AN ABSTRACT OF THE THESIS OF

Bjarni Jonsson for the degree of Master of Science in Fisheries Science presented on October 15, 1996. Title: Polymorphic Segregation in Arctic Charr, *Salvelinus Alpinus* (L.) from Lake Vatnshlidarvatn, Northern Iceland.

Abstract approved:

Redacted for Privacy

Douglas F. Markle

I studied the occurence of two sympatric morphs of arctic charr, Salvelinus alpinus (L.) in Vatnshlidarvatn, a small shallow lake in NW Iceland. The arctic charr were subjectively distinguished by colour and appearance as brown morph or silver morph, and measured for morphological and life history characters. The study revealed the presence of two growth forms represented by the two morphs that differed in age and size at sexual maturation, reproductive investment, and time and place of spawning. The morphs differed significantly in gill raker number and morphometric characters related to manoeuvrability and cruising ability. Morphological segregation was established early in life and is most readily explained as developmental heterochrony. Both morphs were benthivorous, but could be segregated as diet specialist and generalist, with diet segregation being important only when food (especially the benthic crustacean Eurycercus spp.) was scarce, The occurrence of one abundant food resource, and lack of interspecific competition (no other fish species are present) may explain the different feeding strategies. The presence of "empty" niche should induce variability and divergence in morphology and life history to occupy available niche space.

Polymorphic Segregation in Arctic Charr Salvelinus Alpinus (L.) From Lake

Vatnshlidarvatn, Northern Iceland.

by

Bjarni Jonsson

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented October 15, 1996
Commencement June 1997

Master of Science thesis of Bjarni Jonsson presented on October 15, 1996

APPROVED:

Redacted for Privacy

Major Professor, representing Fisheries Science

Redacted for Privacy

Head or Chair of Department of Fisheries and Wildlife

Redacted for Privacy

Dean of Graduate School

I understand that my thesis will become part of the permanent collecton of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Redacted for Privacy

Bjarni Jonsson, Author

ACKNOWLEDGMENT

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF TABLES

Dedication

This thesis is dedicated to my loving daughter, Kristin Kolka.

Polymorphic Segregation in Arctic Charr, Salvelinus Alpinus (L.)
From Lake Vatnshlidarvatn, Northern Iceland

INTRODUCTION

Resource polymorphism, the occurrence of discrete intraspecific morphs displaying differential niche use, is found in various vertebrate species (Skúlason and Smith, 1995). Intraspecific morphs can arise through the utilization of different niches associated with variable habitats and diets (Malmquist et al. 1992, Schluter and McPhail 1992, Robinson et al. 1993, Smith 1993, Day et al. 1994, Snorrason et al. 1994). Divergence of sympatric forms can be facilitated by an absence of competition for these resources from other species (Schluter 1988, Robinson and Wilson 1994). Such resource polymorphism in fish is commonly associated with the presence of discrete benthic and pelagic habitats in lakes. Examples include whitefish (Coregonus and Prosopium spp.), threespine sticklebacks (Gasterosteus aculeatus), sunfishes (Lepomis gibbosus and L. macrochirus), and arctic charr (Salvelinus alpinus) (Skúlason and Smith 1995). The occurrence of sympatric morphs of arctic charr, like many other salmonids, is also known to be related to piscivory and/or cannibalism, and anadromy versus resident life history (Griffiths 1994, Reist et al. 1995, Skúlason and Smith 1995).

Arctic charr, with a northern circumpolar distribution, exhibits great variability in life history, both within and among localities (Johnson 1980, Nordeng 1983). Differences are seen in growth, age and size at sexual maturation, fecundity, and egg size (Jonsson and Hindar 1982, Jonsson et al. 1988, Hindar and Jonsson 1993, Griffiths 1994, Skúlason et al. in press). These life history differences are greatly influenced by feeding behavior and performance (Sparholt 1985, Malmquist et al. 1992, Griffiths 1994). Differences in diet of sympatric morphs are usually characterized by benthivory and planktivory. Morphs can also differ in habitats in large and physically complex water bodies, and due to migration (Griffiths 1994,

Smith and Skúlason in press). Furthermore, seasonality and habitat diversity can ultimately favor the evolution of reproductive segregation (Skúlason et al. 1989b). Thus, resource polymorphism can have important implications for population segregation and speciation (Rice and Hostert 1993, Skúlason and Smith 1995).

Considering the numerous examples of coexisting forms of the species, distinct morphological differentiation among sympatric morphs of arctic charr seems rare (Snorrason et al. 1994). The following studies have reported morphological segregation between forms. In the landlocked lake Thingvallavatn, Iceland, differences in morphology have been observed among four sympatric morphs of arctic charr, (Skúlason, Noakes and Snorrason 1989, Snorrason et al. 1994). In Loch Rannoch, Scotland, three morphs co-occur (Gardner, Walker and Greer 1988, C. Adams in preparation), and in Lake Hazen, Elsmere Island two sympatric morphs are found (Reist et al. 1995).

It is important to investigate ontogenetic trends in shape, for instance to see if adult forms are diverging or converging (Griffiths 1994). Forms may also exhibit differential ontogenetic trajectories in shape early in life, and subsequently maintain their differences by parallel change in shape (Strauss and Fuiman 1985). Bimodal size distribution of arctic charr has been identified in several Icelandic lakes (Skúlason et al. 1992), including the lake Vatnshlidarvatn in NW-Iceland (Tómasson 1987). With the exception of Thingvallavatn, the ecology of such populations is mostly unexplored (Snorrason et al. 1994).

Vatnshlidarvatn is in many ways different from other lakes where sympatric forms of arctic charr have been investigated (Jonsson and Hindar 1982, Hindar and Jonsson, 1982, Johnson 1983, Sparholt 1985, Hindar, Ryman and Stáhl 1986, Skúlason et al. 1989, Svedäng 1990, Hindar and Jonsson 1993, Snorrason et al. 1994, Reist et al. 1995). The lake is small (70 ha), shallow and physically simple, and the only fish present is arctic charr, a common occurrence in arctic lakes. However, compared with arctic lakes, Vatnshlidarvatn is in a warmer climate and is more productive. Thus, this relatively simple lake system, provides an interesting setting for studying evolution of phenotypic segregation.

My objectives are:

First, I test the hypothesis that there are two separate growth forms of arctic charr in Vatnshlidarvatn.

Second, I test if the two forms, subjectively distinguished as brown and silver forms, represent morphologically distinct morphs of arctic charr in the lake.

Thirdly, I test if the brown and silver forms differ in food and habitat use, and if such differences are associated with differences in morphology and life history.

Fourth, I test if segregation of forms is correlated with temporal and/or spatial differences in spawning.

I then relate morphological diversification with ontogenetic trends in shape, and discuss functional, ecological and evolutionary implications of my results comparing the unique characteristics of Vatnshlidarvatn to other systems.

CHAPTER 1

Polymorphic Segregation in Arctic Charr, *Salvelinus Alpinus* (L.)
From a Small Lake, Northern Iceland

Bjarni Jonsson

Introduction

Resource polymorphism, the occurrence of discrete intraspecific morphs displaying differential niche use, is found in various vertebrate species (Skúlason and Smith 1995). Due to their great versatility, teleost fish are able to exploit fluctuating and diverse trophic resources (Liem 1984). Trophic diversification is thought to be important in inducing diverse morphologies within and among species of fish (Echelle and Kornfield 1984).

The arctic charr (Salvelinus alpinus L.), a salmonid fish, has a northern circumpolar distribution, and can be anadromous or residential (Nyman, Hammar and Gydemo 1981, Snorrason et al. 1994). It is frequently found as two or three coexisting forms of different size (Nordeng 1983, Griffiths 1995). Life history of arctic charr is variable, both within and among localities (Hindar and Jonsson 1993, Griffiths 1994), and is characterized by phenotypic plasticity (Nordeng 1983, Hindar and Jonsson 1993). Phenotypic plasticity enables arctic charr to utilize a wide variety of resource types (Skúlason and Smith 1995).

Considering the numerous examples of coexisting forms of the species, distinct morphological differentiation among sympatric morphs of arctic charr is rare (Snorrason et al. 1994). In Lake Thingvallavatn, Iceland, differences in morphology have been observed among four sympatric morphs of arctic charr, (Skúlason, Noakes and Snorrason 1989, Snorrason et al. 1994). In Loch Rannoch, Scotland, three morphs co-occur (Gardner, Walker and Greer 1988, C. Adams in preparation), and in Lake Hazen, Elsmere Island two sympatric morphs are found (Reist et al. 1995).

Some of the morphological studies have failed to take into account allometric changes associated with increasing body size (Griffiths 1994), and age. However, it is important to investigate ontogenetic trends in shape, for instance to see if adult forms are diverging or converging. Forms may also exhibit differential ontogenetic trajectories in shape early in life, and then maintain their differences through the remainder of the ontogeny, by parallel change in shape (Strauss and Famine 1985).

Bimodal size distribution of arctic charr has been identified in several Icelandic lakes (Skúlason et al. 1992), including the lake Vatnshlidarvatn in NW-Iceland (Tómasson 1987). With the exception of Thingvallavatn, the ecology of such populations is mostly unexplored (Snorrason et al. 1994).

Vatnshlidarvatn is in many ways different from other lakes where sympatric forms of arctic charr have been investigated (Jonsson and Hindar 1982, Hindar and Jonsson 1982, Johnson 1983, Sparholt 1985, Hindar, Ryman and Ståhl 1986, Skúlason et al. 1989, Svedäng 1990, Hindar and Jonsson 1993, Snorrason et al. 1994, Reist et al. 1995). The lake is small (70 ha), shallow and physically simple, and the only fish present is arctic charr, a common occurrence in arctic lakes. However, compared with arctic lakes, Vatnshlidarvatn is in a warmer climate and has more productive food resources. Thus, this relatively simple lake system provides an interesting setting for studying evolution of phenotypic segregation.

The study has two objectives:

First, I test the hypothesis that there are two separate growth forms of arctic charr in Vatnshlidarvatn.

Second, I test if there are two morphologically distinct morphs of arctic charr in the lake.

I then relate morphological diversification with ontogenetic trends in shape, and discuss functional and evolutionary implications of my results.

Methods

Study Site

Vatnshlidarvatn (65° N, 19° W) is a shallow 70 ha lake (mean depth 2-3 m, maximum depth 5-6 m, length 1.5 km, width 0.55 km). The bottom is mainly mud, with gravel .close to shore and near the outlet of the lake. The submerged vegetation is

characterized by patches of eelgrass (Myriophyllum spp.). The lake is in a basaltic area at an elevation of 280 m, and is a part of a runoff system, with shallow lakes and wetlands near the origin. The lake has one major inlet and one outlet and is additionally fed by short spring-fed creeks (Fig. 1.1). Water temperature follows seasonal air temperature (mean air temperature in January -5°C, and July 7°C) and can range from 0 - 15 C°. The lake is usually ice-covered from October/November to April/May. Water conductivity is 161 μS/cm (at 25C°), and pH 8.50 (in August 1994).

The lake was formed after the last Pleistocene glaciation, and has been landlocked by a waterfall for the last 6000-8000 years. Arctic charr is the only fish species present in the lake.

Sampling

Arctic charr (n = 848) were sampled in the lake on August 16 1994 with 2x10 bottom gill nets (panel sizes: 1.5 x 25 m, and mesh sizes from 10 mm - 52 mm bar mesh) in two 250 m long series with the mesh sizes placed at random. Gillnetting was done during night for 10 hours. Sub- sample for morphometric measurements was taken by randomly picking 10 fish at a time from each of the gillnets for five rounds to obtain a sample of 492 arctic charr. Most gillnets captured less than 50 fish. The whole sample is used for determination of sexual maturity.

Fork-length on each fish is measured to the nearest 0.1 cm. Degree of sexual maturity is determined according to Dahl (1917). Age is determined from otolith surface analysis (Barber and McFarlane 1987).
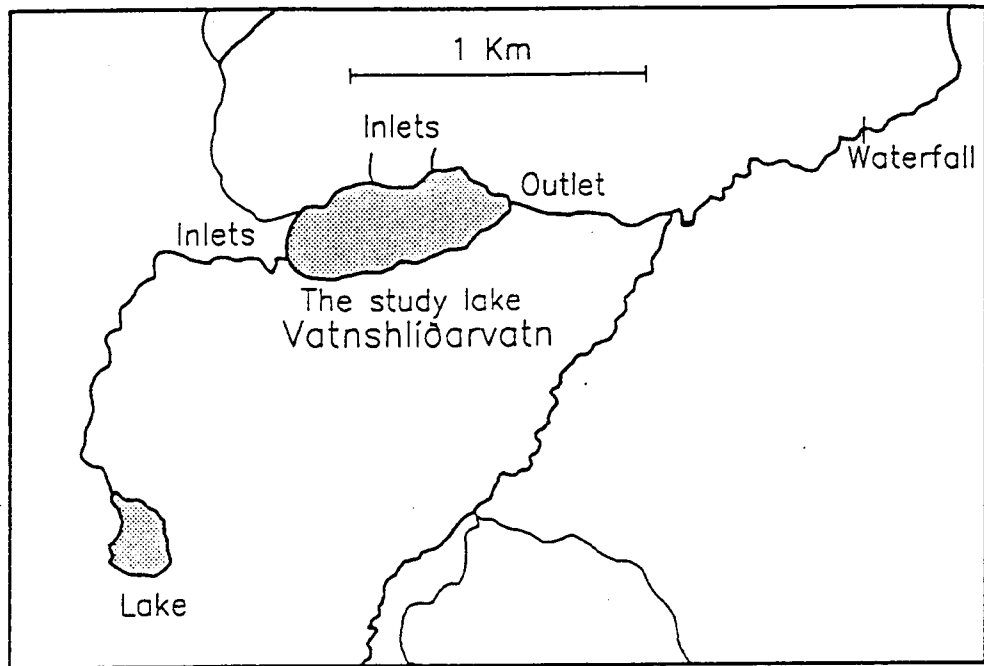
Figure 1.1. Study site, Lake Vatnshlidarvatn and its tributaries.

