasites biogeography: review of the origins and ideas with specific examples from holarctic fishes. *Viet Milieu* **50**(4):221-243.

Cavalli, L., and Chappaz, R. 1996. Diet, growth and reproduction of the Arctic char in a high alpine lake. *J. Fish Biol.* **49**:953-964.

Cavender, TM. 1980. Systematics of *Salvelinus alpinus* from the North pacific basin. *In* EK Balon [ed] Charrs: salmonid fishes of the genus *Salvelinus* p. 295-322. Dr WK Junk. The Hague.

Cavender, TM. 1984. Cytotaxonomy of North American Salvelinus. *In* Johnson L and Burns, BL (eds) Biology of the Arctic charr, Proceedings on International Symposium on Arctic charr, Winnipeg, Manitoba. University of Manitoba, Press Winnipeg. Pp. 431-445

Chakraborty A 2007. Trophic structure of landlocked Arctic char (Salvelinus alpinus) in Iqalugaarjuruluit Lake, Iqaluit Baffin Island. MSc. Thesis. University of Manitoba.

Chambers C, Dick TA 2005. Trophic structure of one deep-sea benthic fish community in the eastern Canadian Arctic: application of food, parasites and multivariate analysis. *Env. Biol. Fish* **74**(3-4):365-378.

Chambers, C., Gallagher, CP., and Dick, TA. (In press). Biology, diet, parasites and stable isotopes of shorthorn sculpin (Myoxocephalus scorpius) from Frobisher Bay, Canada.

Charnov, EL. 1976. Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* **9**: 129-136.

Choudhury, A and Dick, TA. 2001. Sturgeons (Chondrostei: Acipenseridae) and their metazoan parasites: patterns and process in historical biogeography. *J Biogeography*, **28**:1411-1439.

Clarke, WC., Higgs, DA., Markert, JR., Shelbourn, JE., and Castledine, AJ. 1982. Effect of varying dietary protein: lipid ratios on growth and body composition of coho salmon (*Onchorhynchus kisutch*) reared at different temperatures. *Can. Data. Rep. Fish. Aquat. Sci.* 373, iv + 18pp.

Cortés, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Can. J. Fish. Aquat. Sci.* **54**:726-738.

Costello, MJ. 1990. Predator feeding strategy and prey importance: a new graphical analysis. *J. Fish Biol.* **36**:261-263.

Coustau, C. 1991. Analyse genetique et physiologique des interactions hôte-parasite: le systéme *Prosorhynchus squamatus – Mytilus*. PhD thesis, University of Montpellier II, p 1-133.

Craig, P. 1987. Fish resources In Environmental characterization and biological utilization off the North Aleutian Shelf Nearshore Zone. Final Rep. to US Mineral Management Service. LGL Ecological Research Associates. pp 185-321.

Crawford, RE., and Jorgenson, JK. 1993. Schooling behaviour of Arctic cod, *Boreogadus saida*, in relation to drifting pack ice. *Env. Biol. Fish.* **36**:345-357

Crespi, BJ., and Teo, R. 2002. Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. *Evol.* **56**(5):1008-1020.

Cui, Y. and Wootton, RJ. 1988. Bioenergetics of growth of a cyprinid, *Phoxinus phoxinus* (L.): the effect of ration and temperature on growth rate and efficiency. *J. Fish Biol.* **33**:763-773.

Curtis MA, Bérubé M, Stenzel A 1995. Parasitological evidence for specialized foraging behaviour in lake-resident Arctic char (*Salvelinus alpinus*). *Can. J. Fish. Aquat. Sci.* 52 (Suppl. 1), S186-S194.

de March, LB., de March, B., and Eddy, W. 1977. Limnological, fisheries and zoobenthic studies at Stanwell-Fletcher Lake, a large high Arctic lake. Can. Dep. Ind. North. Aff. ESCOM Report A1-04, xiv + 84 pp.

Dechtiar, AO., Christie, WJ. 1988. Survey of the parasite fauna of Lake Ontario fishes, 1961-1971. Great Lakes Fsih. Comm., Tech Rep. **51**:66-106.

Dechtiar, AO., and Lawrie, AH. 1988. Survey of the parasite fauna of Lake Superior fishes, 1969–1975. *In* Nepszy SJ (ed) Parasites of fishes in the Canadian waters of the Great Lakes. Great Lakes Fish. Comm. Tech. Rep. No. 51. pp. 1–18.

Dechtiar, AO., Collins, JJ., and Reckhan, JA. 1988. Survey of the parasite fauna of Lake Huron fishes, 1961-1971. Great Lakes Fish Comm., Tech. Rep. **51**:19-48.

DeLacy, AC., and Morton, WM. 1943. Taxonomy and habits of the charrs, *S. malma* and *S. alpinus*, of the Karluk drainage system. *Trans. Amer. Fish.* Soc. **72**:79-91

DeNiro, MJ., and Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta* **45**:495-506.

Dick TA, Belosevic M. 1981. Parasites of Arctic charr *Salvelinus alpinus* (Linneaus) and their use in separating sea-run and non-migrating charr. *J. Fish Biol.* **18**:339-347.

Dick, TA., and Yang, X. 2002. Arctic charr, *Salvelinus alpinus*. *In* C.D. Webster and C.E., Lim [eds]: nutrient requirements and feeding of finfish aquaculture. CABI Publishing, New York.

dos Santos, J., and Jobling, M. 1991. Factors affecting gastric evcacuation in cod, *Gadus morhua* L., fed single meals of natural prey. *J. Fish Biol.* **38**:697-713.

dos Santos, J., Jobling, M. 1995. Test of food consumption model for Atlantic cod.*ICES J. Mar. Sci.* **52**:209-219.

Dunbar, MJ. 1942. Marine macroplankton from the Canadian eastern Arctic. I. Amphipoda and Schizopoda. *Can. J. Res.* **20**: Sec. D.

Dunbar, MJ. 1946. On *Themisto libellula* in Baffin Island Coastal Waters. *J. Fish Res. Bd. Can.* **6**(6): 419-434.

Dutil, J-D. 1983. Periodic changes in the conditions of the Arctic charr (*Salvelinus alpinus*) of the Nauyuk Lake system. PhD Thesis. The University of Manitoba, Canada. 150p.

Dutil, J-D. 1984. Energetic costs associated with the production of gonads in the anadromous Arctic charr (Salvelinus alpinus) of Nauyuk Lake basin, Canada. *In* Johnson and Burns [eds] Biology of the Arctic charr, Proceedings of the International Symposium on Arctic Charr, Winnipeg, Manitoba. University of Manitoba Press, Winnipeg. p. 263-276.

Dutil, J-D. 1986. Energetic constraints and spawning interval in the anadromous Arctic char (*Salvelinus alpinus*). *Copeia* **4**:945-955.

Dutil, J-D., and Lambert, Y. 2000. Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **57**:826-836.

Eddy, SB., and Lankester, MW. 1978. Feeding and migratory habits of Arctic Charr, *Salvelinus alpinus*, indicated by the presence of the swimbladder nematode *Cystidicola cristivomeri* White. *J. Fish Res. Board Can.* **35**:1488-1491.

Eggers, DM. 1979. Comment on some recent methods for estimating food consumption by fish. *J. Fish Res. Bd. Can.* **36**:1018-1019.

Elliot, JM. 1972. Rates of gastric evacuation in brown trout., *Salmo trutta* L. *Freshwat. Biol.* **2**:1-18.

Elliot, JM. 1975. Number of meals in a day, maximum weight of food consumed in a day and maximum rate of feeding of brown trout, Salmo trutta L. *Freshwat. Biol.* **5**:287-303.

Elliot, JM. 1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. *J. Animal Ecol.* **45**(3):923-948.

Elliot, JM., and Persson, L. 1978. The estimation of daily rates of food consumption for fish. *J. Animal. Ecol.* **47**:977-991.

Field, A. 2005. Discovering statistics using SPSS. Sage Publications London, United Kingdom.

Finstad, A.G. 2005. Salmonids in a changing climate: the winter challenge PhD thesis 1999, Norwegian university of Science of Technology, Faculty of Science and Technology, Trondheim.

Finstad, B., and Heggberget, TG. 1993. Migration, growth and survival of wild and hatchery-reared anadromous Artctic char (*Salvelinus alpinus*) in Finmark, northern Norway. *J. Fish Biol.* **43**:303-312.

Focken, U. 2001. Stable isotopes in animal ecology: the effect of ration size on trophic shift of C and N isotopes between feed and carcass. *Isotopes Environ Health Stud.* **37**:199-211.

Frandsen, F., Malmquist, HJ and Snorrason, SS. 1989. Ecological parasitology of polymorphic Arctic charr, *Salvelinus alpinus* (L.), in Thingvallavatn, Iceland. *J. Fish Biol.* **34**: 281-297.

Fraser NC, Power G. 1989. Influences of lake trout on lake-resident Arctic char in Northern Quebec, Canada. *Trans. Amer. Fish. Soc.* **118**:36-45.

Fraser, D., Adams, CE., and Huntingford, FA. 1998. Trophic polymorphism among Arctic charr *Salvelinus alpinus* L., from Loch Ericht Scotland. *Ecol. Freshwater Fish.* **7**:184-191.

Frimeth JP 1987a. A survey of the parasites of nonanadromous and anadromous brook charr (*Salvelinus fontinalis*) in the Tabusintac River, New Brunswick, Canada. *Can. J. Zool.* **65**:1354-1362.

Frimeth JP 1987b. Potential use of certain parasites of brook charr (*Salvelinus fontinalis*) as biological indicators in the Tabusintac River, New Brunswick, Canada. *Can. J. Zool.* **65**:1989-1995.

Fry B., and Sherr, EB. 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems, *Contrib. Mar. Sci.* **27:**13-47.

Gallagher, CP., and Dick, TA. 2007. The Sylvia Grinnell Arctic char (*Salvelinus alpinus* ) subsistence fishery: biology, population assessment and comparison with historical data. Hunters and Trappers Association (HTA) Report. 25p.

Gannes, LZ., O'Brien, DM., Martinez del Rio, C. 1997. Stable isotopes in animal ecology: assumptions, caveats and a call for more laboratory experiments. *Ecology* **78**:1271-1276.

Gaye-Siesegger, J., Focken, U., Muetzel, S., Abel, H., and Becker, K. 2004. Feeding level; and individual metabolic rate affect $\delta^{13}C$ and $\delta^{15}N$ values in carp: implications for food web studies. *Oecologia* **138**:326-370.

Gibson, DI. 1996. Guide to the parasites of fishes in Canada. Part 4 Trematoda. Canadian Special Publication Fisheries Aquatic Sciences 124. 382p *Eds* Margolis L and Kabata Z.

Gilliam, JF. 1982. Foraging under mortality risk in size-structured populations. PhD Dissertation. Michigan University.

Grainger EH 1953. On the age, growth, migration, reproductive potential and feeding habits of Arctic charr (*Salvelinus alpinus*) of Frobisher Bay, Baffin Island, Canada. *J. Fish. Res. Board Can.*, **10**:326-370.

Grainger, EH. 1971. Biological observations in Frobisher Bay. II Zooplankton data, 1967-9170. Fish. Res. Bd. Can. Technical report No. 266.

Grainger, EH. 1985. Vertical distribution of zooplankton in the central Arctic Ocean. In Louis Rey and Vera Alexander *eds* Proceedings of the Sixth Conference of the Comité Arctique International 13-15 May: p48-60.

Grant, JWA., and Noakes, DLG. 1986. A test of a size-selective predation model with juvenile brook charr, *Salvelinus fontinalis*. *J. Fish. Biol.* 29 (Supplement A):15-23.

Grey, J. 2001. Ontogeny and dietary specialization in brown trout (*Salmo trutta* L.) from Loch Ness, Scotland, examined using stable isotopes of carbon and nitrogen. *Ecol. Freshwater Fish* **10**:168-176.

Grall, J., Le Lc'h, F., Guyonnet, B., and Riera, P. 2006. Community structure and food web based on stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) analysis of a North Eastern Atlantic maerl bed. *J. Exp. Mar. Biol. & Ecol.* **338**:1-5.

Grey, J., Thackeray, SJ., Jones, RI., and Shine, A. 2002. Ferox trout (*Salmo trutta*) as 'Russian dolls': complementary gut content and stable isotope analyses of the Loch Ness foodweb. *Freshwater Biol.* **47**:1235-1243.

Grove, D., Genna, R., Paralika, V., Boraston, J., Hornyold, MG., and Siemens, R. 2001. Effects of dietary water content on meal size, daily food intake, digestion and growth in turbot, *Scophthalmus maximus* (L.). *Aquaculture Research*. **32**:433-442.

Grove, DJ., Moctezuma, MA., Flett, HRJ., Foott, JS., Watson T., and. Flowerdew, M. 1985. Gastric emptying and the return of appetite in juvenile turbot, *Scophthalamus maximus* (L.) fed on artificial diets, *J. Fish Biol.* **26:** 339-354

Guiguer, KRRA., Reist, JD., Power, M., and Babaluk, JA. 2002. Using stable isotopes to confirm the trophic ecology of Arctic charr morphotypes from Lake Hazen, Nunavut, Canada. *J. Fish Biol.* **60**:348-362.

Gulseth, O. A., and Nilssen, KJN. 2001. Life-History traits of char, Salvelinus alpinus, from a high Arctic Watercourse on Svalbard. *Arctic* **54**(1):1-11.

Gurure, RM. 1997. Defining the protein and amino acid requirements of Arctic charr using *in vivo* and modeling techniques. PhD Thesis. The University of Guelph, Canada. 276p.

Gurure, RM., Moccia, RD., and Atkinson, JL. 1995. Optimal protein requirements of young Arctic charr (*Salvelinus alpinus*) fed practical diets. *Aquaculture Nutrition* **1**:227-234.

Hammar J 1998. Interactive symmetry and seasonal niche shifts in sympatric Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*): evidence from winter diet and accumulation of radiocesium. *Nordic J. Freshw. Res.* **74**:33-47.

Hammar J 2000. Cannibals and parasites: conflicting regulators of bimodality in high latitude Arctic char, Salvelinus alpinus. *Oikos* **88**:33-47.

Hanek, G., and Molnar, K. 1974. Parasites of freshwater and anadromous fishes from Matamek River system, Quebec. *J. Fish Res. Board Can.* **31**:1135-1139.

Hayward, RS., Noltie, DB and Wang, N. 1997. Use of compensatory growth to double hybrid sunfish growth rates. *Trans. Amer. Fish. Soc.* **126**:316-322.

Healey, MC. 1972. Bioenergetics of a sand goby (Gobius minutus) population. *J. Fish Res. Bd. Can.* **29**:187-194.

Healey, MC. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia In WJ. McNeil and DC. Himsworth [eds] Salmonid ecosystem of the North Pacific. Oregon State University Press. p. 203-229.

Hess, AD., and Rainwater, JH. 1939. A method for measuring the food preference of trout. *Copeia*. **3**:154-157.

Hesslein, RH., Hallard, KA., and Ramlal, P. 1993. Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}S$, $\delta^{13}C$ and $\delta^{15}N$. *Can. J. Fish. Aquat. Sci.* **50**:2071-2076.

Hicks FJ, Threlfall W 1973. Metazoan parasites of salmonids and coregonids from coastal Labrador. *J. Fish Biol.* **5**:399-415.

Hobson, KA., and Clark, RG. 1992. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. *Condor* **94**:189-197.

Hobson, KA., and Welch, HE. 1992. Determination of trophic relationships within a high Arctic marine food web using δ13C and δ15N analysis. *Mar. Ecol. Prog. Ser.* **84**:9-18.

Hobson, KA., and Welch, EW. 1995. Cannibalism and trophic structure in a high Arctic lake: insights from stable-isotope analysis. *Can. J. Fish. Aquat. Sci.* **52**:1195-1201.

Hobson, KA., Alisauskas, RT., Clark, RG. 1993. Stable-nitrogen enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *The Condor* **95**:388-394.

Hoffman, GL. 1999. Parasites of North American Fishes. Cornell University Press. Ithaca.

Humason, GL. 1979. Animal tissue techniques, 4$^{th}$ edition. WH. Freeman, and Co. San Francisco, California, 661 p.

Hurst, TP. 2004. Temperature and state-dependence of feeding and gastric evacuation in juvenile Pacific halibut. *J. Fish Biol.* **65**:157-169.

Hynes, HBN. 1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in studies of the food of fishes. *J. Anim. Ecol.* **19**:36-58.

Hyslop, EJ. 1980. Stomach contents analysis: a review of methods and their application. *J. Fish Biol.* **17**:411-429.

Irvine, JR., and Northcote, TG. 1983. Selection by young rainbow trout (*Onchorhynchus mykiss*; formerly: *Salmo gairdneri*) in simulated stream environments for live and dead prey of different sizes. Can. J. Fish. aquat. Sci. **40**: 1745–1749.

Isinguzo I, and Dick, TA. 2008. Patterns and processes shaping parasite communities of lake trout (Abstract). In Mills KH, Dyck M, and Harwood LA eds. Proceedings of the second lake trout symposium 2005, Yellowknife, Northwest Territories. Canadian Technical Report of Fisheries and Aquatic Sciences 2778, p187.

Ivlev, VS. 1939. Balance of energy in carps. *Zool. Zh.* **18**:303-18. (In Russian with English summary).

Jensen, AJ. 1980. The 'gut index', a new parameter to measure the gross nutritional state of Arctic char, *Salvelinus alpinus* (L.) and brown trout, *Salmo trutta* L. J. Fish. Biol. **17**(6):741-747.

Jobling, M. 1980. Gastric evacuation in plaice, *Pleuronectes platessa* L.: effects of dietary energy level and food composition. *J. Fish Biol.* **17**:187-196.

Jobling, M. 1983. Influence of body weight and temperature on growth rates of Arctic char, *Salvelinus alpinus* (L.). *J. Fish. Biol.* **22**:471-475.

Jobling, M. 1994. Fish bioenergetics. Fish and Fisheries series 13. Chapman and Hall London UK.

Jobling, M., and Wandsvik, A. 1983. An investigation of factors controlling food intake in Arctic charr, *Salvelinus alpinus*. *J. Fish Biol.* **23**:397-404.

Johnson L 1980. The Arctic charr, *Salvelinus alpinus*, *In* E.K. Balon [ed] Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk Publishers, The Hague. p. 15-98.

Johnson, L. 1989. The anadromous Arctic charr, *Salvelinus alpinus* of Nauyuk Lake, N.W.T., Canada. *Physiol Ecol. Japan, Spec.* **1**:201-227.

Johnson, MW., and Dick, TA. 2001. Parasite effects on the survival, growth, reproductive potential of yellow perch (*Perca flavescens* Mitchill) in Canadian Shield lakes. *Can. J. Zool.* 79:1980-1992

Jónsson, B., and Jónsson, N. 2001. Polymorphism and speciation in Arctic charr. *J. Fish. Biol.* **58**:605-639.

Jørgensten, EH., Johansen, SJS., and Jobling, M. 1997. Seasonal patterns of growth, lipid deposition and lipid depletion in anadromous Arctic charr. *J. Fish Bio.* **51**:312-326.

Kabata, Z. 1969.Revision of the genus *Salmincola* Wilson, 1915 (Copepoda: Lernaeopodidae). *J. Fish. Res. Board Can.* **26**:2987-3041.

Kaeriyama, M. 1986. 1986. Ecological study on early life of chum salmon, *Onchorhynchus keta* (Walbaum). *Sci. Rep. Hokkaido Salmon Hatchery* **40**:31-92.

Karvonen A., Valtonen T 2004. Helminth assemblages of whitefish (*Coregonus lavaretus*) in interconnected lakes: similarity as a function of species specific parasites and geographic separation. *J. Parasitol.* **90**(3): 471-476.

Kendall AW Jr., and Behnke, RJ. 1984. Salmonidae: development and relationships. *In.* Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW Jr., and Richardson SL, eds. Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists, Special Publication 1, Allen Press, Lawrence, Kansas. Pp. 142-149.

Kenkel, NC., Deksen, DA., Thomas, AG., and Watson, PR. 2002. Multivariate analysis in weed science research. *Weed Science*, **50**:281-292.

Kennedy CR 1974. A checklist of British and Irish freshwater fish parasites with notes on their distribution. *J. Fish Biol.* **6**:613-644.

Kennedy CR 1977. The biology, specificity and habitat of species of *Eubothrium* (Cestoda: Pseudophilidea) with reference to their use as biological tags: a review. *J. Fish Biol.* **12**:393-410.

Kennedy CR 1978a. Studies on the biology of *Eubothrium salvelini* and *E. crassum* in resident and migratory *Salvelinus alpinus* and *Salmo trutta* and in *S. salar* in North Norway and the islands of Spitsbergen and Jan Mayen. *J. Fish Biol.* **12**:147-162.

Kennedy CR 1978b. The parasite fauna of resident charr *Salvelinus alpinus* from Arctic islands, with special interest to Bear Island. *J. Fish Biol.* **13**:457-466.

Kennedy, CR 1978c. The biology, specificity and habitat of the species of *Eubothrium* (Cestoda: Pseudophyllidea), with reference to their use as biological tags: a review. *J. Fish Biol.* 12: 393-410.

Kennedy CR 1995. Establishment, survival and site selection of the cestode *Eubothrium crassum* in brown trout, *Salmo trutta. Parasitol.* **111**:233-245.

Kennedy CR, Hartvigsen RA 2000. Richness and diversity of intestinal metazoan communities in brown trout Salmo trutta compared to those of eels *Anguilla anguilla* in their European heartlands. *Parasitol.* **121**:55-64.

Kiljunen, M., Grey, J., Sinisalo, T., Harrod, C., Immonen, H and Jones, RI. 2006. Methodological insights: A revised model for lipid-normalizing $\delta^{13}C$ values from aquatic organisms, with implications for isotope mixing models. J. Applied Ecol. **43**:1213-1222.