Classification

Arctic charr are pre-classified, by eye into either "brown type" or "silver type". The following criteria is used:

Brown type have stocky body, no silvery color on sides, parr marks are sometimes present, there is melanization on operculum and usually on ventral sides of lower jaw, body color is light brownish, and sexually mature individuals have dark bluish back. Silver type, has fusiform body, no parr marks, dark grayish to dark bluish back, silvery sides; melanization on operculum is absent, but sometimes occurs on ventral sides of lower jaw on sexually mature fish. Fish that do not meet these criteria (9% of the sample) are classified as "unknown".

Morphometric and Meristic Measurements

Morphometric characters (adapted from Reist et al. 1995; Fig. 1.2) were measured on 492 fish (left side) to the nearest 0.1 mm with vernier calipers. Measurements made parallel to the longitudinal body axis are: 1) Preorbital length (POL) - the distance from the anteriormost part of the snout to the anterior margin of eye, 2) orbital length (OOL) - the distance from the anterior to the posterior margin of the eye, 3) head length (HL) - the distance from the anteriormost part of the snout to posterior bony margin of the operculum, 4) length of anal fin base (ANL) - the distance from the origin to the insertion of anal fin, 5) caudal penduncle length (CPL) - the distance from the insertion of the anal fin to the origin of the caudal fin rays on the hypural plate (corresponds to the end of the fleshy portion of the body), 6) caudal fin length (CFL) - the distance from the last unmodified vertebrae to the posteriormost tip of compressed caudal fin lobes, 7) Fork depth of caudal fin (FLT) - fork length minus standard length. Measurements made parallel to the dorso- ventral body axis are: 8) Head depth (HDD) - the distance from the bottom of the jaw to the top of the head centered mid-pupil with mouth held closed, 9) Interorbital width (IOW) - the
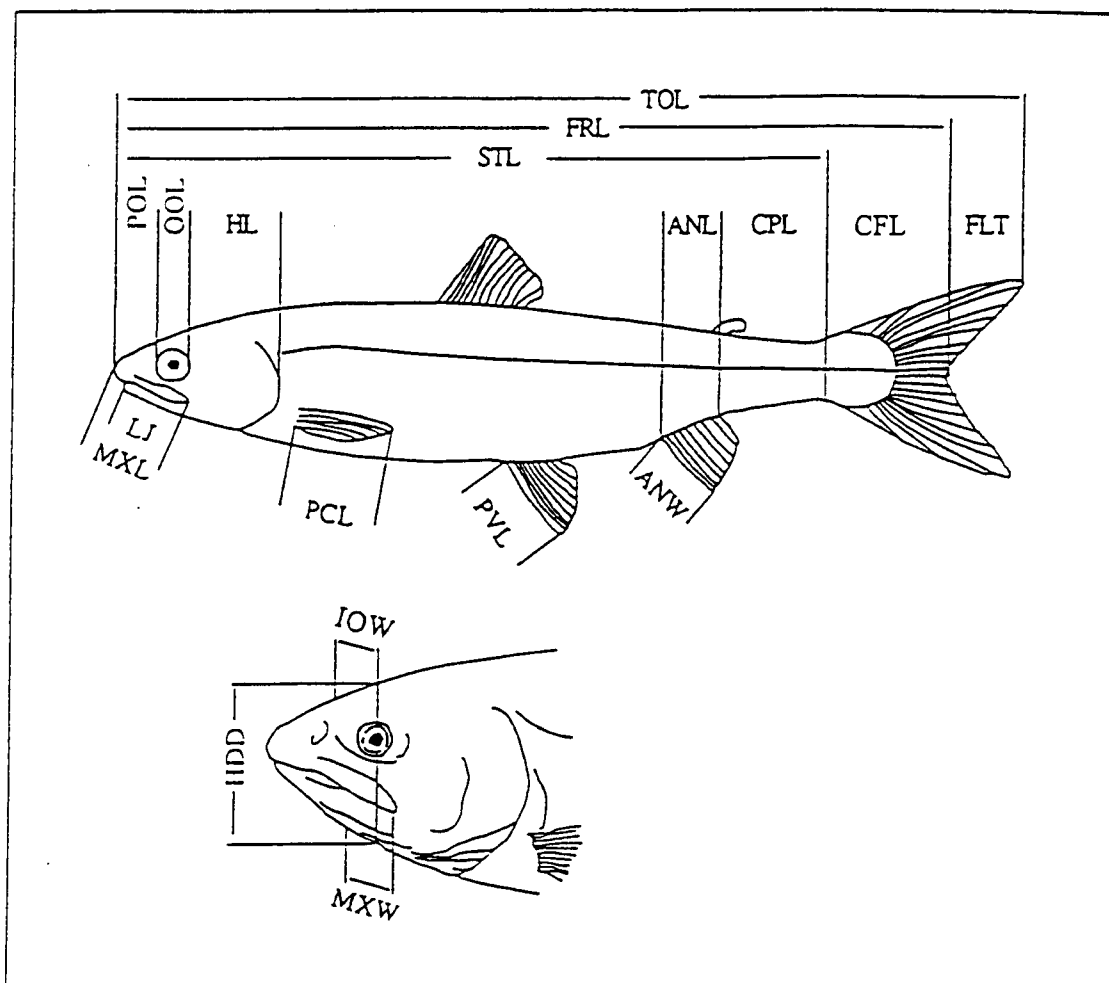
Figure 1.2. Illustration of morphological measurements taken on the left side of each specimen of arctic charr from Vatnshlidarvatn, Iceland. See text for explanations.

distance across the bony margins between the orbits, 10) caudal penduncle depth (CPD) - the depth of the caudal penduncle, anterior to the origin of the caudal fin rays on the hypural plate. The remaining variables are measured following the axis of the body part: 11) Length of upper jaw (MXL) - tip of snout to end of maxilla, 12) length of lower jaw (LJ) - tip of lower jaw to end of maxilla, measured with closed mouth, 13) maxillary width (MXW) - widest distance across the maxilla, 14) pectoral fin length (PCL), 15) pelvic fin length (PVL), 16) length of anal fin (ANW). Fins are measured from the origin of the fin to the tip of the longest ray.

Standard length (STL) is measured to the nearest 1.0 mm - that is the distance from the anteriormost part of the snout to the end of the caudal penduncle, and total length (TOL) as the distance from the anteriormost part of the snout to the posteriormost tip of compressed caudal fin lobes. Body depth is not measured as it would be confounded with the subjective classification of the types.

Measurement precision is verified by blind repeated measurements on 30 specimens. The measurement error varies from 0.3-3.9% depending on the size of the morphometric character involved.

Gill rakers are counted on the first left gill arch of the fish.

Statistical Analysis of Morphological Data

Morphometric data are analyzed using both univariate and multivariate statistical procedures. Prior to analysis, raw measurements (except standard length) are size-adjusted by regression technique, computation of residuals from the regression of untransformed morphological variables on standard length (Reist 1985). This method approaches size-free shape variables. Univariate testing consists of comparison of mean values using analysis of variance ANOVA.

The pattern of morphological variation is analyzed using Principal Component Analysis PCA, and Canonical Discriminant Analysis CDA, (Pimentel 1979). Principal components are derived from the variance-covariance matrix, and the canonical

correlation's are computed using the total variability. PCA reduces and summarizes multivariate trends in shape variation to a set of statistically independent variables (PC axes). CDA derives several independent linear combination of the original variables that have the highest possible multiple correlation with the groups which are being investigated. CDA provides a test of *a priori* designation to types. In order to include "unknowns" in the PCA results, the residual standardization involves three groups; brown type (n=166), silver type (n=281), and unknowns (n=45). In the residual standardization for CDA results, unknowns are excluded.

Two methods are employed for the estimation of bivariate allometric coefficients; the regression method, where allometric coefficients are calculated as slopes of least squares regression lines of ln-transformed variables on ln-standard length (sensu Meyer, 1990), and the covariance-ratio method, which is independent of assumptions on the ratio (denoted by λ) of the error variance of y to that of x (Kuhry and Marcus 1977). Data on a third, so-called "instrumental" variable is required for the estimation of the covariance ratio (here, head length, HL). T-tests for homogeneity of slopes are made according to Sokal and Rohlf (1981).

For the estimation of multivariate allometric coefficients, PCA's are computed on each of the two types and sexes separately from the covariance matrixes on ln transformed data (Jolicoeur 1963). The multivariate coefficients are determined according to Shea (1985), as ratios of the first component loading of the other variables relative to that of standard length. Standard length is included in the analysis, in order to make the multivariate and bivariate allometric coefficients comparable.

Results

Growth and Sexual Maturity

There are two growth forms of arctic charr in Vatnshlídarvatn (Fig. 1.3). Silver type charr continues to grow relatively fast until eight years of age, after which they grow slower, but the growth of the brown type charr decreases after they are six years of age. The observed maximum age of the brown type is twelve years, but silver type charr has the maximum observed age of nine years. The silver type grows faster than the brown type after two years old, and there is little overlap in size of types after four years of age.

Almost all males and most females of the brown type are sexually mature at two years of age. Some males mature at one year. However, 50% sexual maturity of male and female silver type charr is not attained until seven and five years of age respectively (Fig. 1.4).

Univariate Results

There are significant differences at the 0.003 level among the sexes of the brown and silver type for most adjusted character means (Table 1.1). The greatest differences observed among both sexes, are in caudal penduncle length, CPL, the paired fins, PCL and PVL, and anal fin width, ANW (Table 1.1). There are significant differences between many adjusted character means of the two types for five year old (5+) males and females alone, although caudal penduncle length, CPL and anal fin width, ANW, of the males appear to be linked with the development of sexual maturity (silver type become sexually mature at five years of age). Differences between adjusted means of the sexes combined were highly significant for all characters except fork depth of
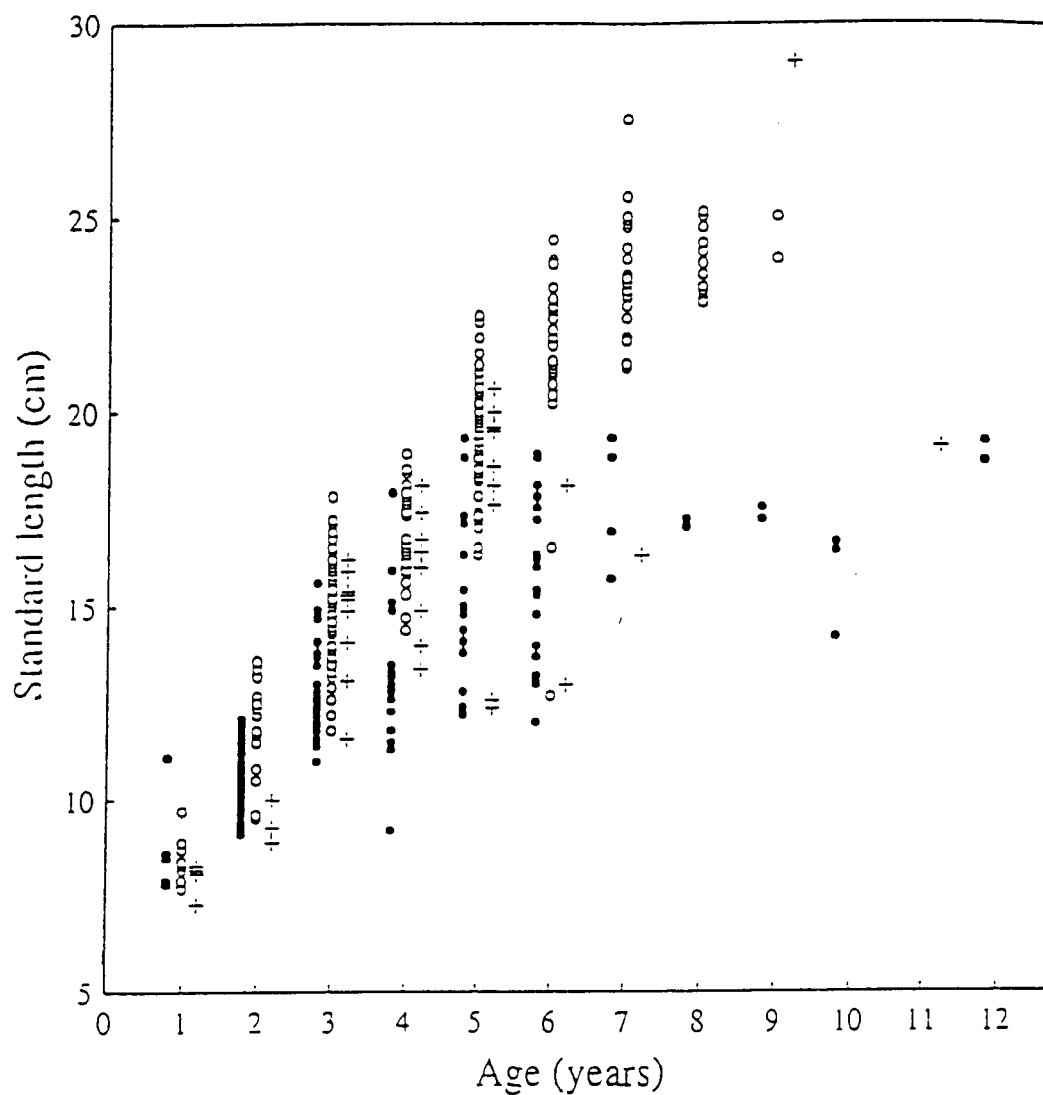
Figure 1.3 Length - age relationships of arctic charr from Vatnshlidarvatn, Iceland. Triangles are males and circles females. Brown type shaded symbols and silver type open symbols. Crosses are unknown arctic charr.
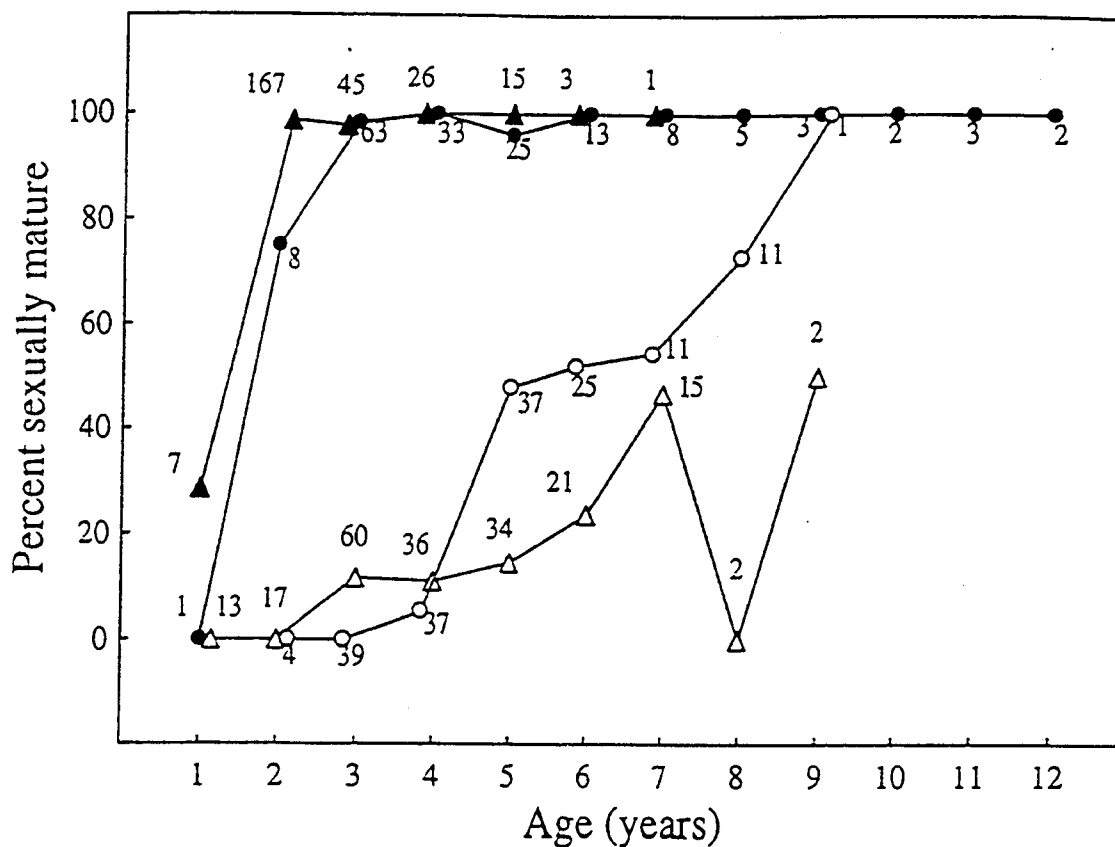
Figure 1.4. Percentage of sexually mature male (triangles) and female (circles) arctic charr from Vatnshlidarvatn, Iceland. Brown type shaded symbols and silver type open symbols. Male sample size is given above symbols and female sample size below symbols.