Klemetsen, A., Amundsen, PA., Dempson, JB., Jonsson, B., Jonsson, N., O'Connell, MF., and Mortensen, E. 2003. Atlantic salmon Salmo salar L., brown trout Salmo trutta L. and Arctic char *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* **12**:1-59.

Knudsen P, Amundsen PA, and Klemetsen A 2003. Inter- and intra-morph patterns of helminth communities of sympatric whitefish morphs. *J. Fish Biol.* **62**:847-859.

Knudsen R, Klemetsen A, and Staldvik F. 1996. Parasites as indicators of individual feeding specialization in Arctic char during winter in northern Norway. *J. Fish. Biol.* 48:1256-1265.

Koed, A. 2001. The effects of meal size, body size and temperature on gastric evacuation in pikeperch. *J. Fish Biol.* **58**:281-290.

Kristofferson, AH., and Sopuck, RD. 1983. The effects of exploitation on the Arctic char population of the Sylvia Grinnell River, NWT Can. Manuscr. Rep. Fish. Aquat. Sci. 1721: 35p.

Laffargue, P., Baudouin, G., Sasal, P., Arnaud, C., Anras, MB., and Lagardére. 2004. Parasitic infection of sole Solea solea by Prosorhynchus spp. metacercariae (Digenea,

Bucephaliadae) in Atlantic nurseries under mussel cultivation influence. *Inter-Research* **58**:179-184.

Lambert, Y., and Dutil, JD. 1997. Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. *Can. J. Fish. Aquat. Sci.* **54**:2388-2400

Lankester, MW, and Smith, JD. 1980. Host specificity and distribution of swim-bladder nematodes, *Cystidicola farionis* Fischer, 1798 and *C. cristivomeri* White, 1941 (Habronetoidea), in salmonid fishes of Ontario. *Can. J. Zool.* **58**:1298-1305.

Larsson, S. 2005. Thermal preference of Arctic char, *Salvelinus alpinus*, and brown trout, *Salmo truuta*: implications ofor their niche segregation. *Env. Biol. Fish.* **73**:89-96.

Larsson, S., and Berglund, I. 1998. Growth and food consumption of 0+ Arctic charr fed pelleted or natural food at six different temperatures. *J. Fish Biol.* **52**: 230-242.

Leeson, S., and Summers, J. 2001. Nutrition of the chicken. University Books. University of Guelph, Ontario Canada.

Legendre, P., and Legendre, L.1998. Numerical Ecology. Developments in Environmental modeling 20. Elsevier BV. Amsterdam.

Logan, JL., Haas, H. Deegan, L. Gaines, E. 2006. Turnover rates of nitrogen stable isotopes in the salt marsh mummichog, *Fundulus heteroclitus*, *Oecol.* **147:**391-395.

Lønne, OJ., and Gulliksen, B. 1989. Size, age and diet of Polar Cod, *Boreogadus saida* (Lepechin 1773), in ice-covered waters. *Polar Biology* **9**:187-191.

MacNeil, MA., Drouillard KG., and. Fisk, AT. 2006. Variable uptake and elimination of stable isotopes between tissues in fish, *Can. J. Fish. Aquat. Sci.* **63**:345-

Margolis L 1965. Parasites as an auxillary source of information about the biology of Pacific salmons (genus *Onchorhynchus*). *J. Fish. Res. Bd. Can.* 22:1387-1395.

Margolis L, Kabata Z. 1988. Guide to the parasites of fishes of Canada. Part II – Crustacea. Can. Spec. Publ. Fish Aquat. Sci. 101: 184p.

Margolis L. and Arthur, JR. 1979. Synopsis of the parasites of fishes of Canada. *Bull. Fish. Res. Board. Can.* 199: 269 pp.

Margolis, L., and Esch, GW., Holmes, JC., Kurtis, AM., and Schad, GA. 1982. The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitology). *J. Parasitol.*, **68**(1):131-133

Martin, NV., and Olver, CH. 1980. The lake charr, *Salvelinus namaycush. In* E.K. Balon ed Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk. The Hague. p. 205-277.

Martino, RC., Cyrino, JEP., Portz, L., and Trugo, L. 2002. Effect of dietary lipid level on nutritional performance of the surubim, *Pseudoplatystoma coruscans*. *Aquaculture* **209**:209-218.

Matthews, RA. 1973. The life-cycle of *Prosorhynchus crucibulum* (Rudolphi, 1819) Odhner, 1905, and a comparison of its cercaria with that of *Prosorhynchus squamatus* Odhner, 1905, *Parasitology* **66**:133-164.

McCarthy, ID., Fraser, D., Waldron, S., and Adams, CE. 2004. A stable isotope analysis ot trophic polymorphism among Arctic charr from Loch Ericht, Scotland. *J. Fish. Biol.* **65**:1435-1440.

McDonald TE, Margolis L. 1995. Synopsis of the parasites of fishes of Canada. Supplement (1978-1993). *Canadian Special Publication of Fisheries and Aquatic Sciences* 122,. National Research Council of Canada Ottawa. 265p

McPhail, JD. 1961. A systematic study of the *Salvelinus alpinus* complex in North America. *J. Fish Res. Board Can.* 18(5):793-816.

McPhail, JD, and Lindsey, CC. 1970. Freshwater fishes of northwestern Canada and Alaska. *Bull. Fish. Res. Board Can.* Pp 173:381.

Michener, RH., and Kaufman, L. 2007. Stable isotope ratios as tracers in marine food webs: An update. R. Michener and K. Lajtha [eds] Ecological methods and concepts: Stable isotopes in ecology and environmental science 2nd ed. Blackwell Publishing, UK.

Miglavis, I., and Jobling, M. 1989. The effects of feeding regime on proximate body composition and patterns of energy deposition in juvenile Arctic char, *Salvelinus alpinus*. *J. Fish Biol.* 35:1-11.

Mills D 1971. Salmon and trout: A resource, its ecology, conservation and management. St. Martin's Press New York.351p.

Minagawa, M., and Wada, E. 1984. Stepwise enrichment of 15N along food chains: further evidence and the relation between δ15N and animal age. *Geochim Cosmochim Acta* **48**:1135-1140.

Moncreiff., CA., and Sullivan, MJ. 2001. Trophic importance of spiphytic alge in subtropical seagrass beds: Evidence from multiple stable isotope analyses. *Mar. Ecol. Pro. Ser.* **215**:93-106

More, JW., and More, IA. 1974. Food and growth of Arctic char, *Salvelinus alpinus* (L), in the Cumberland Sound area of Baffin Island. *J. Fish. Biol.* **6**:79-92.

More, JW. 1975. Distribution, movements, and mortality of anadromous Arctic char, *Salvelinus alpinus* L., in the Cumberland Sound. *J. Fish Biol.* 7(3):339-348.

Mudry, DR., and Anderson, R. 1977. Helminth and arthropod parasites of fishes in the mountain national parks of Canada. *J. Fish Biol.* **11**:21-33.

Mudry, DR,, and McCart, C. 1976. Metazoan parasites of Arctic charr (*Salvelinus alpinus*) from the north slope of Canada and Alaska. *J Fish Res. Bd Can.* **33**:271-275.

Muzzall, PM. 1989. Endohelminths of salmonids from two localities in eastern Lake Michigan, with emphasis on *Echinorhynchus salmonis*. *Can J. Zool.* **67**:1604-1607.

Muzzall, PM. 1995. Parasites of Lake Trout, *Salvelinus namaycush*, from the Great Lakes: a review of the literature 1874-1994. *J. Great Lakes Res.* **21**(4):594-598.

Muzzall, PM., and Peebles, CR. 1986. Helminths of pink salmon, *Onchorhynchus gorbusha*, from five tributaries of Lake Superior and Lake Huron. *Can. J. Zool.* 64:508-511.

Muzzall PMC, Bowen CA II 2000. Helminths in an intensively stocked population of lake trout, *Salvelinus namaycush*, from Lake Huron. *J. Parasitol.*. **86**(3):639-642.

Nelson, GA., and Ross, MR. 1995. Gastric evacuation in little skate. *J. Fish. Biol.* **46**:977-986.

Newman, RM., and Waters, TF. 1984. Size-selective predation on *Gammarus pseudolimnaeus* by trout and sculpins. *Ecology* **65**:1535-1545.

NRC [National Research Council]. 1981. Nutrient requirements of coldwater fishes. Washington DC. National Academy Press, USA.

NRC [National Research Council]. 1993. Nutrient requirement of fish. Washington, DC. National Academy Press, USA.

Olsen, RE., Henderson, RJ., and McAndrew, BJ. 1990. The conversion of linoleic and linolenic acid to longer chain polyunsaturated fatty acids by *Tilapia* (*Orechromis*) *nilotica in vivo*. *Fish Physiol. Biochem.* **8**:261-270.

Owens, NJP. 1987. Natural variations in $^{15}N$ in the marine environment. *Advances of Marine Biology* **24**:389-1257

Pääkkönen, J-PJ., and Marjomäki, TJ. 1997. Gastric evacuation rate of burbot fed single-fish meals at different temperatures. *J. Fish Biol.* **50**:555-563.

Pearcy, W., Nishiyama, T., Fujii, T., and Masuda, K. 1984. Diel variations in the feeding habits of Pacific salmon caught in gill nets during a 24-hour period in the Gulf of Alaska. *Fish. Bull.* **82**:391-399.

Percy, JA. 1993a. Reproduction and growth of the Arctic hyperiid amphipod *Themisto libellula* Mandt. *Polar Biol.* **13**: 131-139.

Percy, JA. 1993b. Energy consumption and metabolism during startvation in the Arctic hyperiid amphipod *Themisto libellula* Mandt. *Polar Biol.* **13**:549-555.

Percy, JA., and Fife, FJ. 1980. The proximate composition and calorific content of Arctic marine invertebrates from Frobisher Bay. Candian Data report of Fisheries and Aquatic Sciences. No. 214.

Percy, JA., and Fife, FJ. 1981. The biochemical composition and energy content of Arctic marine macrozooplankton. *Arctic* **34**(4):307-313.

Peterson, BJ., and Fry, B. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* **18**:293-320.

Phillips, DL. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. *Oecologia* **127**:166-170.

Pike, D., and Dahlke, L. 1990. Arctic char of the Sylvia Grinnell River. AFSAC.p19.

Pinkas, L., Oliphant, MS., and Iverson, ILK. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Fish Game, **152**:1-105.

Power, G 1980. The brook charr, *Salvelinus fontinalis In* E.K. Balon [ed], Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk Publishers. The Hague. Pp. 141-203.

Power, M., Power, G., Caron, F., Doucett, RR., and Guiguer, KRA. 2002. Growth and dietary niche in Salvelinus alpinus and Salvelinus fontinalis as revealed by stable isotope analysis. *Environmental Biology of Fishes* **64**:75-85.

Pugachev ON 1984. Parasites of freshwater of North-East Asia (In Russian). USSR Academy of Sciences.

Quinn, TP. 2005. The behaviour ecology of Pacific salmon and trout. University of Washington Press. Washington.

Radujkovic, BM., Orecchia, P., and Paggi, L. 1989. Parasites des poisons marins du Monténégro: Digénes. *Acta Adriatica* **30**:137-187.

Rau, GH., Mearns, AJ., Young, DR., Olson, RJ., Scafer, HA., and Kaplan, IR. 1983. Animal $^{13}C/^{12}C$ correlates with trophic level in pelagic food webs. *Ecology* **64**:1314-1318.

Reimers, N. 1957. Some aspects of the relation between stream foods and trout survival. *California Fish Game* **43**:43-69.

Reinitz, GL., Orme, LE., Lemm, CA., and Hitzel, FN. 1978. Influence of varying lipid concentrations with two protein concentrations in diets for rainbow trout (*Onchorhynchus mykiss*; formerly: *Salmo gairdneri*). *Trans. Amer. Fish. Soc.* **107**: 751-754.

Reist, JD., Wrona, FJ., Prowse, TD., Power, M., Dempson, JB., King, JR and Beamish, RJ. 2006. An overview of effects of climate change on selected Arctic freshwater and anadromous fishes. *Ambio* **35**(7):381-387.

Ricker, WE. 1971. Methods for assessment of fish Production in freshwater. IBP Handbook No. 3. Blackwell Scientific Publications, Oxford.

Rikardsen, AH., Amundsen, P.-A, Bjørn, PA., and Johansen, M. 2000. Comparison of growth, diet and food consumption of sea-run and lake-dwelling Arctic charr. *J. Fish. Biol.* **57**:1172-1188.

Rikardsen, AH, Amundsen, PA., and Bodin, PJ. 2002. Foraging behaviour changes of Arctic char during smolt migration in northern Norway. *J. Fish Biol.* **60**:489-491.

Rikardsen, AH., and Johansen, M. 2003. A morphometric method for estimation of total lipid levels in live Arctic char: a case study of its application on wild fish. J. Fish Biol. **62**(3):724-734

Rikardsen, AH., Dempson, JB, Amundsen, P-A, Bjørn, PA, Finstad, B and Jensen, AJ. 2007. Temporal variability in marine feeding of sympatric Arctic char and sea trout. *J. Fish Biol.* **70**:837-852.

Rikardsen, AH., Haugland, M., Bjørn, Finstad, B., Knudsen, R., Dempson, JB, Holst, JC., Hvidsten, NA and Holm, M. 2004a. Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. *J. Fish Biol.* **64**:1655-1679.

Rikardsen, AH., Thorpe, JE., and Dempson B. 2004b. Modelling the life-history variation of Arctic char. *Ecology of Freshwater Fish.* **13**:305-311.

Rikardsen, AH.and Amundsen, PA. 2005. Pelagic marine feeding behaviour of Arctic char *Salvelinus alpinus* and sea trout *Salmo trutta*. *J. Fish Biol.* **66**:1163-1166.

Ringler, NH. 1979. Selective predation by drift-feeding brown trout (*Salmo trutta*). *J. Fish. Res. Bd. Can.* **36**:392-403.

Sainte-Marie, B. 1986. Feeding and swimming of lysianassid amphipods in a shallow cold-water bay. *Mar. Biol.* **91**:219-229.

Saksvik M, Nilsen F, Nylund A and Berland B 2001. Effect of marine Eubothrium sp. (Cestoda: Pseudophyllidea) on the growth of Atlantic salmon, *Salmo salar* L. *J Fish Diseases* **24**:111-119.

Salvanes, AGV., Aksnes, DL., and Giske, J. 1995. A surface-dependent gastric evacuation model for fish. *J. Fish. Biol.* **47**:679-695.

Sandeman IM., Pippy JHC 1967. Parasites of freshwater fishes (Salmonidae and Coregonidae) of Insular Newfoundland. *J. Res. Bd. Canada*, **24**(9):1911-1943.

Sanford, CPJ. 1990. The phylogenetic relationships of salmonoid fishes. *Bull. Brit. Mus. Nat. Hist. (Zoology)*. **56**(2):145-153.

Sars, GO. 1890. An account of the Crustacea of Norway. Volume 1. Amphipoda. Bergen and Oslo. Copenhagen.

Sars. GO. 1899. An account of the Crustacea of Norway. Volume II. Isopoda. Bergen, Christiania.

Scholz T, Kuchta R, Shinn AP, Šnabel V and Hanzelova V 2003. Host specificity and geographical distribution of *Eubothrium* in European salmonid fish. *J. Helminth.* 77:255-262.

Scott WB, Crossman EJ 1973. Freshwater fishes of Canada. *Bull. Fish. Res. Board Can.* 184: 966 pp.

Scott WB, Scott MG. 1988. Atlantic Fishes of Canada. *Can. Bull. Fish. Aquat.* 219:731 p.

Specziár, A. 2002. *In situ* estimates of gut evacuation and its dependence on temperature in five cyprinids. *J. Fish Biol.* **60**:1222-1236.

Squires, HJ. 1990. Decapod Crustacea of the Atlantic coast of Canada. Canadian Bulletin of Fisheries Aquatic Sciences. 221:477pp.

Starostka, VJ., and Applegate, RL. 1970. Food selectivity of bigmouth buffalo, *Ictiobus cyprinellus*, in Lake Poinsett, South Dakota. *Trans. Amer. Fish Soc.*, 3:571-575.

Stearley RF, Smith GR 1993. Phylogeny of the pacific trouts and salmons (*Onchorhynchus*) and genera of the family Salmonidae. *Trans. Am. Fish. Soc.* 122:1-33.

Stephens, DW and Krebs, JR. 1986. Foraging Theory: Monographs in behaviour and ecology. 248p. Princeton University Press. Princeton, New Jersey.

Straty, RR., and Jaenicke, HW. 1980. Estuarine influenced of salinity, temperature, and food on the behaviour, growth, and dynamics of Bristol Bay sockeye salmon. p. 247-265 In WJ. McNeil and DC. Himsworth [eds] Salmonid eosystem of the North Pacific. Oregon State University Press. p.247-265.

Suzuki, KW., Kasai, A., Nakayama, K., and Tanaka, M. 2005. Differential isotopic enrichment and half-life among tissues in Japanese temperate bass (*Lateolabrax japonicus*) juveniles: implications for analyzing migration. *Can. J. Fish. Aquat. Sci.* **62**:671-678.

Tabachek, JL. 1986. Influence of sietary protein and lipid levels on growth, body composition and utilization efficiencies of Arctic charr (*Salvelinus alpinus* L.). *J. Fish Biol.* **29**:139-151.

Tabachek, JL. 1988. The effects of feed particle size on the growth and feed efficiency of Arctic charr (*Salvelinus alpinus*, L.). *Aquaculture*, **71**:319-330.

Takeuchi, J., Watanabe, T., and Ogino, C. 1978. Optimum ratio of protein to lipids in diets of rainbow trout. *Bull. Jap. Soc. Sci. Fish.* **44**:683-688.

Temming, A., and Herrmann, J.-P. 2001. Gastric evacuation of horse mackerel. II. The effects of different prey types on the evacuation model. *J. Fish. Biol.* **58**:1246-1256.

Temming, A., Bøhle, B., Skagen, DW., and Knudsen, FR. 2002. Gastric evacuation in mackerel: the effects of meal size, prey type and temperature. *J. Fish Biol.* **61**:50-70.

ter Braak, CFJ. 1996. Unimodal models to relate species to environment. Agricultural Mathematics Group, Wageningen, The Netherlands.

ter Braak, CFJ., and Šmilauer, P. 2002. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4.5). Biometris, Wageningen and České Budějovice, The Netherlands.

Thomas, CJ., and Cahoon, LB. 1993. Stable isotope analyses differentiated between different trophic pathways supporting rocky-reef fishes. *Mar. Ecol. Progr. Ser.* **95**: 19-24.

Tieszen, LL., Boutton, TW., Tesdahl, KG., and Slade, NA. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. *Oecologia* **57**:32-37

Van Dijk, PLM., Hardewig, I and Holker, F. 2005. Energy reserves during food deprivation and compensatory growth in juvenile roach: the importance of season and temperature. *J. Fish Biol.* **66**:167-181.

Vander Zanden, MJ., Cabana, G., and Rasmussen, JB. 1997. Comparing the trophic position of littoral fish estimated using stable nitrogen isotopes ($\delta^{15}N$) and dietary data. *Can. Fish. Aquat. Sci.* **54**:1142-1158.

Vander Zanden, MJ., and Rasmussen, JB. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food web studies. *Limnol. Oceanogr.* **46**(8):2061-2006.

Vanriel P. and Johnson, L. 1995. Action principles as determinants of ecosystem structure: the autonomous lake as a reference system, *Ecol.* **76:** 1741–1757

Viherluoto, M., Kuosa, H., Flinkman, J., and Viitasalo, M. 2004. Food utilisation of pelagic mysids, Mysis mixta and M. relicta, during their growing season in the northern Baltic Sea. *Mar. Biol.* **136**(3):553-559.

Vik R 1963. Studies on the helminth fauna of Norway. IV. Occurrence and distribution of *Eubothrium crassum* (Bloch, 1779) and E. salvelini (Schrank, 1770) (Cestoda) in Norway, with notes on their life cycles. *Nytt Mag. Zool.* **11**:47-73.

Vinni, M., Lappalainen, J., and Horppila, J. 2005. Temporal and size-related changes in the frequency of empty stomachs in smelt. *J. Fish Biol.* **66**:578-582.

von Bertalanffy, L. 1957. Quantitative laws inmetabolism and growth. *Quant. Rev. Biol.* **32**:217-231.

Wankowski JWJ 1979. Morphological limitations, prey size selectivity, and growth response of juvenile Atlantic salmon, *Salmo salar. J. Fish. Biol.*, **14**:89-100.

Wankowski JWJ, Thorpe JE 1979. The role of food particle size in the growth of juvenile Atlantic salmon *Salmo salar. J. Fish. Biol.* **14**: 239–247.

Watanabe, T., 1977. Sparing action of lipids on dietary protein in fish-low protein with higher calorie content. *Technocrat* **10**:34-39.

Watson, RA., and Dick, TA. 1979. Metazoan parasites of whitefish *Coregonus clupeaformis* (Mitchell) and cisco *C. artedii* Lesueur from Southern Indian Lake, Manitoba. *J. Fish Biol.* **15**:579-587.

Weslawski, JM., Stempniewicz and Galaktionov, K. 1994. Summer diet of seabirds from the Frans Josef Land archipelago, Russain Arctic. *Polar Research* **13**(2):172-181.

Winberg, GG. 1956. Rate of metabolism and food requirements of fishes. Belorussian State University, Minsk. (Translated from Russian by Fish. Res. Bd. Can. Transl. Seer. No. 194, 1960).