TABLE 1.1 Difference between least - square means (LSMean) among all male and female brown and silver types, estimated from the common - within - groups regression lines of the variable against standard length. ANOVA tests for differences between adjusted means of brown versus silver type, among all males, five year old (5+) males, all females, Five year old (5+) females, and between types of the sexes combined. Differences are considered significant at the 0.003 level (16 tests, Bonferoni adjustment) No significant differences in allometric slopes are observed between types of either sex at the 0.05 level

Trait[a]	LSMean Brown – Silver	Males All $F_{1,242}$	P	5+ $F_{1,77}$	P	LSMean Brown – Silver	Females All $F_{1,200}$	P	5+ $F_{1,116}$	P	Males and female All $F_{1,359}$	P
POL	0.041	18.41	< 0.001	16.94	< 0.001	0.029	8.50	0.004	3.23	0.074	9.93	< 0.001
OOL	0.028	11.98	< 0.001	0.00	0.992	0.031	12.05	< 0.001	1.41	0.237	11.59	< 0.001
IIL	0.030	41.63	< 0.001	10.54	0.002	0.012	7.09	0.008	1.34	0.249	14.47	< 0.001
MXL	0.057	59.32	< 0.001	18.20	< 0.001	0.026	15.28	< 0.001	7.77	0.006	21.44	< 0.001
LJ	0.060	56.16	< 0.001	12.39	< 0.001	0.023	12.29	< 0.001	5.49	0.020	16.19	< 0.001
HDD	0.048	33.04	< 0.001	5.90	0.017	0.036	32.20	< 0.001	7.84	0.006	29.16	< 0.001
MXW	0.066	17.94	< 0.001	4.15	0.045	− 0.008	0.55	0.460	1.80	0.183	6.70	0.001
IOW	0.050	48.48	< 0.001	14.44	< 0.001	0.046	38.77	< 0.001	7.33	0.008	33.72	< 0.001
PCL	0.082	111.87	< 0.001	20.06	< 0.001	0.053	47.72	< 0.001	8.80	0.004	56.33	< 0.001
PVL	0.087	90.66	< 0.001	16.94	< 0.001	0.049	32.77	< 0.001	8.78	0.004	42.70	< 0.001
ANL	0.067	55.59	< 0.001	10.70	0.002	0.035	15.09	< 0.001	6.92	0.010	24.40	< 0.001
ANW	0.107	65.72	< 0.001	2.39	0.126	0.056	27.63	< 0.001	5.16	0.025	29.17	< 0.001
CPL	− 0.132	77.67	< 0.001	3.41	0.069	− 0.147	84.09	< 0.001	16.21	< 0.001	70.99	< 0.001
CPD	0.042	30.96	< 0.001	4.48	0.038	0.012	1.81	0.180	1.17	0.282	11.44	< 0.001
CFL	− 0.003	0.13	0.722	0.42	0.517	− 0.043	18.90	< 0.001	20.99	< 0.001	9.15	< 0.001
FLT	0.020	1.56	0.212	0.03	0.874	0.043	4.11	0.044	1.66	0.200	5.59	0.004

[a] For key to abbreviations, see legend to Fig. 1.2

caudal fin, FLT (Table 1.1). Adjusted means for male and female brown type are higher than means of the corresponding sex of the silver type, for all body measurements except two, caudal peduncle length, CPL, and caudal fin length, CFL.

PCA Results

The residual standardization is efficient in removing size differences between types, significant correlation is not indicated between any principal components and standard length ($p > 0.05$). Principal component one (PC1) accounts for 40% of the variation and has a negative loading for caudal peduncle length and positive loading for all other characters (Table 1.2). Differences in mean scores of individuals between types is highly significant (pooled variances t test of PC1: $t = 10.823$, $Df = 445$, $p < 0.001$). Principal component two (PC2) accounts for 9.4% of the variation and has high positive loading for caudal fin length and caudal peduncle length; and negative loading for orbital length and anal fin width (Table 1.2). Between group differences in mean individual scores is highly significant (pooled variances t test of PC2: $t = -8.523$, $Df = 445$, $p < 0.001$).

Examination of the bivariate plots of PC1 and PC2 scores reveals grouping with respect to *a priori* designation of types (Fig. 1.5). Although considerable overlap is evident, brown type charr tend to score positively on PC1 and negatively on PC2. Silver type charr tend to score negatively on PC1 and positively on PC2. Unknown individuals overlap with both types (Fig. 1.5).

Males of both type tend to score higher than females on both PC1 and PC2 (Fig. 1.5). Mean scores for males in various age classes are also better separated on PC1 than mean scores for females, but scores for females are more widely distributed on PC2 (Fig. 1.6a, b).

Significant age trends in scores on PC1 and PC2 are indicated from linear regression ($p < 0.001$). However, despite this age effect, the brown and silver type charr are relatively well separated on means plots for age classes on the first two

TABLE 1.2 Loadings of the first two principal components (PC), total canonical structure (TCS) and within standardized canonical coefficients (SCC) from the canonical discriminant analysis.

Trait[a]	PC1	PC2	TCS	SCC
POL	0.699	0.272	0.326	0.004
OOL	0.242	− 0.474	0.327	0.031
HL	0.768	0.181	0.399	0.030
MXL	0.865	0.133	0.473	0.003
LJ	0.833	0.155	0.410	− 0.166
HDD	0.730	− 0.079	0.530	0.051
MXW	0.401	0.027	0.236	0.019
IOW	0.777	− 0.021	0.590	0.185
PCL	0.812	− 0.017	0.735	0.537
PVL	0.831	− 0.011	0.641	0.013
ANL	0.680	0.008	0.542	0.222
ANW	0.410	− 0.453	0.542	0.000
CPL	− 0.409	0.566	− 0.790	− 0.540
CPD	0.416	− 0.269	0.280	− 0.009
CFL	0.084	0.694	− 0.327	− 0.287
FLT	0.437	0.210	0.208	− 0.023
Eigenvalue	6.395	1.504		0.577

[a] For key to abbreviations, see legend to Fig. 1.2
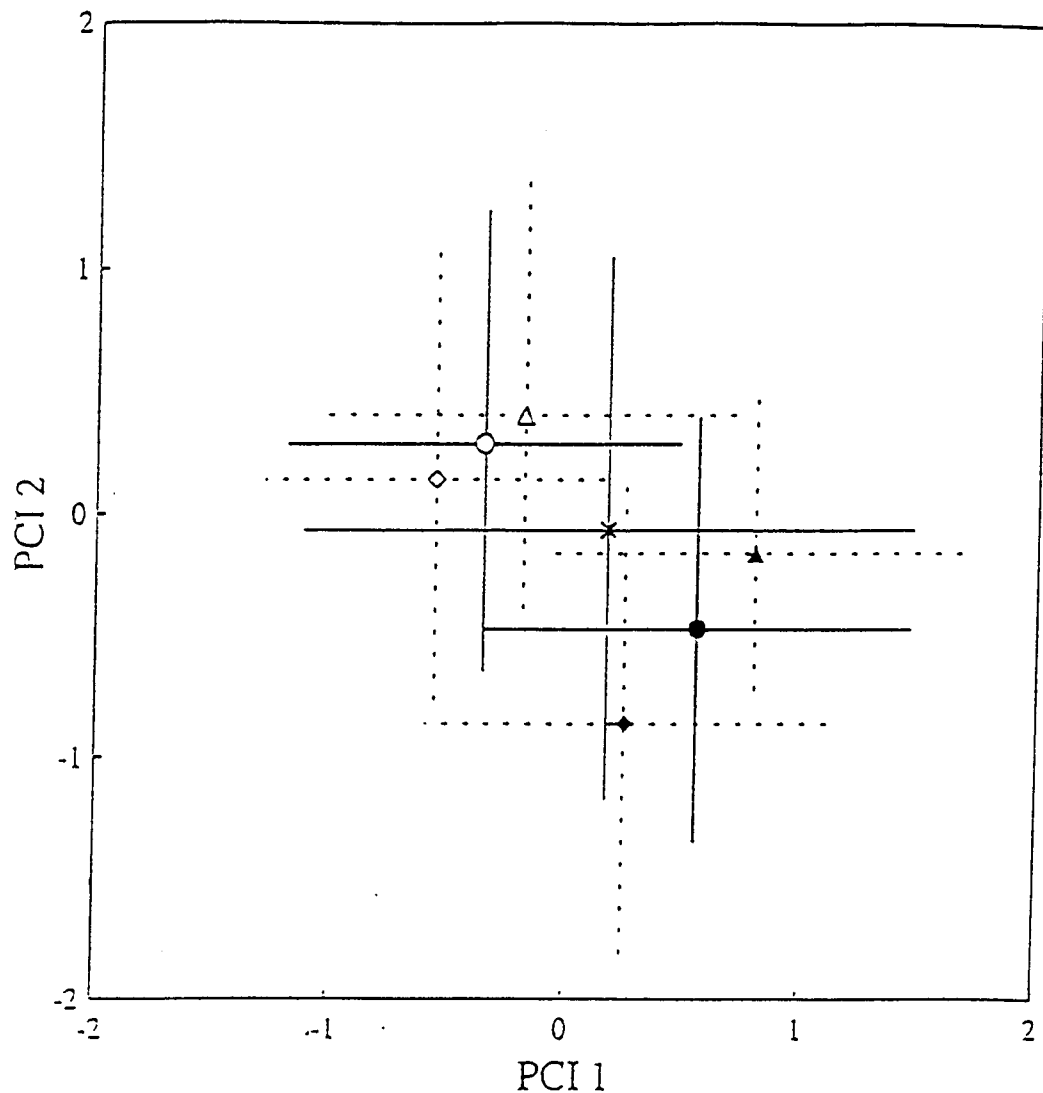
Figure 1.5. Plot of mean scores with standard deviations (1 SD) from between group PCAs, based on a variance-covariance matrix. Multivariate analysis of 16 mensural characters, size adjusted by regression technique, computation of residuals from the regression of untransformed morphological variables on standard length (STL). Groups are, brown type (●), silver type (○), and unknown (X) arctic charr from Vatnshlidarvatn, Iceland. Mean scores for sexes also shown sepparately on the plot, triangles, males, boxes, females.

components. The oldest silver type and the youngest brown type charr are the age classes of both sexes that tend to overlap (Fig. 1.6a, b).

CDA Results

Canonical discriminant analysis, indicates that the two types are significantly different in morphology (Wilks's lamda = 0.634, $F_{15,431}$ = 16.6, p< 0.001).