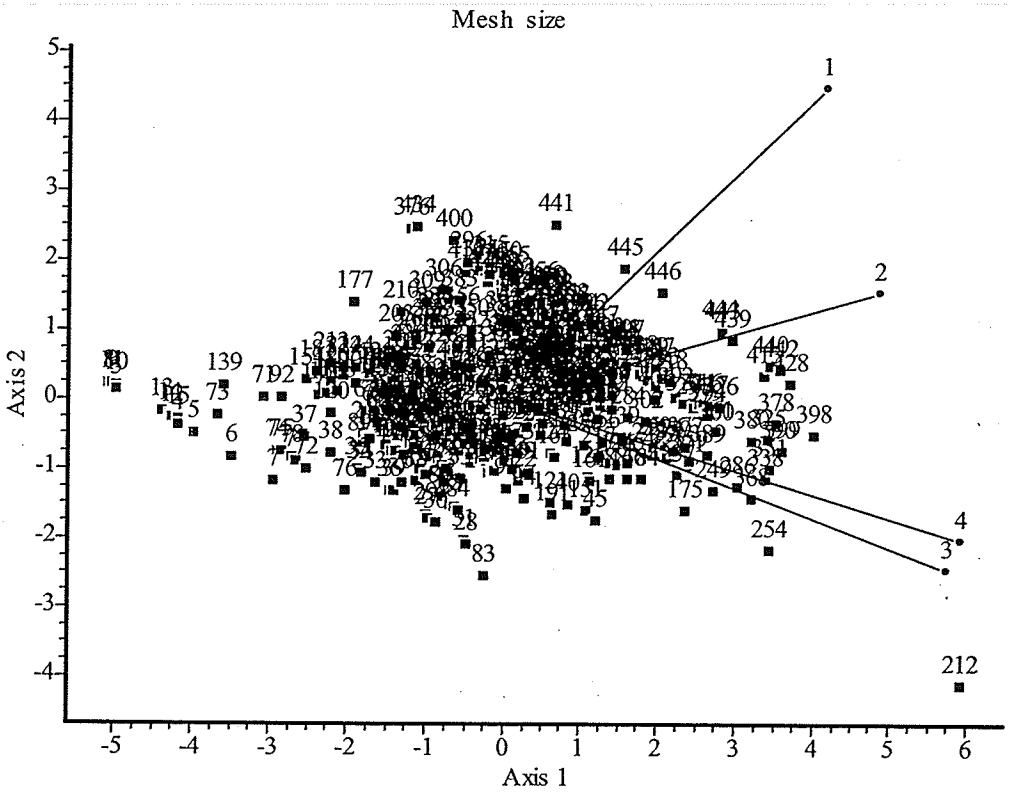
Windell, JT. 1966. Rate of digestion in bluegill sunfish. *Invest. Indiana Lakes and Streams* 7:185-214.

Windell, JT., and Norris, DO. 1969. Gastric digestion and evacuation in rainbow trout. *Progve Fish Cult.* **31**:20-26.

# APPENDICES

## Appendix 1. List and codes of variables used in multivariate analyses in Chapter Two

| Variables | Codes | Variables | Codes |
|---|---|---|---|
| **Sampling locations** | | **Diet items** | |
| Sylvia Grinnell | SG | *Themisto libellula* | *Them* |
| Kagnitsuatsia | KG | Polychaete sp. | *Py* |
| Causeway | CW | *Thysanoessa* sp. | *Thys* |
| Apex | AP | *Mysis* sp. | *Mys* |
| Tar inlet | TI | *Onesimus littoralis* | *Ones* |
| Foul inlet | FI | *Gammarus* sp. | *Gam* |
| Bay of Two Rivers | BT | *Calanus* sp. | *Cal* |
| | | Sculpins | *scp* |
| **Fish condition** | | **Other environmental factors** | |
| Weight of gonad | Gd | July sampling period | Jy |
| Gonadosomatic index | GSI | August sampling period | Aug |
| Condition factor | K | Julian date of low tide | JDLT |
| Liver weight | Lv | Julian date of high tide | JDHT |
| Liversomatic index | LSI | Subnet 2 | Sn2 |
| Weight of visceral fat | VF | Subnet 8 | Sn8 |
| Visceral fat-gonad weight ratio | VG | Subnet 9 | Sn9 |
| Weight of full stomach | Sf | Subnet 10 | Sn10 |
| Weight stomach content | Sc | Experimental net | ExN |
| **Covariables** | | | |
| Weight of fish | Wt | | |
| Fork length | FL | | |
| Total length | TL | | |
| Age | A | | |




Appendix 2. PCA ordination of the relationship between mesh sizes, fish weight, fork length and age. Variables are represented by numbers: 1 = Mesh size; 2 = Fish weight; 3 = Fish fork length and 4 = Age.

Appendix 3. Combinations used in multivariate analyses in Chapter Two.

| Model Runs | Data files | Response variables (species) | Explanatory variables (Environmental variables) | Figure (ordination diagram) | Type of analysis |
|---|---|---|---|---|---|
| 1 | Pooled food species<br>Sampling location | Pooled food species | Sampling locations | 4 | pCCA |
| 2 | Sampling locations<br>Fish condition data | Sampling locations | Fish condition data | 5 | pCCA |
| 3 | Fish condition data<br>Other env. Factors | Fish condition data | Other env. Factors | 6 | CCA |

Appendix 4. Presence of diet species by sampling locations

| Food species | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| *Themisto libellula* | | | | | | | |
| Polychaete sp. | | | | | | | |
| *Thysanoessa* sp. | X | X | X | X | X | X | |
| *Mysis* sp. | X | X | X | X | X | X | |
| *Onesimus littoralis** | X | X | X | X | X | X | X |
| *Gammarus* sp. | X | X | X | X | X | X | |
| *Calanus* sp. | | | | | | | X |
| Sculpins | | | | | | | X |

* May be found in all sampling locations
1 = Sylvia Grinnell River; 2 = Kagnitsuatsia; 3 = Causeway; 4 = Apex; 5 = Tar Inlet; 6 = Foul Inlet and 7 = Bay of Two Rivers.

Appendix 5. Summary of dependent t-tests for weight among age classes and among sex using 2002 samples.

| Variable | Sampling Period | Age Classes | P-value | Sig. Abbreviation |
|---|---|---|---|---|
| Fish weight | July | 8 vs. 9 | 0.341 | NS |
| | | 8 vs. 10 | 0.025 | S |
| | | 9 vs. 10 | 0.020 | S |
| | August | 8 vs. 9 | 0.398 | NS |
| | | 8 vs. 10 | 0.605 | NS |
| | | 9 vs. 10 | 0.831 | NS |

Appendix 6. Summary of MANOVA results of male char weight, length, age, and ratios of visceral fat, liver weight and gonad weight to fish weight in July over time.

| Variable | Year (a) | Year (b) | P-value | Sig. Abbreviation |
|---|---|---|---|---|
| Fish weight | 2002 | 2004 | 0.051 | NS |
| | | 2005 | 0.000 | S |
| | 2004 | 2002 | 0.051 | NS |
| | | 2005 | 0.000 | S |
| | 2005 | 2002 | 0.000 | S |
| | | 2004 | 0.000 | S |
| Fork length | 2002 | 2004 | 0.006 | NS |
| | | 2005 | 0.000 | S |
| | 2004 | 2002 | 0.006 | S |
| | | 2005 | 0.000 | S |
| | 2005 | 2002 | 0.000 | S |
| | | 2004 | 0.000 | S |
| Age | 2002 | 2004 | 1.000 | NS |
| | | 2005 | 0.090 | NS |
| | 2004 | 2002 | 1.000 | NS |
| | | 2005 | 0.050 | NS |
| | 2005 | 2002 | 0.090 | NS |
| | | 2004 | 0.050 | NS |
| Ratio of Visceral fat/fish weight | 2002 | 2004 | 0.016 | S |
| | | 2005 | 0.000 | S |
| | 2004 | 2002 | 0.016 | S |
| | | 2005 | 0.039 | S |
| | 2005 | 2002 | 0.000 | S |
| | | 2004 | 0.039 | S |
| Ratio of liver weight/fish weight | 2002 | 2004 | 1.000 | NS |
| | | 2005 | 0.004 | S |
| | 2004 | 2002 | 1.000 | NS |
| | | 2005 | 0.000 | S |
| | 2005 | 2002 | 0.004 | S |
| | | 2004 | 0.000 | S |
| Ratio of gonad weight/fish weight | 2002 | 2004 | 0.366 | NS |
| | | 2005 | 0.050 | NS |
| | 2004 | 2002 | 0.366 | NS |
| | | 2005 | 0.695 | NS |
| | 2005 | 2002 | 0.050 | NS |
| | | 2004 | 0.695 | NS |

Appendix 7. Summary of MANOVA results of male char weight, length, age, and ratios of visceral fat, liver weight and gonad weight to fish weight in August over time

| Variable | Year (a) | Year (b) | P-value | Sig. Abbreviation |
|---|---|---|---|---|
| Fish weight | 2002 | 2004 | 1.000 | NS |
| | | 2005 | 0.089 | NS |
| | 2004 | 2002 | 1.000 | NS |
| | | 2005 | 0.288 | NS |
| | 2005 | 2002 | 0.089 | NS |
| | | 2004 | 0.288 | NS |
| Fork length | 2002 | 2004 | 1.000 | NS |
| | | 2005 | 0.995 | NS |
| | 2004 | 2002 | 1.000 | NS |
| | | 2005 | 0.737 | NS |
| | 2005 | 2002 | 0.995 | NS |
| | | 2004 | 0.737 | NS |
| Age | 2002 | 2004 | 1.000 | NS |
| | | 2005 | 1.000 | NS |
| | 2004 | 2002 | 1.000 | NS |
| | | 2005 | 1.000 | NS |
| | 2005 | 2002 | 1.000 | NS |
| | | 2004 | 1.000 | NS |
| Ratio of Visceral fat/fish weight | 2002 | 2004 | 0.016 | S |
| | | 2005 | 0.038 | S |
| | 2004 | 2002 | 0.016 | S |
| | | 2005 | 1.000 | NS |
| | 2005 | 2002 | 0.038 | S |
| | | 2004 | 1.000 | NS |
| Ratio of liver weight/fish weight | 2002 | 2004 | 1.000 | NS |
| | | 2005 | 1.000 | NS |
| | 2004 | 2002 | 1.000 | NS |
| | | 2005 | 1.000 | NS |
| | 2005 | 2002 | 1.000 | NS |
| | | 2004 | 1.000 | NS |
| Ratio of gonad weight/fish weight | 2002 | 2004 | 0.934 | NS |
| | | 2005 | 1.000 | NS |
| | 2004 | 2002 | 0.934 | NS |
| | | 2005 | 1.000 | NS |
| | 2005 | 2002 | 1.000 | NS |
| | | 2004 | 1.000 | NS |

Appendix 8: Summary of MANOVA results of female char weight, length, age, and ratios of visceral fat, liver weight and gonad weight to fish weight in July over time

| Variable | Year (a) | Year (b) | P-value | Sig. Abbreviation |
|---|---|---|---|---|
| Fish weight | 2002 | 2004 | 0.000 | S |
| | | 2005 | 0.000 | S |
| | 2004 | 2002 | 0.000 | S |
| | | 2005 | 0.000 | S |
| | 2005 | 2002 | 0.000 | S |
| | | 2004 | 0.000 | S |
| Fork length | 2002 | 2004 | 0.004 | S |
| | | 2005 | 0.000 | S |
| | 2004 | 2002 | 0.004 | S |
| | | 2005 | 0.010 | S |
| | 2005 | 2002 | 0.000 | S |
| | | 2004 | 0.010 | S |
| Age | 2002 | 2004 | 0.071 | NS |
| | | 2005 | 0.002 | S |
| | 2004 | 2002 | 0.071 | NS |
| | | 2005 | 0.127 | NS |
| | 2005 | 2002 | 0.002 | S |
| | | 2004 | 0.127 | NS |
| Ratio of Visceral fat/fish weight | 2002 | 2004 | 1.000 | NS |
| | | 2005 | 0.002 | S |
| | 2004 | 2002 | 1.000 | NS |
| | | 2005 | 0.000 | S |
| | 2005 | 2002 | 0.002 | S |
| | | 2004 | 0.000 | S |
| Ratio of liver weight/fish weight | 2002 | 2004 | 1.000 | NS |
| | | 2005 | 0.222 | NS |
| | 2004 | 2002 | 1.000 | NS |
| | | 2005 | 0.163 | NS |
| | 2005 | 2002 | 0.222 | NS |
| | | 2004 | 0.163 | NS |
| Ratio of gonad weight/fish weight | 2002 | 2004 | 0.007 | S |
| | | 2005 | 1.000 | NS |
| | 2004 | 2002 | 0.007 | S |
| | | 2005 | 0.699 | NS |
| | 2005 | 2002 | 1.000 | NS |
| | | 2004 | 0.699 | NS |

Appendix 9. Summary of MANOVA results of female char weight, length, age, and ratios of visceral fat, liver weight and gonad weight to fish weight in August over time

| Variable | Year (a) | Year (b) | P-value | Sig. Abbreviation |
|---|---|---|---|---|
| Fish weight | 2002 | 2004 | 0.010 | S |
| | | 2005 | 0.000 | S |
| | 2004 | 2002 | 0.001 | S |
| | | 2005 | 0.266 | NS |
| | 2005 | 2002 | 0.000 | S |
| | | 2004 | 0.266 | NS |
| Fork length | 2002 | 2004 | 0.000 | S |
| | | 2005 | 0.005 | S |
| | 2004 | 2002 | 0.000 | S |
| | | 2005 | 0.000 | S |
| | 2005 | 2002 | 0.005 | S |
| | | 2004 | 0.000 | S |
| Age | 2002 | 2004 | 0.015 | S |
| | | 2005 | 0.299 | NS |
| | 2004 | 2002 | 0.015 | S |
| | | 2005 | 1.000 | NS |
| | 2005 | 2002 | 0.299 | NS |
| | | 2004 | 1.000 | NS |
| Ratio of Visceral fat/fish weight | 2002 | 2004 | 1.000 | NS |
| | | 2005 | 0.038 | S |
| | 2004 | 2002 | 1.000 | NS |
| | | 2005 | 0.014 | S |
| | 2005 | 2002 | 0.038 | S |
| | | 2004 | 0.014 | S |
| Ratio of liver weight/fish weight | 2002 | 2004 | 1.000 | NS |
| | | 2005 | 1.000 | NS |
| | 2004 | 2002 | 1.000 | NS |
| | | 2005 | 1.000 | NS |
| | 2005 | 2002 | 1.000 | NS |
| | | 2004 | 1.000 | NS |
| Ratio of gonad weight/fish weight | 2002 | 2004 | 0.005 | S |
| | | 2005 | 1.000 | NS |
| | 2004 | 2002 | 0.005 | S |
| | | 2005 | 0.010 | S |
| | 2005 | 2002 | 1.000 | NS |
| | | 2004 | 0.010 | S |

Appendix 10. Mean ± SD of ratio of visceral fat weight(VF)/fish weight (FW) of male and female Arctic char over time

| Sex | Year | n | Total mean ± SD of ratio of VF/FW in July | n | Total mean ± SD of ratio of VF/FW in August |
|---|---|---|---|---|---|
| Male | 2002 | 27 | 0.0046 ± 0.0030 | 24 | 0.0085 ± 0.0059 |
| | 2004 | 31 | 0.0076 ± 0.0045 | 57 | 0.0118 ± 0.0041 |
| Female | 2002 | 45 | 0.0064748 ± 0.0043027 | 50 | 0.008433 ± 0.0040178 |
| | 2004 | 44 | 0.0065245 ± 0.0028779 | 54 | 0.0145971 ± 0.006718 |
| Ratio of total ratio of male/female visceral fat weight/fish weight | 2002 | | 0.71045 | | 1.01 |
| Ratio of total ratio of male/female visceral fat weight/fish weight | 2004 | | 1.16484 | | 0.81 |

Appendix 11. Mean ± SD of ratio of liver weight (LV)/fish weight (FW) of male and female Arctic char over time

| Sex | Year | n | Total mean ± SD of ratio of LV/FW in July | n | Total mean ± SD of ratio of LV/FW in August |
|---|---|---|---|---|---|
| Male | 2002 | 26 | 0.0153553 ± 0.0039875 | 23 | 0.0202433 ± 0.0059859 |
| | 2004 | 32 | 0.0144373 ± 0.0030388 | 57 | 0.019548 ± 0.0049926 |
| Female | 2002 | 47 | 0.0187576 ± 0.0112833 | 51 | 0.0198405 ± 0.0056142 |
| | 2004 | 42 | 0.0185996 ± 0.0057971 | 54 | 0.0232572 ± 0.036592 |
| Ratio of total ratio of male/female liver weight/fish weight | 2002 | | 0.81862 | | 1.02 |
| Ratio of total ratio of male/female of liver weight/fish weight | 2004 | | 0.77622 | | 0.84 |

Appendix 12. Mean ± SD of ratio of gonad weight (GD)/fish weight (FW) of male and female Arctic char over time

| Sex | Year | n | Total mean ± SD of ratio of GD/FW in July | n | Total mean ± SD of ratio of GD/FW in August |
|---|---|---|---|---|---|
| Male | 2002 | 27 | 0.0008901 ± 0.0007511 | 26 | 0.0013037 ± 0.0035275 |
| | 2004 | 31 | 0.0023485 ± 0.0040576 | 54 | 0.0019916 ± 0.0073571 |
| Female | 2002 | 46 | 0.007745 ± 0.0068181 | 52 | 0.0053502 ± 0.0088932 |
| | 2004 | 41 | 0.0150396 ± 0.0141257 | 58 | 0.0065817 ± 0.0128747 |
| Ratio of total ratio of male/female gonad weight/fish weight | 2002 | | 0.11 | | 0.24 |
| Ratio of total ratio of male/female of gonad weight/fish weight | 2004 | | 0.16 | | 0.30 |

Appendix 13. Intra-annual diet species abundances among male and female char in 2002 and 2004

| | Year 2002 | | | | Year 2004 | | | |
|---|---|---|---|---|---|---|---|---|
| Food species | Male: Early July | Female: Early July | Male: Late August | Female: Late August | Male: Early July | Female: Early July | Male: Late August | Female: Late August |
| *Mysis* spp. | 195.17 | 154.45 | 271.01 | 248.00 | 65.68 | 92.44 | 27.88 | 403.23 |
| Sculpins | 0.32 | 3.13 | 20.83 | 17.81 | 0.29 | 0.33 | 0.36 | 16.38 |
| *Themisto libellula* | 12.39 | 29.50 | 76.92 | 79.09 | 17.07 | 15.94 | 43.32 | 103.15 |
| *Onesimus littoralis* | 2.88 | 19.42 | 7.15 | 9.09 | 7.36 | 0.11 | 8.20 | 7.15 |
| *Thysanoessa* spp. | 19.88 | 11.50 | 4.02 | 7.79 | 5.32 | 23.56 | 0.00 | 0.46 |
| *Calanus* spp. | 0.27 | 1.68 | 17.63 | 84.30 | 0.00 | 0.17 | 0.12 | 5.15 |
| *Gammarus* spp. | 5.07 | 15.45 | 0.35 | 0.28 | 0.39 | 0.61 | 0.52 | 0.23 |
| Polychaetes | 24.44 | 49.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 |

Appendix 14. Summary of dependent (paired) t-tests of stomach fullness and content data of male and female char over time

| Variable | Sampling period | Year | P-value | Sig. Abbreviation* |
|---|---|---|---|---|
| Ratio of weight of stomach fullness/fish weight | July vs. August | 2002 | 0.013 | S |
| | July vs. August | 2004 | 0.721 | NS |
| Ratio of weight of stomach contents/fish weight | July vs. August | 2002 | 0.290 | NS |
| | July vs. August | 2004 | 0.714 | NS |

Appendix 15. Mean ± SD of ratio of weight of stomach fullness (SF)/fish weight (FW) of male and female char over time

| Sex | Year | n | Total mean ± STD of ratio of SF/FW in July | n | Total mean ± STD of ratio of SF/FW in August |
|---|---|---|---|---|---|
| Male | 2002 | 39 | 0.0525 ± 0.0255 | 33 | 0.04139 ± 0.01941 |
| | 2004 | 40 | 0.0534 ± 0.02022 | 50 | 0.03824 ± 0.02307 |
| | | | | 43 | |
| Female | 2002 | 35 | 0.0467 ± 0.0236 | 43 | 0.3736 ± 0.01696 |
| | 2004 | 35 | 0.05075 ± 0.02484 | 44 | 0.04783 ± 0.07453 |

Appendix 16. Mean ± SD of ratio of weight of stomach contents (SC)/fish weight (FW) of male and female char over time

| Sex | Year | n | Total mean ± STD of ratio of SC/FW in July | n | Total mean ± STD of ratio of SC/FW in August |
|---|---|---|---|---|---|
| Male | 2002 | 39 | 0.0371 ± 0.02651 | 30 | 0.03003 ± 0.01864 |
| | 2004 | 40 | 0.03702 ± 0.01783 | 50 | 0.02461 ± 0.02186 |
| | | | | 43 | |
| Female | 2002 | 35 | 0.03112 ± 0.0228 | 43 | 0.02640 ± 0.0162 |
| | 2004 | 35 | 0.03682 ± 0.0257 | 44 | 0.03359 ± 0.06373 |

Appendix 17. $\delta^{13}C$ and $\delta^{15}N$ ratios based on location

| Location | n | Mean ± SD $\delta^{13}C$ | Mean ± SD $\delta^{15}N$ |
|---|---|---|---|
| Sylvia Grinnell River | 12 | -20.16 ± 3.75 | 13.15 ± 3.51 |
| Kagnitsuatsia | 25 | -19.06 ± 0.62 | 14.54 ± 1.85 |
| Causeway | 12 | -20.04 ± 4.03 | 13.29 ± 1.70 |
| Bay of Two Rivers | 14 | -20.06 ± 0.78 | 12.73 ± 2.91 |
| Foul Inlet | 2 | -17.71 ± 0.47 | 14.33 ± 1.48 |