Pooled within canonical coefficients clearly show discrimination contrast in caudal penduncle length versus pectoral fin length (Table 1.2). The distribution of canonical scores for the silver type is positively skewed and is wider than the distribution of the scores for the brown type (Fig. 1.7). *A posteriori* classification accuracy is good; 86% and 76% of the brown and silver type charr are correctly classified respectively. Both types show trends of higher scores with increasing age. The "misclassified" fish, 43 females and 45 males, are mostly young brown type and the oldest silver type fish (Fig. 1.8), which have overlapping shape scores in PCA (Fig. 1.6a, b).

Gill Rakers

The silver and brown type charr differ significantly in gill raker numbers with the mean numbers of 22.2 and 23.1 respectively ($F_{2,488}$ = 13.3 p<0.001). No significant correlation is observed between gill rakers and sex or size of either type.
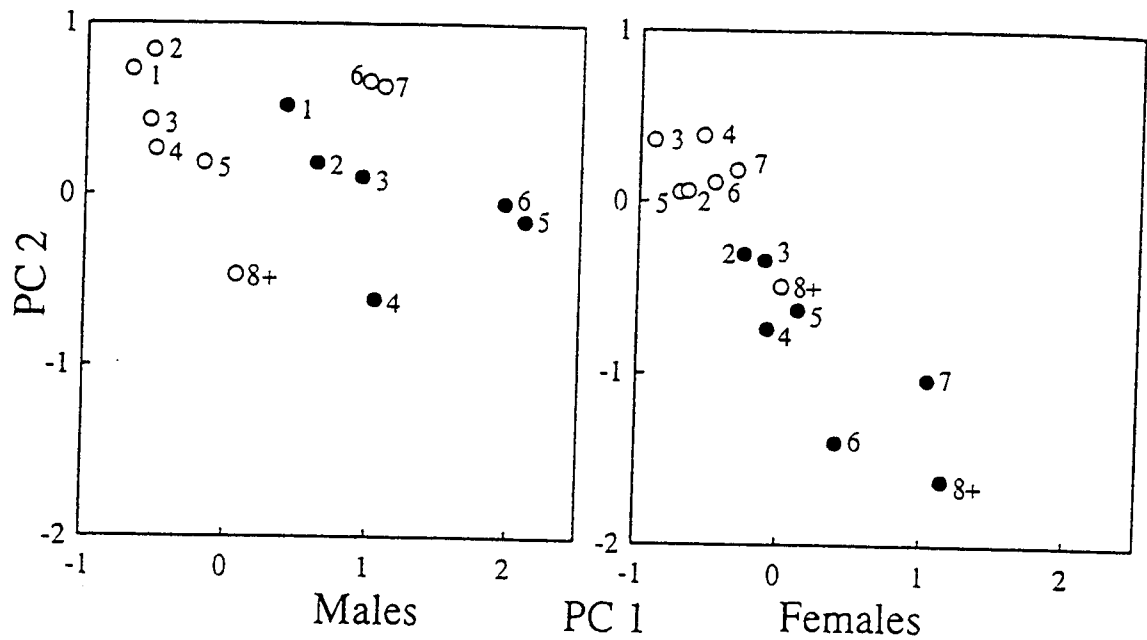
Figure 1.6a, b. Plot of mean scores from between group PCAs, based on a variance-covariance matrix. Multivariate analysis of 16 mensural characters, size adjusted by regression technique, computation of residuals from the regression of untransformed morphological variables on standard length (STL). Means for age groups of male and female arctic charr from Vatnshlidarvatn, Iceland. Brown type closed symbols, silver type open symbols (1 – 7 denote one year to seven year old fish, 8+ are fish eight years and older combined).
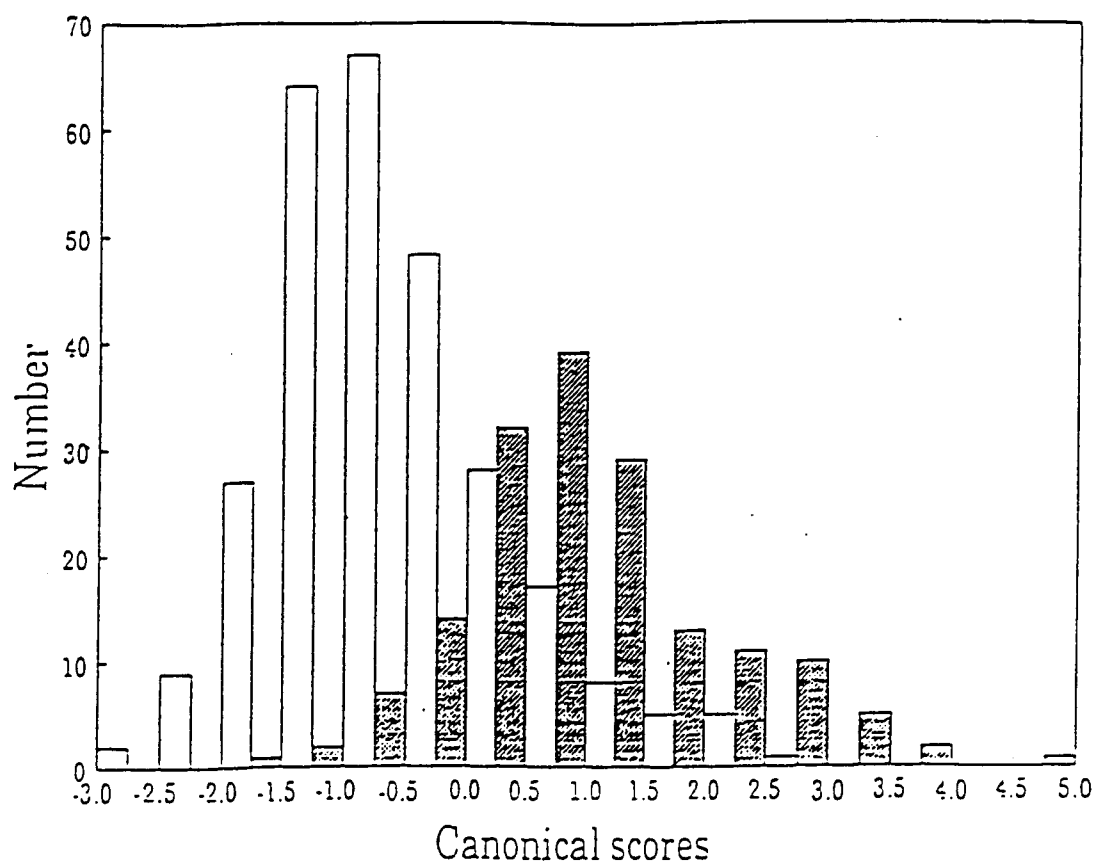
Figure 1.7. Histogram of the distribution of scores from canonical discriminant analysis of brown and silver type arctic charr from Vatnshlidarvatn, Iceland. Multivariate analysis of 16 mensural characters, size adjusted by regression technique, computation of residuals from the regression of untransformed morphological variables on standard length (STL). Shaded bars brown type, open bars silver type.
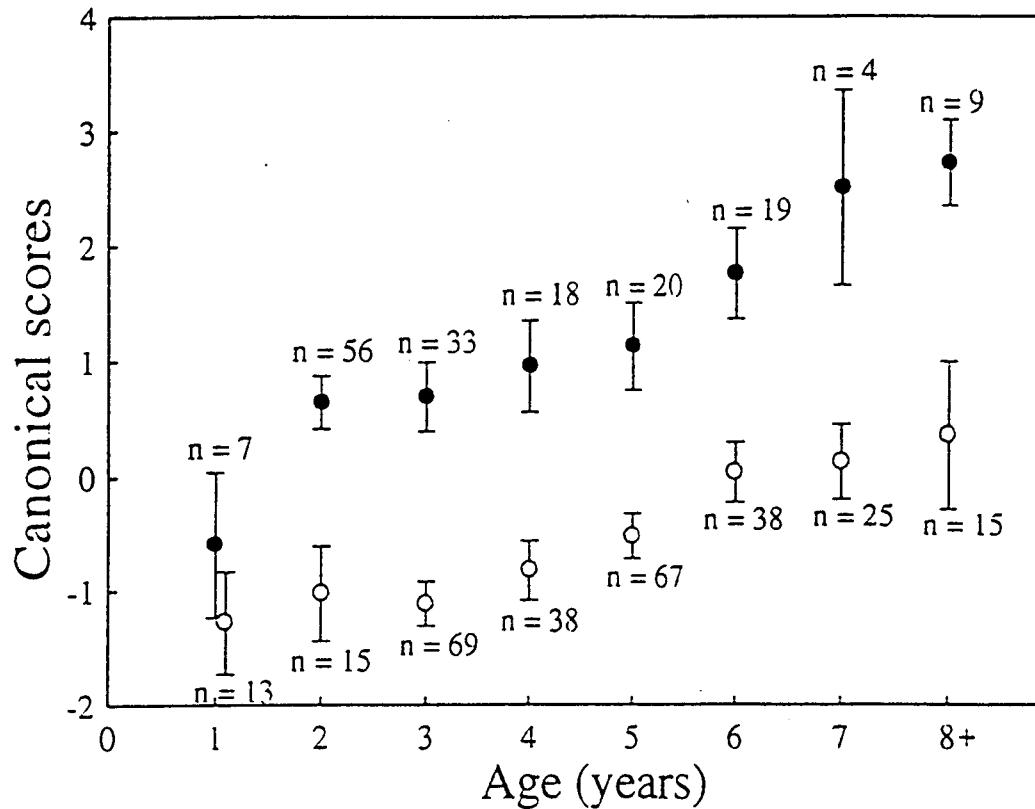
Figure 1.8. Plot of means and 95% confidence intervals of scores from canonical discriminant analysis of brown and silver type arctic charr from Vatnshlidarvatn, Iceland. Multivariate analysis of 16 mensural characters, size adjusted by regression technique, computation of residuals from the regression of untransformed morphological variables on standard length (STL). Shaded symbols brown type, open symbols silver type. (1 – 7 denote one year to seven year old fish, 8+ are fish eight years and older combined).

Allometric Slopes

Ontogenetic patterns of morphological differentiation between types are investigated through the calculation of bivariate and multivariate allometric coefficients. Tests are performed for statistical differences in the bivariate allometries (Table 1.3).

Compared to the other tests, the regression method underestimates allometric slopes, particularly for the brown type. Such underestimation can be expected, unless the correlation coefficient is 1.0 (Harvey and Pagel 1993). Allometric slopes calculated from the covariance-ratios are similar to the multivariate allometric slopes produced from the first PCA, as the ratio of characters with standard length (Table 1.3).

Brown males grow relatively faster than silver males in most body characters other than fish length, and brown females tend to grow faster in most head characters than the silver females, while the latter tend to grow faster in tail area measurements. These differences are not significant at the 0.05 level (Table 1.3, legend).

Discussion

Growth and Sexual Maturation

The data suggest that there are two growth forms of arctic charr in Vatnshlidarvatn (Fig. 1.3). This can not be explained by sexual dimorphism in size (Fig. 1.3).

Two alternative maturation strategies are evidently present among the arctic charr; the brown type becomes sexually mature at young ages and small sizes, while the silver type experiences extended growth to older ages and larger sizes before they reach maturity (Fig. 1.3 and 1.4).

TABLE 1.3 Bivariate and multivariate allometric coefficients of 16 mensural characters in arctic charr from Vatnshlidarvatn, Iceland. Bivariate slopes calculated as regression coefficients of y variables on STL, standard length (x variable), and as covariance ratio, HL, head length, as third variable (PCL, pectoral fin length used as third variable for HL). Multivariate slopes calculated as first component loadings (PC1) of log- transformed data from within group PCAs (sex and type separately), based on a variance- covariance matrix, divided by the loading for STL, standard length.

| | Bivariate slopes | | | | | | | | Multivariate slopes | | | |
| | Regression | | | | Covariance ratio | | | | Standardized | | | |
Trait[a]	B1	S1	B0	S0	B1	S1	B0	S0	B1	S1	B0	S0
POL	1.13	1.10	1.14	1.12	1.18	1.11	1.19	1.14	1.19	1.11	1.21	1.14
OOL	0.58	0.64	0.62	0.58	0.61	0.64	0.66	0.59	0.61	0.64	0.66	0.59
HL	0.94	0.95	0.88	0.95	0.98	0.96	0.92	0.97	0.97	0.96	0.92	0.97
MXL	1.14	1.08	1.07	1.07	1.19	1.09	1.12	1.09	1.19	1.09	1.12	1.09
LJ	1.15	1.12	1.08	1.09	1.20	1.13	1.13	1.11	1.20	1.14	1.13	1.11
HDD	1.01	0.98	0.99	1.00	1.04	0.98	1.03	1.02	1.04	0.99	1.03	1.02
MXW	0.98	0.95	0.85	0.89	1.00	0.95	0.89	0.90	1.05	0.96	0.90	0.91
IOW	1.05	1.04	1.02	1.07	1.10	1.05	1.05	1.09	1.09	1.05	1.05	1.09
PCL	1.03	1.02	0.96	1.00	1.07	1.02	1.01	1.02	1.07	1.03	1.02	1.03
PVL	1.05	1.00	0.98	0.98	1.10	1.01	1.03	1.00	1.11	1.01	1.04	1.01
ANL	1.06	1.00	1.03	1.01	1.10	1.00	1.08	1.02	1.11	1.01	1.10	1.03
ANW	1.10	1.13	1.04	1.07	1.15	1.13	1.07	1.07	1.15	1.14	1.09	1.10
CPL	1.03	0.96	0.86	0.95	0.99	0.98	0.84	0.93	1.01	0.97	0.89	0.95
CPD	0.99	1.01	0.89	1.03	1.02	1.01	0.91	1.05	1.01	1.01	0.91	1.05
CFL	0.91	0.95	0.72	0.91	0.95	0.95	0.73	0.92	0.95	0.96	0.75	0.93
FLT	0.85	0.88	0.95	1.03	0.91	0.78	1.05	1.05	0.95	0.91	1.16	1.12

[a] For key to abbreviations, see legend Fig. 1.2
B1 = brown males; S1 = silver males; B0 = brown females; S0 = silver females

Ontogeny of Morphological Segregation

The study supports the hypothesis that arctic charr in Vatnshlidarvatn constitute two different morphs. Similar trends of morphological segregation are indicated by all the morphometric methods employed (Tables 1.1 and 1.2). The silver morph has an elongated and fusiform body, while the brown morph has a stocky body and relatively long paired fins. This dimorphism is not dependent on fish size, sex, age or state of maturity. The segregation between morphs is independently reinstated by the brown morph having significantly greater gill raker number than the silver morph.