Appendix 18. List of abbreviations used in Chapter Three.

| Sections | Abbreviations | Full meaning |
|---|---|---|
| Fish data | MFW | Mean fish weight |
| | MFL | Mean fish (fork) length |
| | MWS | Mean weight of stomach content |
| | K | Condition factor |
| | Lv | Liver weight |
| | LSI | Liversomatic index |
| | V | Weight of visceral fat |
| | VSI | Visceralfatsomatic index |
| | GSI | Gonadosomatic index |
| | V/G | Ratio of visceral fat to gonad weight |
| Food data | | |
| | %O | Percent frequency occurrence |
| | %N | Percent by number |
| | %V | Percent by volume |
| | IRI | Index of relative importance |
| | %IRI | Percent index of relative importance |
| | 3-D | 3-dimensional graphing |
| | DE | Digestible energy |
| | GE | Gross energy |
| | ME | Metabolizable |
| Stable isotopes data | | |
| | $\delta^{13}C$ | 13Carbon stable isotope ratio |
| | $\delta^{15}N$ | 15N stable isotope ratio |
| | ‰ | Parts per mille |
| Statistics | | |
| | ANOVA | Analysis of variance |
| | MANOVA | Multiple analysis of avriance |
| | CA | Correspondence analysis |
| | S | Significant difference |
| | NS | No significant difference |

Appendix 19. Mean of means (± SD) of fish weight, length and age for the 3 sampling years.

| Time | Weight (g) | Fork length (mm) | Age (Yrs.) |
|---|---|---|---|
| 2002 | 1046.14 ± 531.89 | 420.35 ± 108.33 | 10.50 ± 4.18 |
| 2004 | 1223.47 ± 452.06 | 447.69 ± 88.29 | 10.00 ± 3.32 |
| 2005 | 1646.86 ± 776.21 | 503.61 ± 101.15 | 9.71 ± 2.69 |

Appendix 20. Intra-annual fish length of char by age classes (7, 8 and 9) based on 2002 samples

| | Age 7 (n) | Age 8 (n) | Age 9 (n) | Age 10 |
|---|---|---|---|---|
| Total mean ± SD of fork length (mm) in July | 338.67 ± 81.34 (9) | 389.74 ± 70.80 (19) | 435.80 ± 38.95 (20) | 449.94 ± 53.39 (18) |
| Total mean ± SD of fork length (mm) in August | 374.18 ± 54.0 (56) | 432.99 ± 55.13 (91) | 459.96 ± 56.23 (126) | 473.82 ± 73.90 (147) |
| Percent (%) increase in length | 10% | 11% | 6% | 5% |

Appendix 21. Multiple comparisons based on Bonferroni post-hoc tests among effects (MW, ML, and MWS)* and sample periods

| Dependable variable | Year (a) | Year (b) | Mean Difference (a-b) | Standard Error | Sig (P < 0.05) | Abbrev. |
|---|---|---|---|---|---|---|
| MW | 2002 | 2004 | -101.934 | 199.294 | 1.000 | NS |
| | | 2005 | -948.239 | 210.948 | 0.000 | S |
| | 2004 | 2002 | 101.934 | 199.294 | 1.000 | NS |
| | | 2005 | -846.305 | 218.652 | 0.002 | S |
| | 2005 | 2002 | 948.239 | 210.948 | 0.000 | S |
| | | 2004 | 846.305 | 218.652 | 0.002 | S |
| ML | 2002 | 2004 | -9.219 | 49.356 | 1.000 | NS |
| | | 2005 | -46.626 | 52.242 | 1.000 | NS |
| | 2004 | 2002 | 9.219 | 49.356 | 1.000 | NS |
| | | 2005 | -37.407 | 54.150 | 1.000 | NS |
| | 2005 | 2002 | 46.626 | 52.242 | 1.000 | NS |
| | | 2004 | 37.407 | 54.150 | 1.000 | NS |
| MWS | 2002 | 2004 | 1.255 | 19.070 | 1.000 | NS |
| | | 2005 | -82.331 | 20.185 | 0.001 | S |
| | 2004 | 2002 | -1.255 | 19.070 | 1.000 | NS |
| | | 2005 | -83.586 | 20.923 | 0.001 | S |
| | 2005 | 2002 | 82.331 | 20.185 | 0.001 | S |
| | | 2004 | 83.586 | 20.923 | 0.001 | S |

(*): MW = mean fish weight; ML = mean fish length and MWS = mean weight of stomach contents

Appendix 22. ANOVA results of condition factors for the 3 sampling years.

| Tests | Sum of Squares | df | Mean Square | F-ratio | Sig. | Abbrev. |
|---|---|---|---|---|---|---|
| Between groups | 0.034 | 2 | 0.017 | 0.335 | 0.716 | NS |
| Within groups | 61.355 | 1211 | 0.051 | | | |
| Total | 61.389 | 1213 | | | | |

Appendix 23. Multiple comparisons of condition factors for the 3 sampling years using Bonferroni post-hoc tests.

| Year (a) | Year (b) | Mean Difference (a-b) | Std. Error | Sig. | 95% Confidence Interval | | Abbrev. |
|---|---|---|---|---|---|---|---|
| | | | | | Lower Bound | Upper Bound | |
| 2002 | 2004 | 0.0110 | 0.01468 | 1.000 | -0.0242 | 0.0462 | NS |
| | 2005 | -0.0110 | 0.02605 | 1.000 | -0.0626 | 0.0623 | NS |
| 2004 | 2002 | -0.0111 | 0.01468 | 1.000 | -0.0462 | 0.0242 | NS |
| | 2005 | -0.0111 | 0.02434 | 1.000 | -0.0695 | 0.0472 | NS |
| 2005 | 2002 | 0.0001 | 0.02605 | 1.000 | -0.0623 | 0.0626 | NS |
| | 2004 | 0.0111 | 0.02434 | 1.000 | -0.0472 | 0.0695 | NS |

Appendix 24. Summary of mean ± SD of condition factor (K values) for the 3 sampling years.

| Year | Mean ± SD | n |
|---|---|---|
| 2002 | 1.13 ± 0.24 | 340 |
| 2004 | 1.12 ± 0.22 | 782 |
| 2005 | 1.13 ± 0.21 | 98 |

Appendix 25. Mean ± SD of fish condition data of for the 3 sampling years.

| Year of sampling | Liver weight (g) (n) | Visceral fat weight (V) (g) (n) | LSI (n) | VSI (n) | GSI (n) |
|---|---|---|---|---|---|
| | (470) | (470) | (470) | (470) | (470) |
| 2002 | 22.9 ± 16.3 | 8.70 ± 7.65 | 1.89 ± 1.06 | 0.69 ± 0.47 | 0.82 ± 1.31 |
| | (184) | (184) | (184) | (184) | (184) |
| 2004 | 28.10 ± 17.68 | 15.45 ± 11.36 | 1.96 ± 0.97 | 1.04 ± 0.60 | 0.62 ± 1.18 |
| | (79) | (79) | (79) | (79) | (79) |
| 2005 | 41.21 ± 20.24 | 21.98 ± 13.57 | 2.04 ± 0.47 | 0.95 ± 0.51 | 0.48 ± 0.63 |

Appendix 26. Multiple comparison of MANOVA results based on Bonferroni post-hoc tests among effects (LSI and GSI)* for the 3 sampling periods.

| Dependable variable | Year (a) | Year (b) | Mean Difference (a-b) | Standard Error | Sig | Abbrev. |
|---|---|---|---|---|---|---|
| LSI | 2002 | 2004 | -0.0848 | 0.09075 | 1 | NS |
| | | 2005 | -0.1381 | 0.12797 | 0.843 | NS |
| | 2004 | 2002 | 0.0848 | 0.09075 | 1 | NS |
| | | 2005 | -0.0532 | 0.14108 | 1 | NS |
| | 2005 | 2002 | 0.1381 | 0.12797 | 0.843 | NS |
| | | 2004 | 0.0532 | 0.14108 | 1 | NS |
| GSI | 2002 | 2004 | 0.1859 | 0.11086 | 0.282 | NS |
| | | 2005 | 0.3393 | 0.15632 | 0.091 | NS |
| | 2004 | 2002 | -0.1859 | 0.11086 | 0.282 | NS |
| | | 2005 | 0.1534 | 0.17235 | 1 | NS |
| | 2005 | 2002 | -0.3393 | 0.15632 | 0.091 | NS |
| | | 2004 | -0.1534 | 0.17235 | 1 | NS |

(*): LSI = Liversomatic index and GSI = Gonadosomatic index.

Appendix 27. Summary of one-way ANOVA results of GSI, LSI and VSI* for the 3 sampling years.

| Variable | Time | P-value (Sig.: P < 0.05) | Sig. Abbreviation |
|---|---|---|---|
| GSI | 2002 vs. 2004 | 0.007 | S |
| | 2004 vs. 2005 | 0.138 | NS |
| | 2002 vs. 2005 | 0.452 | NS |
| LSI | 2002 vs. 2004 | 0.071 | NS |
| | 2004 vs. 2005 | 0.466 | NS |
| | 2002 vs. 2005 | 0.025 | S |
| VSI | 2002 vs. 2004 | 0.000 | S |
| | 2004 vs. 2005 | 0.851 | NS |
| | 2002 vs. 2005 | 0.000 | S |

(*): Visceralfatsomatic index

Appendix 28. $\delta^{13}C$ and $\delta^{15}N$ of invertebrates based on 2004 samples

| Food species | $\delta^{13}C$ | $\delta^{15}N$ | C:N |
|---|---|---|---|
| *Themisto libellula* | -20.3 | 10.9 | -0.54 |
| *Thysanoessa inermis* | -19.91 | 11.52 | -0.58 |
| *Thysanoessa raschii* | -19.13 | 10.55 | -0.55 |
| *Mysis mixta* | -18.78 | 10.83 | -0.58 |
| *Mysis oculata* | -18.49 | 11.35 | -0.61 |
| *Gammarus campylops* | -19.32 | 7.04 | -0.36 |
| *Gammarus pulex* | -17.05 | 6.68 | -0.39 |
| *Onesimus littoralis* | -19.31 | 6.72 | -0.35 |

Appendix 29. $\delta^{13}C$ and $\delta^{15}N$ isotope ratios of polar cod based on 2005 samples

| Polar cod ID | $\delta^{13}C$ | $\delta^{15}N$ | C:N | Polar cod weight (g) | Polar cod size (TL) (mm) |
|---|---|---|---|---|---|
| Cod-36 | -21.11 | 12.76 | -0.60 | 60.3 | 200 |
| Cod-37 | -20.82 | 12.97 | -0.62 | 50.6 | 190 |
| Cod-38 | -19.48 | 12.24 | -0.63 | 37.6 | 170 |
| Cod-39 | -22.2 | 13.09 | -0.59 | 10.9 | 94 |
| Cod-40 | -20.87 | 13.35 | -0.64 | 9.9 | 113 |
| Cod-41 | -22.36 | 12.38 | -0.55 | 12.3 | 118 |
| Cod-43 | -20.09 | 11.73 | -0.58 | 14.9 | 115 |
| Cod-44 | -23.18 | 13.45 | -0.58 | 15.9 | 121 |
| Cod-45 | -22.27 | 12.28 | -0.55 | 15.6 | 120 |
| Cod-46 | -20.16 | 11.54 | -0.57 | 10.3 | 105 |
| Cod-47 | -20.55 | 12.01 | -0.58 | 34.9 | 142 |
| Cod-48 | -22.39 | 13.42 | -0.60 | 25.7 | 134 |

Appendix 30. Fractional contribution of the most imporatant diet items to char $\delta^{13}C$ and $\delta^{15}N$ ratios based on 3-source mixing model. Data used for invertebrates were from 2002 and data for polar cod was from 2005 samples.

| Food species | n* | Status | Designation | δJ ($\delta^{13}C$) | δK ($\delta^{15}N$) | *f*A | *f*B | *f*C |
|---|---|---|---|---|---|---|---|---|
| Arctic char | 7 | Consumer | D | -19.87 | 13.04 | | | |
| *Mysis* spp | 2 | Diet | A | -18.63 | 11.09 | 3.000313 | | |
| *Themisto libellula* | 1 | Diet | B | -20.3 | 10.9 | | 23.10314 | |
| Polar cod | 12 | Diet | C | -21.29 | 12.6 | | | -25.1035 |

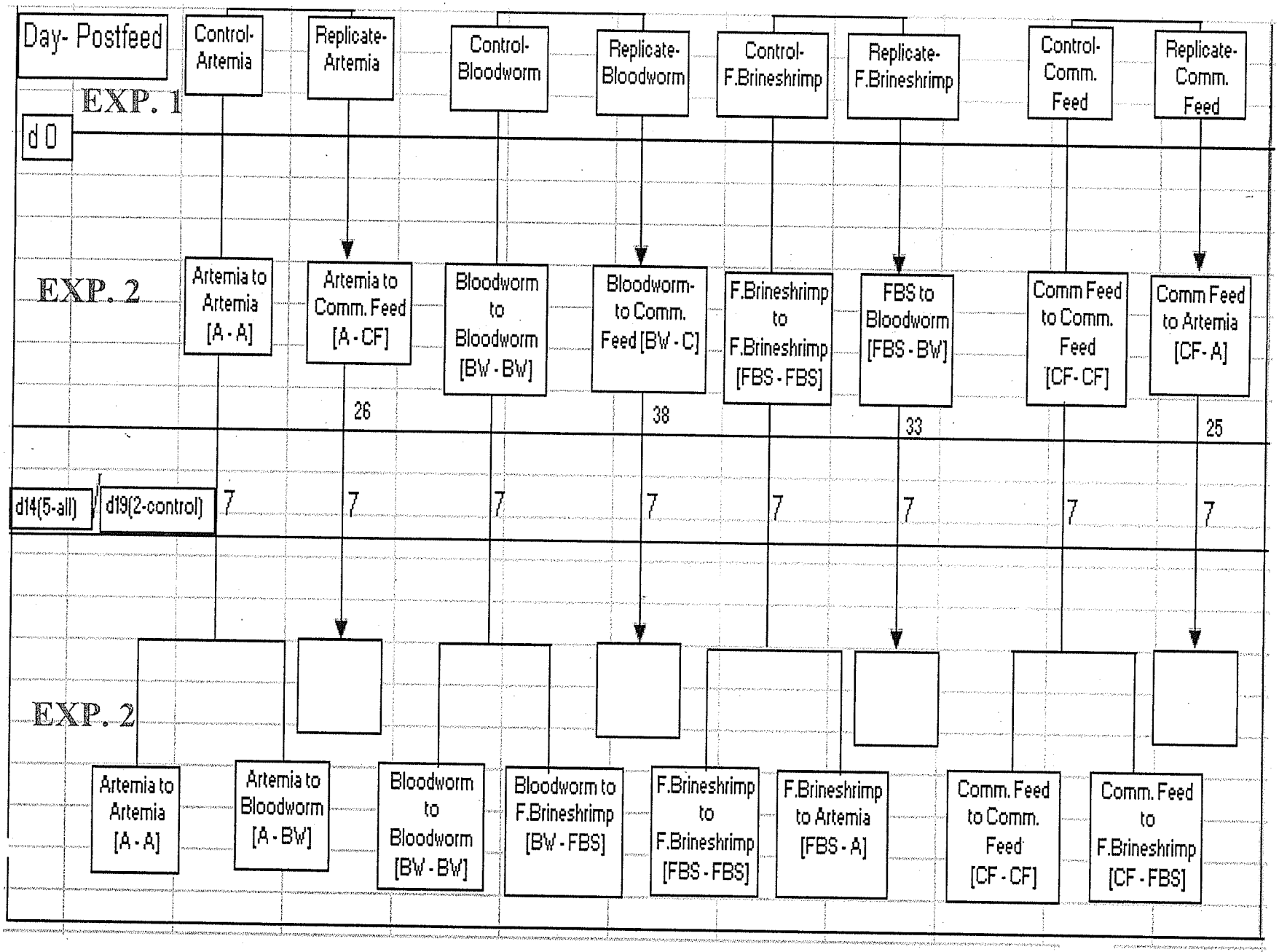
*Mean values were calculated where n > 1; 3-source mixing linear model from Phillips (2001)

Appendix 31. Specific growth rates of char in Experiment 1 (% $day^{-1}$)

| Time (days) | AR | BW | BS | CF |
|---|---|---|---|---|
| 30 | 1.24 | 1 | 1.2 | 1.21 |
| 56 | 1.21 | 1.2 | 1.25 | 1.13 |
| 100* | 1.13 | 1.02 | 1.13 | 1.15 |
| 114 | 1.11 | 0.99 | 1.12 | 1.12 |
| **Mean ± STD** | **1.17 ± 0.06** | **1.05 ± 0.10** | **1.18 ± 0.06** | **1.15 ± 0.04** |

(*): Batch weights

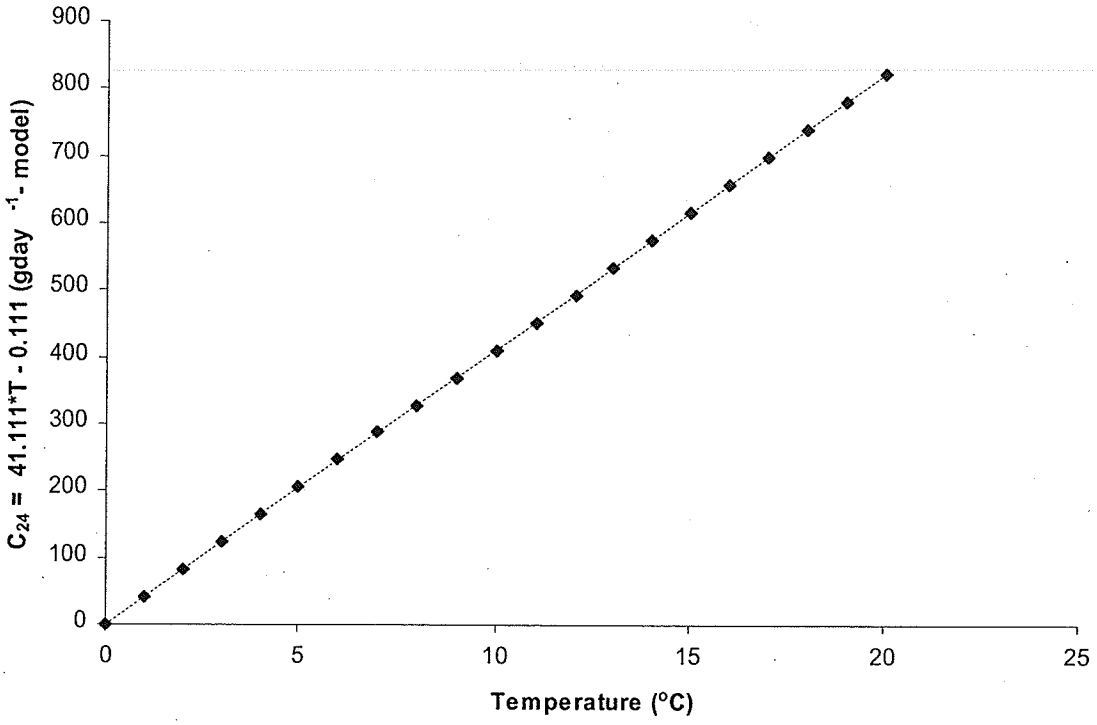
Appendix 32. Flow chart showing the design of experiments 1 and 2. Legend: A = *Artemia* nauplii; BW = Bloodworm; FBS = Frozen brine shrimp and CF = Commercial Feed.


Day- Postfeed
EXP. 1
d 0
Control-Artemia
Replicate-Artemia
Control-Bloodworm
Replicate-Bloodworm
Control-F.Brineshrimp
Replicate-F.Brineshrimp
Control-Comm. Feed
Replicate-Comm. Feed
EXP. 2
Artemia to Artemia [A - A]
Artemia to Comm. Feed [A - CF]
Bloodworm to Bloodworm [BW - BW]
Bloodworm-to Comm. Feed [BW - C]
F.Brineshrimp to F.Brineshrimp [FBS - FBS]
FBS to Bloodworm [FBS - BW]
Comm Feed to Comm. Feed [CF- CF]
Comm Feed to Artemia [CF- A]
26
38
33
25
d14(5-all)
d19(2-control)
7
EXP. 2
Artemia to Artemia [A - A]
Artemia to Bloodworm [A - BW]
Bloodworm to Bloodworm [BW - BW]
Bloodworm to F.Brineshrimp [BW - FBS]
F.Brineshrimp to F.Brineshrimp [FBS - FBS]
F.Brineshrimp to Artemia [FBS - A]
Comm. Feed to Comm. Feed [CF - CF]
Comm. Feed to F.Brineshrimp [CF - FBS]

Appendix 33. Mean ± SD ratio of weight of stomach contents to fish weight of small and large char.

| Char group | n | Fork length (mm) | Fish weight (g) | Weight of stomach contents (g) | Ratio of weight *Stc/Fw |
|---|---|---|---|---|---|
| Small char | 4 | 68.5 ± 8.39 | 3.33 ± 1.16 | 0.2 ± 0.06 | 0.06 ± 0.022 |
| Large | 2 | 132 ± 31.11 | 24.45 ± 14.78 | 1.25 ± 0.29 | 0.06 ± 0.023 |

(*): Stc = stomach contents and Fw = fish weight




Appendix 34. Hypothetical estimation of mean amount of diet consumption per 1 °C rise/decline in temperature. Legend: *x*-axis = temperature (°C) and *y*-axis = mean weight of stomach content (g)/day.