Evolutionary change in the timing of ontogenetic events, heterochrony, is most likely responsible for the morphological differentiation between arctic charr morphs in Vatnshlidarvatn. The brown morph has higher adjusted means than the silver morph, in the univariate analysis for all morphometric measurements except caudal penduncle length, CPL, and caudal fin length, CFL (Table 1.1). Further, none of the ontogenetic slopes are significantly different between the morphs (Table 1.3). Therefore, differences in morphology between morphs can only be explained by different ontogenetic trajectories of younger fish than currently examined. Because fish in this study are older than one year, early determination of morphological differences is suggested. The divergence is then accomplished by acceleration or retardation in the development of morphometric characters with respect to growth in size, resulting in the altered growth patterns observed in adult morphology. These findings are substantiated by the parallel morphological change of the brown and silver morphs with age in the PCA (Fig. 1.6a, b), and the CDA (Fig. 1.8) analysis. The results are in agreement with the view of Strauss (1990) that larval ontogenetic characters should be emphasized along with static adult traits, when studying evolutionary segregation in fish. The importance of such early differentiation has been underlined for arctic charr morphs from Lake Thingvallavatn (Skúlason et al. 1989).

The ontogenetic changes in shape might decrease resource competition between age classes, as age groups can differ both in size and shape (Meyer 1990). The age

effects in this study highlight the importance of considering age in morphological studies in the future.

Functional Significance of Morphological Divergence

The divergence in head morphology among arctic charr morphs in Thingvallavatn (Snorrason et al. 1994), and Loch Rannoch (Gardner et al. 1988), are among the best documented cases of morphological segregation in sympatric morphs of salmonids. My study shows an alternative mechanism of morphological divergence, being more related to swimming performance and maneuverability than head morphology. The stocky body, and relatively long paired fins and short caudal penduncle of the brown morph (Table 1.1) are all characters allowing for greater maneuverability, important for selective feeding (Stoner and Livingston 1984, Toline and Baker 1993). Slimmer bodies and longer caudal regions should enhance sustained swimming and speed performance in the silver morph (Taylor and Foote 1991), compared to the brown morph. Similar pattern of morphological segregation has been observed between sympatric arctic charr morphs in Lake Hazen, Elsemere Island (Reist et al. 1995), between sockeye salmon and kokanee (Oncorhynchus nerka W.) (Taylor and Foote 1991), and between allopatric anadromous and resident arctic charr in Norway (Damsgård 1991), indicating that this mode of morphological diversification might be more pervasive throughout the Salmonidae than previously noted. The shape of the silver morph bears resemblance with anadromous salmonids. During smolting, fish become silvery and develop elongated, and fusiform body (Birt and Green 1986, Damsgård 1991). Historically landlocked arctic charr exhibit basic smolting characteristics (Schmitz 1992), although less so than anadromous fish (Staurnes et al. 1992). The silver morph in Vatnshlidarvatn could be displaying remnants of smolt transformation, while the brown morph is not. Early sexual maturation of the brown morph could constrain the ability to smoltify. Evolutionary departure from anadromy has been suggested among nonanadromous atlantic salmon

(Salmo salar L.), as adaptation to avoid energetically intensive process no longer relevant in their life history (Birt and Green 1986). The sacrifice of cruising ability for greater maneuverability could also be important in enhancing such developmental changes.

Explanations for Polymorphism

This is the first report of morphological segregation of a salmonid species in a shallow landlocked lake (maximum depth 5-6m). Further, diet analysis indicates that both arctic charr morphs in Vatnshlidarvatn are mainly benthic feeders, showing segregation when food is limiting, with cannibalism being very uncommon (B. Jónsson chapter 2). Polymorphism in the Salmonidae has most often been observed in lakes with discrete benthic and pelagic habitats resulting in ecological segregation of morphs into benthivory and planktivory (Skúlason and Smith 1995). Piscivory and/or cannibalism, and anadromy versus resident life history is also commonly encountered (Griffiths 1994, Reist et al. 1995, Smith and Skúlason in press). None of this holds for the polymorphism observed in Vatnshlidarvatn.

The small size, shallowness, and geographic simplicity of the lake, retards the divergence into benthic and limnetic morphs of arctic charr. The lake is landlocked, so anadromy is not possible. The development of local subpopulations in the lake is also unlikely, due to its small size. Two benthic morphs of arctic charr have been found in Thingvallavatn (Snorrason et al. 1994), and in Loch Rannoch (Gardner et al. 1988), but these two lakes are much larger and more physically complex than Vatnshlidarvatn.

The arctic charr morphs in Vatnshlidarvatn exhibit polymorphism in the absence of ecological conditions generally thought to be necessary for its maintenance. This is in agreement with Liem (1984), that the great versatility of teleost fish enables them to sustain considerable overlap in resource use. The present results suggest the existence of alternative mechanism of segregation among Salmonidae. Other fish than arctic

charr are absent from Vatnshlidarvatn and thus there is no interspecific competition. This combined with abundant food resources provides unique opportunities for arctic charr to expand their niche breadth, without cannibalism, anadromy, or segregation into benthivory and planktivory. The morphological divergence is correlated with life history differences, such as in growth (Fig. 1.3), age at sexual maturity (Fig. 1.4), feeding, and reproductive strategies, but wide overlap in diet and microhabitat use is also apparent (B. Jónsson chapter 2). The conditions prevailing in the lake, and the presence of "empty niche" might increase realized capacities of the morphs together, by inducing variability and divergence in morphology and life history to fully occupy available niche space.

References

Barber WA, McFarlane GA. 1987. Evaluation of three techniques to age Arctic char from Alaskan and Canadian waters. *Transactions into the American Fisheries Society* **116**: 874-881.

Birt T P, Green JM, Davidson WS. 1986. Midichondrial DNA variation reveals genetically distinct sympatric populations of anadromous and nonanadromous Atlantic salmon, *Salmo salar. Canadian Journal of Fisheries and Aquatic Sciences* **48**: 577-582.

Dahl K. 1917. Studier and forsök over örret og örretvand. Kristiania: Centraltrykkeriet.(Studies on trout and trout-lakes). [In Norwegian.]

Damsgård B. 1991. Smolting characters in anadromous and resident Arctic charr, Salvelinus alpinus (L.). *Journal of Fish Biology* **39**: 765-774.

Echelle AA, Kornfield I, eds. 1984. *Evolution of Fish Species Flocks*. Orono: University of Maine Press.

Gardner AS, Walker AF, Greer RB. 1988. Morphometric analysis of two ecologically distinct forms of Arctic charr, *Salvelinus alpinus* (L.), in Loch Rannoch, Scotland. *Journal of Fish Biology* **32**: 901-910.

Griffiths D. 1994. The size structure of lacustrine Arctic charr (Pisces: Salmonidae) populations. *Biological Journal of the Linnean Society* **51**: 337-357.

Harvey PH, Pagel MD. 1993. *The Comparative Method in Evolutionary Biology.* Oxford: Oxford University Press.

Hindar K, Jonsson B. 1982. Habitat and food segregation of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet lake, Western Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **39**: 1030-1045.

Hindar K, Jonsson B. 1993. Ecological polymorphism in Arctic charr. *Biological Journal of the Linnean Society* **48**: 63-74.

Hindar K, Ryman N, Ståhl G. 1986. Genetic differentiation among local populations and morphotypes of Arctic charr, *Salvelinus alpinus*. *Biological Journal of the Linnean Society* **27**: 269-285.

Johnson L. 1983. Homeostatic characteristics of single species fish stocks in arctic lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 987-1024.

Jolicoeur P. 1963. The multivariate generalization of the allometry equation. *Biometrics* **19**: 497-499.

Jonsson B, Hindar K. 1982. Reproductive strategy of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet lake Western Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **39**: 1404-1413.

Kuhry B, Marcus LF. 1977. Bivariate linear models in biometry. *Systematic Zoology* **26**: 201-209.

Liem KF. 1984. Functional versatility, speciation, and niche overlap: are fishes different? In: Meyers DG, Strickler JR, eds. *Trophic interactions within aquatic ecosystems*. Westview press. 269-305.

Marcus LF. 1988. Traditional morphometrics. In: Rohlf FJ, Bookstein FL, eds. *Proceedings of the Michigan morphometrics workshop*. 77-122.

Meyer A. 1990. Morphometrics and allometry in the trophically polymorphic cichlid fish, *Cichlasoma citrinellum*: Alternative adaptations and ontogenetic changes in shape. *Journal of Zoology London* **221**: 237-260.

Nordeng H. 1983. Solution to the "char problem" based on Arctic char (*Salvelinus alpinus*) in Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 1372-1387.

Nyman L, Hammar J, Gydemo R. 1981. The systematics and biology of landlocked populations of Arctic char from Northern Europe. Institute of Freshwater Research Drottningholm. Report No. 59: 128-41.

Pimentel RA. 1979. *Morphometrics*. Iowa: Kendal/Hunt Publishing Company.

Reist JD. 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. *Canadian Journal of Zoology* **63**: 1429-1439.

Reist JD, Gyselman E, Babaluk JA, Johnson JD, Wissink R. 1995. Evidence for two morphotypes of Arctic char (*Salvelinus alpinus* (L.)) from Lake Hazen, Ellesmere Island, Northwest Territories, Canada. *Nordic Journal of Freshwater Research* **71**: 396-410.

Rencher AC. 1988. On the use of correlations to interpret canonical functions. *Biometrika* **75**: 363-365.

Schmitz M. 1992. Annual variations in rheotactic behavior and seawater adaptability in landlocked Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 448-452.

Shea BT. 1985. Bivariate and multivariate growth allometry: statistical and biological considerations. *Journal of Zoology London* (A) **206**: 367-390.

Skúlason S, Antonsson T, Gudbergsson G, Malmquist H J, Snorrason SS. 1992. Variability in Icelandic Arctic charr. *Icelandic Agricultural Sciences* : 143-153.

Skúlason S, Noakes DLG, Snorrason, SS. 1989. Ontogeny of trophic morphology in four sympatric morphs of arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. *Biological Journal of the Linnean Society* **38**: 281-301.

Skúlason S, Smith TB. 1995. Resource polymorphism in vertebrates. *Tree* **10**: 347-388.

Smith TB, Skúlason S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. In press *Annual Review of Ecology and Systematics*

Snorrason SS, Skúlason S, Jonsson B, Malmquist HJ, Jónasson PM, Sandlund OT, Lindem T. 1994. Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces; Salmonidae): morphological divergence and ontogenetic niche shifts. 1994. *Biological Journal of the Linnean Society* **52**: 1-18.

Sokal RR, Rohlf FJ. 1981. *Biometry*. New York: W.H. Freeman and Co.

Sparholt H. 1985. The population, survival, growth, reproduction and food of arctic charr, *Salvelinus alpinus* (L.), in four unexploited lakes in Greenland. *Journal of Fish Biology* **26**: 313-330.

Staurnes M, Sigholt T, Lysfjord G, Gulseth OA. 1992. Difference in the seawater tolerance of anadromous and landlocked populations of Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 443-447.

Stoner AW, Livingston RJ. 1984. Ontogenetic patterns in diet and feeding morphology in sympatric sparid fishes from seagrass meadows. *Copeia*: 174-187.

Strauss RE. 1990. Heterochronic variation in the developmental timing of cranial ossifications in pociliid fishes (Cyprinodontiformes). *Evolution* **44**: 1558-1567.

Strauss RE, Fuiman LA. 1985. Quantitative comparisons of body form and allometry in larval and adult pacific sculpins (Teleostei: Cottidae). *Canadian Journal of Zoology* 63: 1582-1589.

Svedäng H. 1990. Genetic basis of life-history variation of dwarf and normal Arctic charr, *Salvelinus alpinus* (L.), in Stora Rösjön, central Sweden. *Journal of Fish Biology* **36**: 917-932.

Taylor EB, Foote CJ. 1991. Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). *Journal of Fish Biology* **38**: 407-419.

Toline CA, Baker AJ. 1993. Foraging tactic as a potential selection pressure influencing geographic differences in body shape among populations of dace (*Phoxinus eos*). *Canadian Journal of Zoology* **71**: 2178-2184.

Tómasson T. 1987, *unpublished.* The connection between growth and size at sexual maturity in Icelandic arctic charr (*Salvelinus alpinus*). A paper prepared for the International conference on alternative life history styles of fishes and other organisms. Grahamstown, South Africa.

CHAPTER 2

Feeding and Reproduction of Polymorphic Arctic Charr, *Salvelinus Alpinus* (L.) From a Small Lake, Northern Iceland

Bjarni Jonsson

Introduction

Intraspecific morphs can arise through the utilization of different niches associated with variable habitats and diets (Malmquist et al. 1992, Schluter and McPhail 1992, Robinson et al. 1993, Smith 1993, Day et al. 1994, Snorrason et al. 1994). Divergence of sympatric forms can be facilitated by an absence of competition for these resources from other species (Schluter 1988, Robinson and Wilson 1994). Such resource polymorphism in fish is commonly associated with the presence of discrete benthic and pelagic habitats in lakes. Examples include whitefish (Coregonus and Prosopium spp.), threespine sticklebacks (Gasterosteus aculeatus), sunfishes (Lepomis gibbosus and L. macrochirus), and arctic charr (Salvelinus alpinus) (Skúlason and Smith 1995). The occurrence of sympatric morphs of arctic charr, like many other salmonids, is also known to be related to piscivory and/or cannibalism, and anadromy versus resident life history (Griffiths 1994, Reist et al. 1995, Skúlason and Smith 1995).

Arctic charr, with a northern circumpolar distribution, exhibits great variability in life history, both within and among localities (Johnson 1980, Nordeng 1983). Differences are seen in growth, age and size at sexual maturation fecundity, and egg size (Jonsson and Hindar 1982, Jonsson et al. 1988, Hindar and Jonsson 1993, Griffiths 1994, Skúlason et al. in press). These life history differences are greatly influenced by feeding behavior and performance (Sparholt 1985, Malmquist et al. 1992, Griffiths 1994). Differences in diet of sympatric morphs are associated with segregation in feeding habitats, such as diversification into benthivory and planktivory. Morphs can also diversify in diet between local habitats in large and physically complex water bodies, and due to migration (Griffiths 1994, Smith and Skúlason in press). Furthermore, conditions like seasonality and habitat diversity can then favor evolution of reproductive segregation (Skúlason et al. 1989b). Thus resource polymorphism can have important implications for population segregation and speciation (Rice and Hostert 1993, Skúlason and Smith 1995).

In a few cases, significant differences in morphology have been observed for instance, in Thingvallavatn Iceland where four sympatric morphs co-occur (Skúlason et al. 1989a, Snorrason et al. 1994), in Loch Rannoch Scotland where three morphs co-occur (Gardner et al. 1988, C. Adams personal comm.), between two morphs in Lake Hazen Elsmere Island (Reist et al. 1995), and in Lake Vatnshlidarvatn Iceland where there are two morphs (B. Jónsson chapter 1).

Bimodal size distribution of arctic charr has been noticed in several Icelandic lakes (Skúlason et al.1992) including the lake Vatnshlidarvatn (Tómasson 1987). Life histories and ecology of such populations are, however relatively unexplored, except in Thingvallavatn (Snorrason et al. 1994).

Vatnshlidarvatn in NW- Iceland is in many ways different from other lakes where sympatric forms of arctic charr have been investigated (Jonsson and Hindar 1982, Johnson 1983, Sparholt 1985, Hindar et al. 1986, Skúlason et al. 1989b, Svedäng 1990, Hindar and Jonsson 1993, Snorrason et al. 1994, Reist et al. 1995). The lake is only 70 ha, shallow and uniform, and the only fish present is arctic charr, a common occurrence in arctic lakes. However, compared to arctic lakes, Vatnshlidarvatn is in a warmer climate and has more productive food resources. It is interesting that this uniform lake contains two morphologically distinct morphs of arctic charr, distinguished as brown morph and silver morph (B. Jónsson chapter 1), which serves a unique opportunity for studying evolution of phenotypic segregation.

My objectives are:
to test if the two morphological forms, the brown and the silver morphs differ in food and habitat use.
Second, to test if there are differences in life history between morphs, and if such differences are associated with differences in resource use.
Thirdly, I test if segregation of morphs is correlated with temporal and spatial differences in spawning.

I then discuss ecological and evolutionary implications of my results and compare the unique characteristics of Vatnshlidarvatn to other systems.

<u>Methods</u>

Study Site

Vatnshlidarvatn (Fig. 1.1 chapter 1) is a shallow lake in northern Iceland (65° N, 19° W), 70 ha in size (mean depth 2-3 m, maximum depth 5-6 m). The bottom is mainly mud, with gravel close to shore and near the outlet of the lake. The submerged vegetation is characterized by patches of eelgrass (<u>Myriophyllum spp.</u>). The lake is in a basalt area at an elevation of 280 m, and is a part of a runoff system, with shallow lakes and wetlands near the origin. The lake has one major inlet and outlet and is also fed by short spring-fed creeks. Water temperature follows seasonal air temperature (mean air temperature in January -5°C, and July 7°C), ranging from 0 - 15 C°. The lake is usually ice-covered from October/November to April/May. Water conductivity is 161 μS/cm (at 25C°), and pH 8.50 (in August 1994). The lake was formed after the Pleistocene glaciation, and has been landlocked by a waterfall for the last 6000-8000 years. Arctic charr is the only fish present in the lake, and it has been subject to minimal commercial harvest in recent years.

Sampling

Arctic charr (n = 848) were sampled on August 16 1994 with 2x10 bottom gill nets set out at night for 10 hours (panel sizes: 1.5 x 25 m, and mesh sizes from 10 mm - 52 mm bar mesh) in two 250 m long series with the mesh sizes in a random order. The sub- sample for diet analysis was taken by picking at random 10 fish at a time from each of the gill nets (n = 346). Two more samples for diet analysis were taken by the same gill nets in September 28 1994 (n = 213), and July 15 1995 (n = 130) to look at diet at different dates. Stomachs from all fish in these samples were examined. Additional qualitative data needed for the estimation of fecundity, egg size,

gonadosomatic index, spawning time and location were sampled by beach zeines and gill nets in the lake, and electrofishing in the inlets and in the outlet in September and October 1994.

Classification

Arctic charr are pre-classified, by eye into either "brown morph" or "silver morph". The following criteria is used:

The brown morph have stocky body, no silvery color on sides, parr marks are sometimes present, there is melanization on operculum and usually on ventral sides of lower jaw, body color is light brownish, and sexually mature individuals have dark bluish back. The silver morph, has fusiform body, no parr marks, dark grayish to dark bluish back, silvery sides; melanization on operculum is absent, but sometimes occurs on ventral sides of lower jaw on sexually mature fish. Silver females, and males of both morphs can display bright spawning colors. Fish that do not meet these criteria (9% of the sample) are classified as "unknown".

Diet

The prey in each stomach are identified to one of 10 food categories and the number of individuals in each category counted. The food categories are:

1. Lymnea peregra; 2. Pisidium spp; 3. Eurycercus spp.; 4. Miscellaneous Crustacea; 5. Orthocladinae spp.; 6. Chironomidinae spp.; 7. Tanipoidinae spp.; 8. Miscellaneous Insecta; 9. Lepidurus arcticus; 10. Fish eggs.

Percentage by number (% N) of each food taxon is determined as:

$$\% N = 100 N_i / N_j$$

where N_i is the total number of organisms of food category i, and N_j is the total number of organisms of all food categories. Overlap in diet (Levins index LO), and

diet breadth (Levins index B) of the two morphs, are estimated (Ludwig and Reynolds 1988).

Diet overlap (LO) of morph 1 with morph 2 is given by:

$$LO_{1,2} = \frac{\sum_{j}^{r} [\, (p_{1j})(p_{2j}) \,]}{\sum_{j}^{r} (p_{1\,j}^{2})}$$

Where r is the number of food categories, p is percent of each food category in the diet, and subscripts i, j represent the ith type and the jth food category. LO can range between 0 and 1, from no overlap to complete overlap. Diet breadth is measured as:

$$B_{i} = \frac{1}{\sum_{j}^{r} (p_{i\,j}^{2})}$$

Where r is the number of food categories, p is percent of each food category in the diet, and subscripts i, j represent the ith morph and the jth food category. The denominator is termed the breadth of the ith morph.

B can range from 1, one food category present in the diet, to 10, when contribution of all food categories in the diet is equal. To facilitate diet comparison between types, diet overlap and dietary breadth are analyzed both for fish of all sizes, and for fish in the size range 15.1 - 22 cm separately.

Parasites

The presence/absence of the following parasites is noted: Cestoda - Diphyllobotrium spp. and Eubotrium salvelini; Nematoda - Philonema oncorhynchi; Trematoda - Phyllodistomum conostomum (kidney fluke); and Crustacea - Salmonicola edwardsii. The complete sample from August 16 1994 (n = 848) is used

for investigation of parasite infection, except for <u>Phyllodistomum conostomum</u> that is only examined in fish from the sample taken on July 15 1995.

Growth and Sexual Maturation

Fish are weighed to the nearest 1 g, and fork-length measured to the nearest 0.1 cm. Age is determined from otolith surface analysis (Barber and McFarlane 1987). Empirical growth rates are calculated using modified form of the von Bertalanffy´s function according to Everhart and Youngs 1981

$$L_A = L_\infty(1 - e^{-kA})$$

where L_A is fork length at age A, L_∞ is asymptotic length, and k is Brody´s growth coefficient of von Bertalanffy equation.

Stage of sexual maturity is determined according to Dahl (1917).

Empirical growth rates (von Bertalanffy), as well as percentage of sexually mature male and female brown and silver morph, and sex ratios are calculated using the whole gill nets sample from August 16, 1994.

Reproduction

Thirty ripe (stage 6) eggs are randomly picked from each of 38 silver and 61 brown female morph, blotted and individual eggs weighed to the nearest 0.1 mg.

Fecundity is estimated (total counts of eggs) in 54 silver and 68 brown female morph in maturity stages 4-6. Ovulating females are not included.

Gonadosomatic index - GSI of females is estimated as 100 times ovarian weight (OW, g) divided by somatic weight (SW, g) less intestines:

GSI = 100* OW/SW

For comparison of egg size, fecundity, and GSI between the morphs, raw measurements are size adjusted by regression technique, computation of residuals from the regression of variables on fork length (adapted from Reist et al. 1995).

Age-specific fecundities (PF_i, percent) are estimated as:

$$PF_i = N_i \, F_i \, 100 / \sum_{x=a}^{n} N_x \, F_x$$

where N_i is number of mature females in the ith age class of a morph, F_i is the age-specific fecundity estimated from the mean fork-lengths of the fish, a denotes the age of the youngest sexually mature female, and n is the age of the oldest sexually mature female.

Reproductive value of each age class $v(x)$, or the relative number of eggs that remain to be spawned to females at a given age, is calculated according to Gotelli (1995) as:

$v(x)$ = number of eggs produced by female morph of age x or older divided by number of female morph of age x. Average egg number for sexually mature female morph is calculated in each age class. Age specific fecundities, (PF_i, percent), and reproductive value, $v(x)$ are calculated using the whole gill nets sample from August 16 1994.

Liver- somatic index, LSI is calculated as:

LSI = (liver weight/body weight less gonads and intestines) x 100

Condition factor, K is calculated as:

K = (Weight in gr/Length^3) x 100

For dry weight, fish were dried in a vacuum oven at a temperature of 70 °C until changes in weight between successive weightings were less than 0.1%. Dry weight was measured as percentage of wet weight:

Dry weight % = (dry weight/body weight less gonads and intestines) x 100

Water temperature was monitored in the lake and the inlets and the outlet, during the spawning season of both morphs in 1994.

<u>Results</u>

Diet

About 70% of all food items eaten by the brown morph in July is <u>Eurycercus</u>

<u>spp.</u> and the percentage increases throughout the summer, 94% in August and 98% in

September (Fig. 2.1). In Icelandic lakes <u>Eurycercus spp.</u> appears in July and is at its

peak abundance in August/September (Adalsteinsson 1979). The second most

important food item of the brown morph in July are <u>Tanypodinae</u> larvae and pupae,

constituting 14% of the food items (Fig. 2.1). <u>Pisidium</u> 24% and <u>Eurycercus spp.</u> 37%

are the most important food items of the silver morph in July. Other important food

items of this morph in July include <u>Chironominae</u> and <u>Tanypodinae</u> larvae and pupae,

12% and 10% respectively. At other sampling dates the silver morph feeds, mostly on

<u>Eurycercus spp.</u> At all other sampling dates the silver type eats more <u>Pisidium</u> than the

brown morph (Fig. 2.1). Cannibalism is observed in one individual of silver morph.

<u>Lepidurus arcticus</u>, which is the largest food item available besides arctic charr is only

infrequently found in the diet of either morph. Differences in diet in July are not

explained by size differences between the morphs (Fig. 2.2).

Levins index indicates that the diet of the two morphs overlaps greatly at all

sampling dates.(Table 2.1). The dietary breadth of the silver morph is greater than the

brown morph, except in August (Table 2.1) when both morphs feed almost exclusively

on <u>Eurycercus spp.</u>, and this difference between the morphs is independent of size

(Table 2.1).

Parasites

No of the individuals examined are infected by <u>Eubotrium salvelini</u> or

<u>Philonema oncorhynchi</u>, and only one fish (brown morph) is infected by

<u>Diphyllobotrium sp</u>. The kidney fluke, <u>Phyllodistomum conostomum</u> is found in
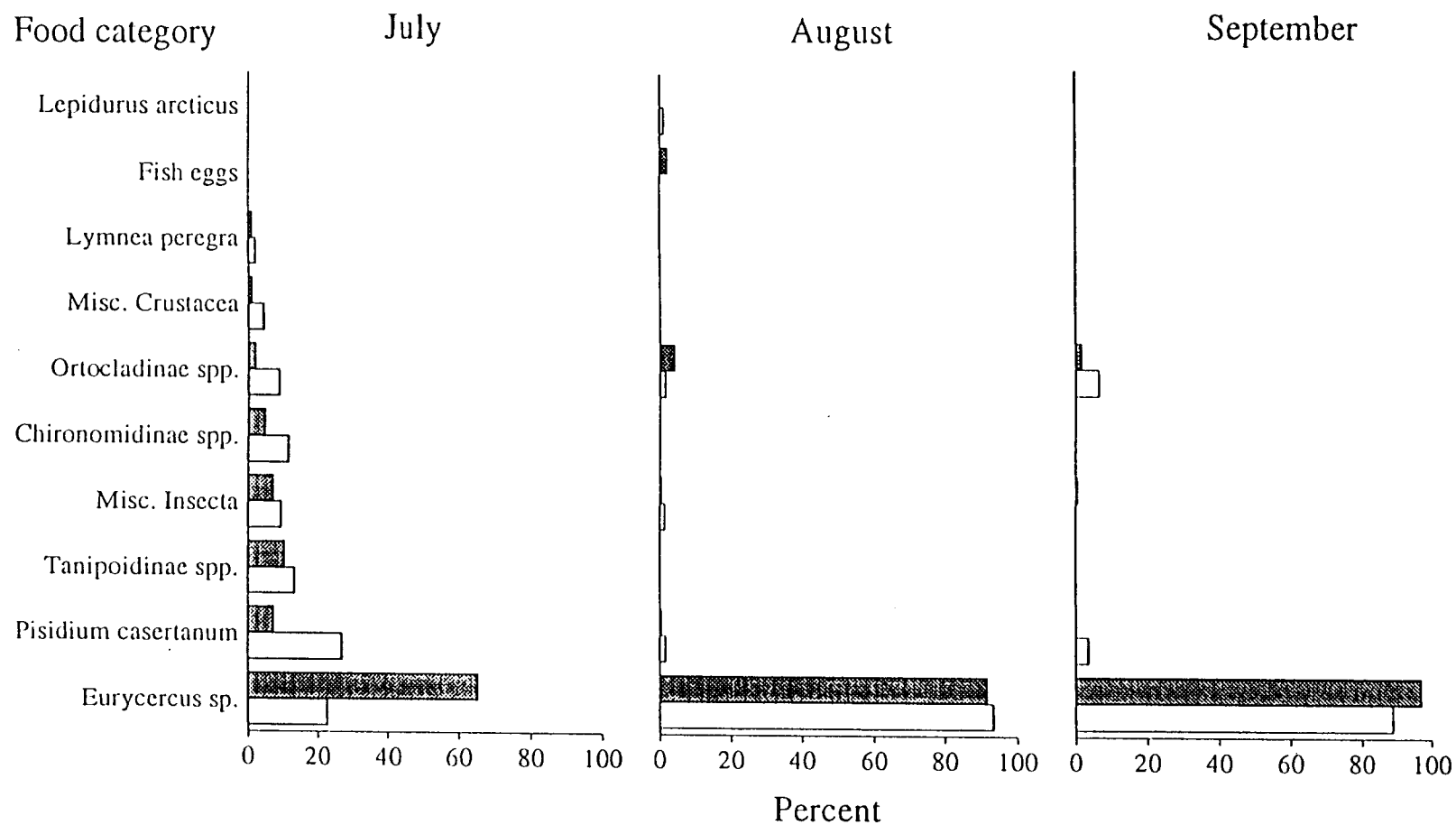
Figure 2.1 Percent contribution of each food category in the diet of arctic charr in Vatnshlidarvatn (number of food items). Samples from August 16. And September 28. 1994 and July 12. 1995. Brown morph shaded bars and silver morph open bars.
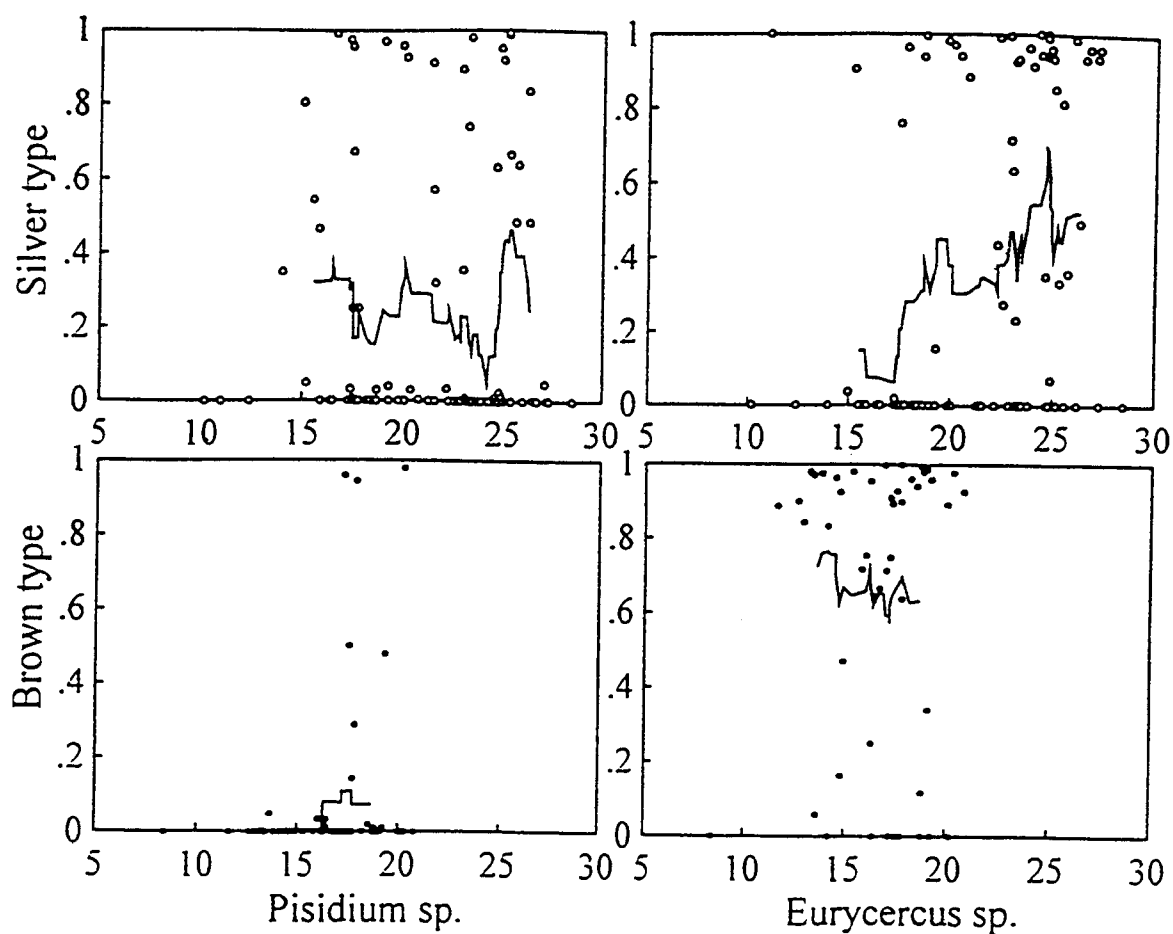
Figure 2.2. Percent contribution of Pisidium spp. and Eurycercus spp. In the stomachs of the brown and silver morph of different size in July 1995. Individual fish represented as points on the graph. Lines represent moving average, average contribution of pisidium spp. and Eurycercus spp. for individual of a given size and the six fishes larger and six fishes smaller than the individual. Moving average are calculated for the morphs separately.

TABLE 2.1 Levins index for diet overlap, and Levins's B for dietary breadth of the brown and silver arctic charr morphs in Vatnshlidarvatn at three sampling dates. The number 2 represents fish in the size range 15.1 - 22.1 cm fork length, and T stands for fish of all sizes.

Morph	Size	Diet overlap			Dietary breadth		
		July	August	September	July	August	September
Brown	2	0.56	1.00	0.92	2.05	1.18	1.06
	T	0.66	1.00	0.92	1.87	1.17	1.04
Silver	2	0.97	0.98	1.00	3.52	1.14	1.25
	T	1.00	0.98	1.00	3.15	1.12	1.23

15.4% of the brown morph (n=65), and 15.5% of the silver morph (n=206). Significant differences between morphs are found in the occurrence of <u>Salmonicola edwardsii</u>, brown morph 7.4%, and silver morph 19.5% (z- test for equality of the odds, 1-sided p-value <0.001).

Growth

The two morphs of arctic charr in Vatnshlidarvatn exhibit different growth trajectories (Fig. 2.3). They are of similar size one and two years old after which they diverge in growth. The silver morph with the theoretical asymptotic sizes 33.4 cm ($k =$ 0.179) for males and 31.6 cm ($k = 0.180$) for females, grow relatively fast until eight years of age, after which they grow slower. The brown morph with the asymptotic size of 18.0 cm ($k = 0.369$) for males, and 20.1 cm ($k = 0.364$) for females, exhibit slow growth after they are six years of age (Fig. 2.3). The brown morph, with a maximum observed age of twelve years, may be more long-lived than the silver morph, that has the maximum age of nine years (Fig. 2.3) There is little overlap in size of the two morphs after four years of age, and there are no indications that the brown morph become silver morph later in life.

Age at Sexual Maturity

The two charr morphs differ in age at first sexual maturity (Fig. 1.4 chapter 1). Almost all males and most females of the brown morph are sexually mature at age two. Some males become mature one year old. Females of the silver morph reach 50% sexual maturity at five years of age and males at seven years of age, but large proportion of the silver morph, over five years old is not sexually mature (Fig. 1.4 chapter 1). The youngest sexually mature silver morph males are sexually mature three years old, and females four years old (Fig. 1.4 chapter 1).
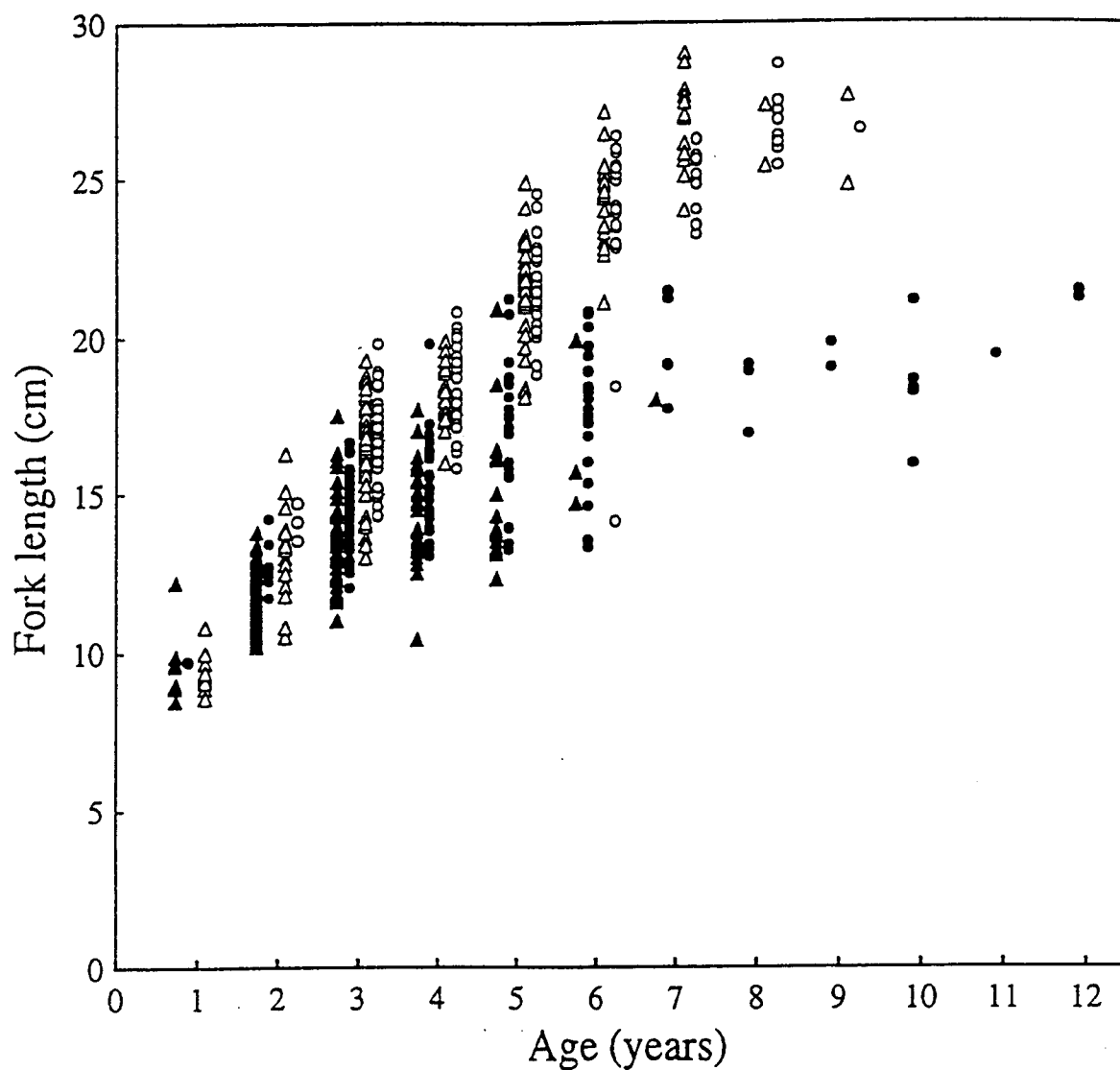
Figure 2.3 Length-age relationships. Triangles males and circles females. Brown morph shaded symbols and Silver morph open symbols.

Sex Ratios

Males represent higher proportion than females of both morphs, 61.4% (95% CI 56.8-66%) of the brown morph and 54.8% (95% CI 49.7-60.0%) of the silver morph are males. The skewed sex ratio holds for fish until they are five year old, but is most extreme in age two in both morphs (Fig. 1.4 chapter 1). The difference in sex ratios between the morphs is significant (z-test for equality of the odds of males between the morphs, 1-sided p-value = 0.03). The morphs also differ significantly in the sex ratios of sexually mature fish. Males constitute 61.4% of the sexually mature brown morph, and 40.8% of the silver morph (z-test for equality of the odds, 1-sided p-value = 0.011).

Reproduction

Fecundity is a function of size (Fig. 2.4 and 2.5). No significant differences are noticed between morphs, after standardizing for fish length ($F_{1,128}$ = 0.013, p>0.05). Multiple regression shows that including age in the regression of fecundity on fish length does not improve the fit (p>0.05 extra sum of squares F-tests). Thus differences between morphs are mainly attributed to size differences.

Age-specific fecundity indicates the relative contribution of each age class to the total female fecundity within each morph and the morphs together. In the silver morph fecundity is mostly based on five to eight year old females. In the brown morph the peak fecundity is attributed to three year old females, but remains high until seven years of age (Fig. 2.6). The reproductive value, or the relative number of eggs expected to be spawned by an individual of a given age, is higher for brown than the silver females for all age classes considered (Table 2.2).

Egg size does not differ between the two morphs when compared directly ($F_{1,97}$ = 0.025, p>0.05) and increases with fish size (Fig. 2.7) and age (Fig. 2.8). However,
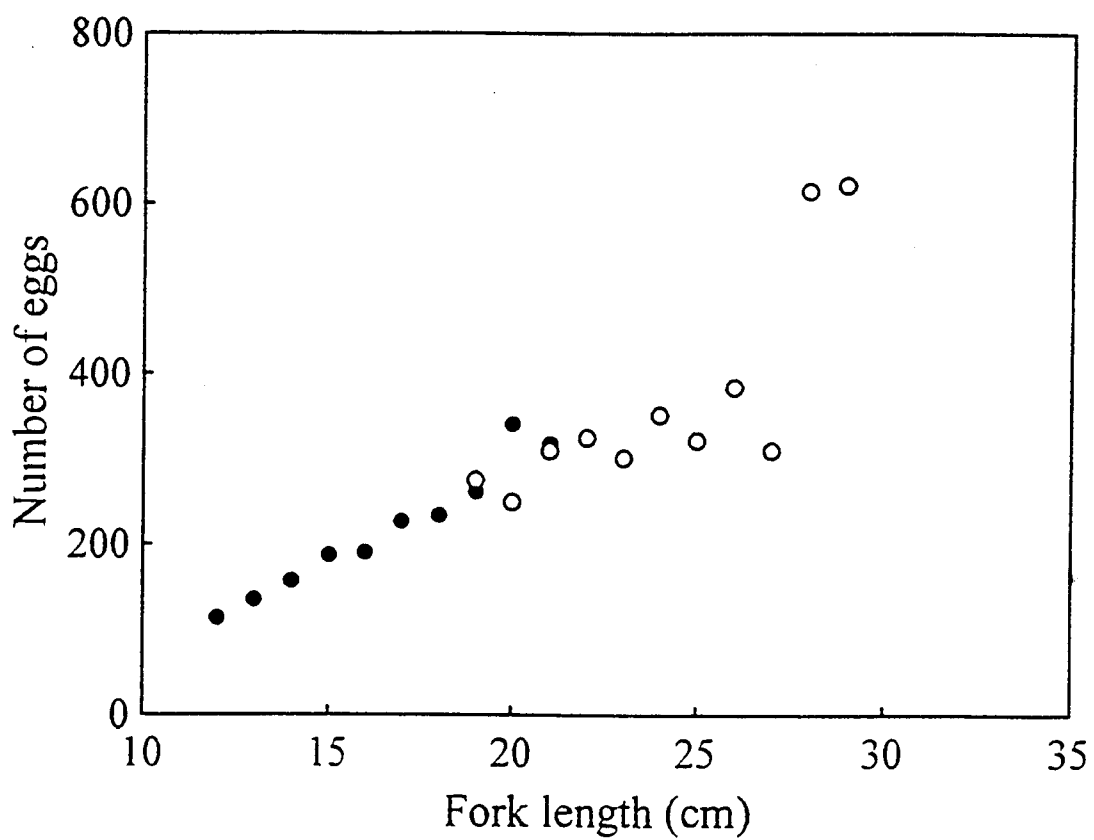
Figure 2.4 Fecundity of females in relation to fork length (cm). Brown morph (●) and Silver morph (○).Vertical bars are ± 1 SD.
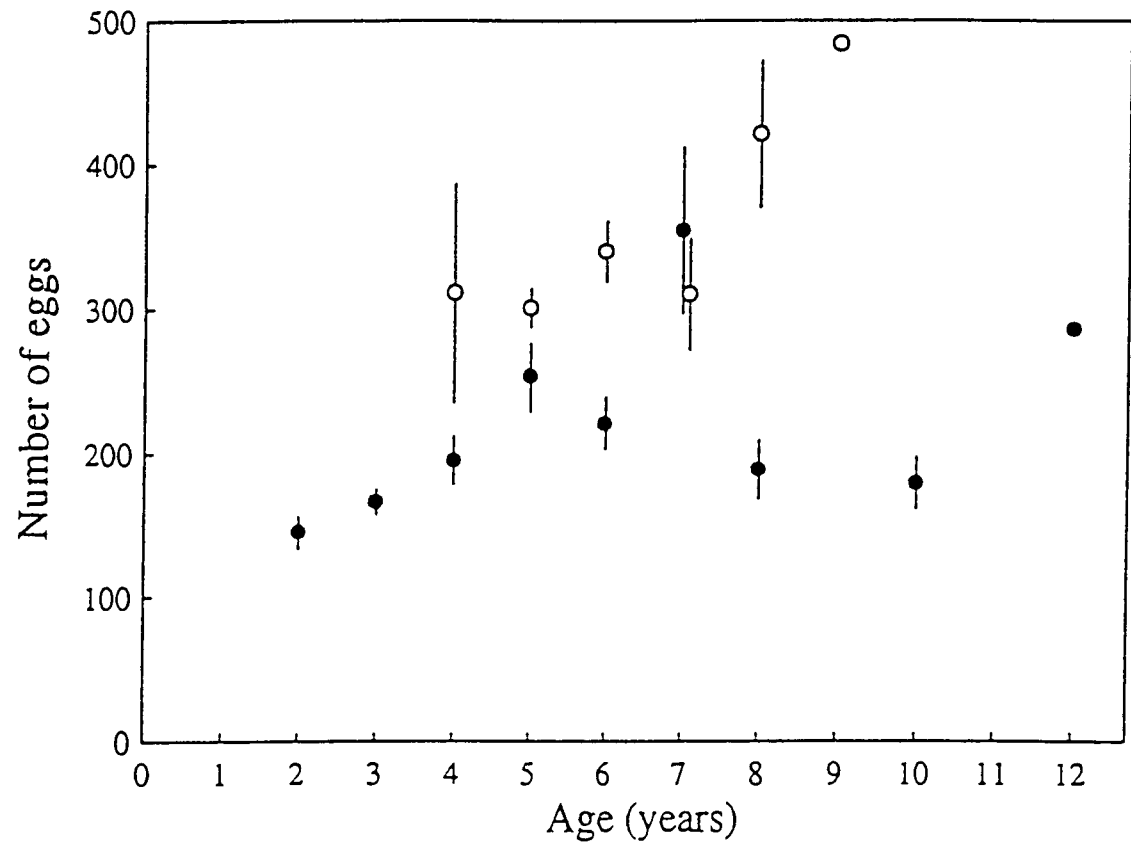
Figure 2.5 Fecundity of females in relation to age (years). Brown morph (●) and Silver

morph (O). Vertical bars are ± 1 SD.
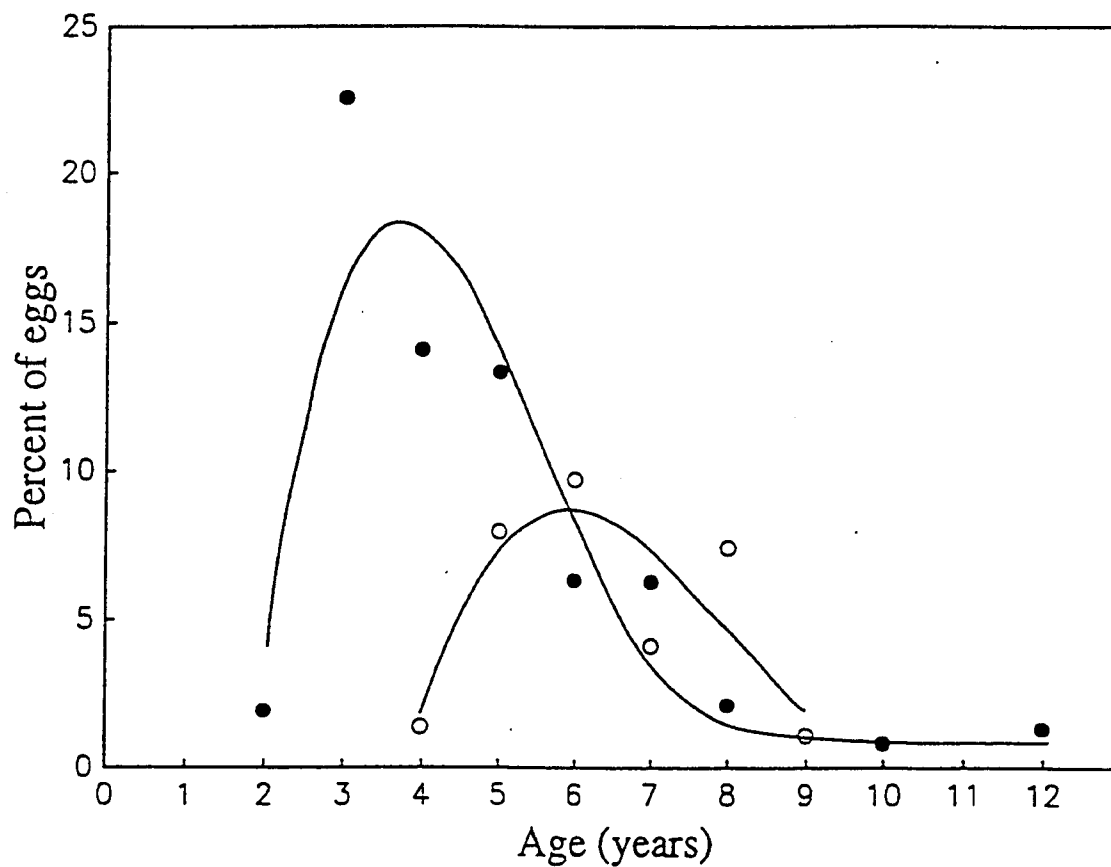
Figure 2.6 Age-specific morph fecundities of Brown morph (●) and Silver morph (O).

TABLE 2.2. Reproductive value of female brown and silver morph in age groups three years old (3+) and onward. Reproductive value $v(x)$ is calculated as number of offspring produced by female morph of age x or older divided by number of individuals of age x. Age classes younger than three years old (3+) are omitted from the analysis due to potential size dependent gill net selectivity. Time - specific liftable is created from the whole gill net sample from August 16 1994, and age structure of the morphs used to construct a single cohort for each morph.

| Morph | Age in years | | | | | | | | | |
	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+
Brown	506	654	606	699	776	674	808	823	430	286
Silver	368	388	371	405	519	350	484	–	–	–

Figure 2.7 Egg weight (mg) in relation to fork length (cm). Brown morph (●) and Silver morph (○) (± 1 SD Brown morph = +, and Silver morph = x).

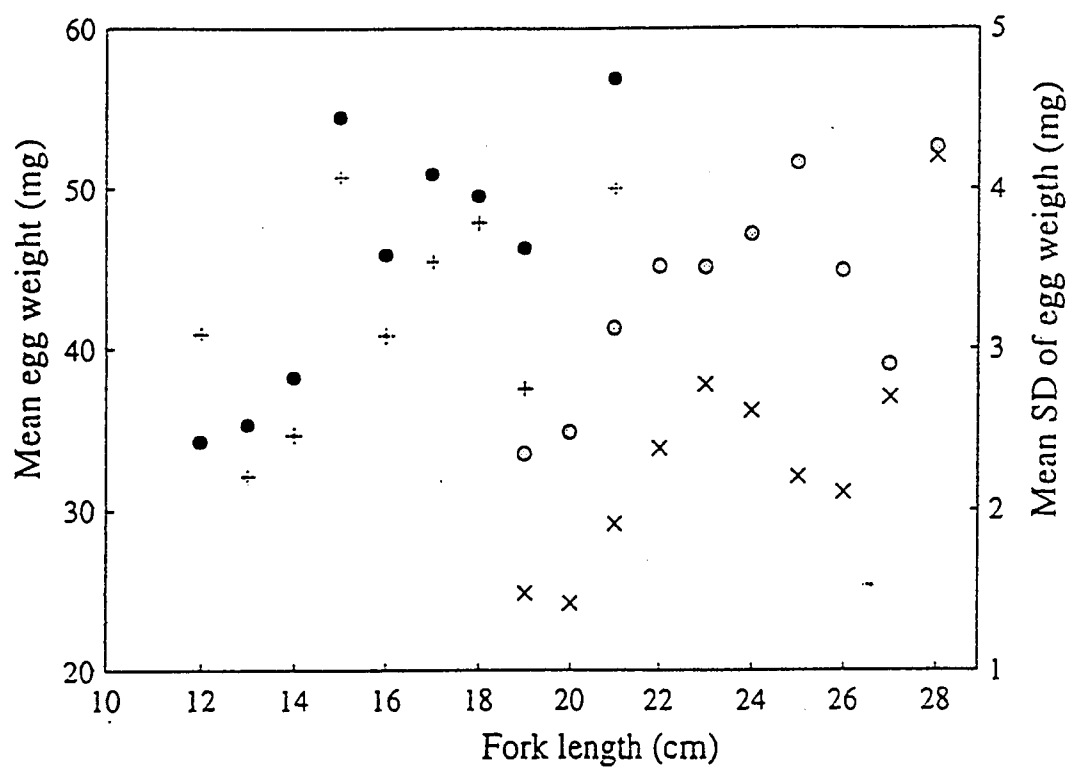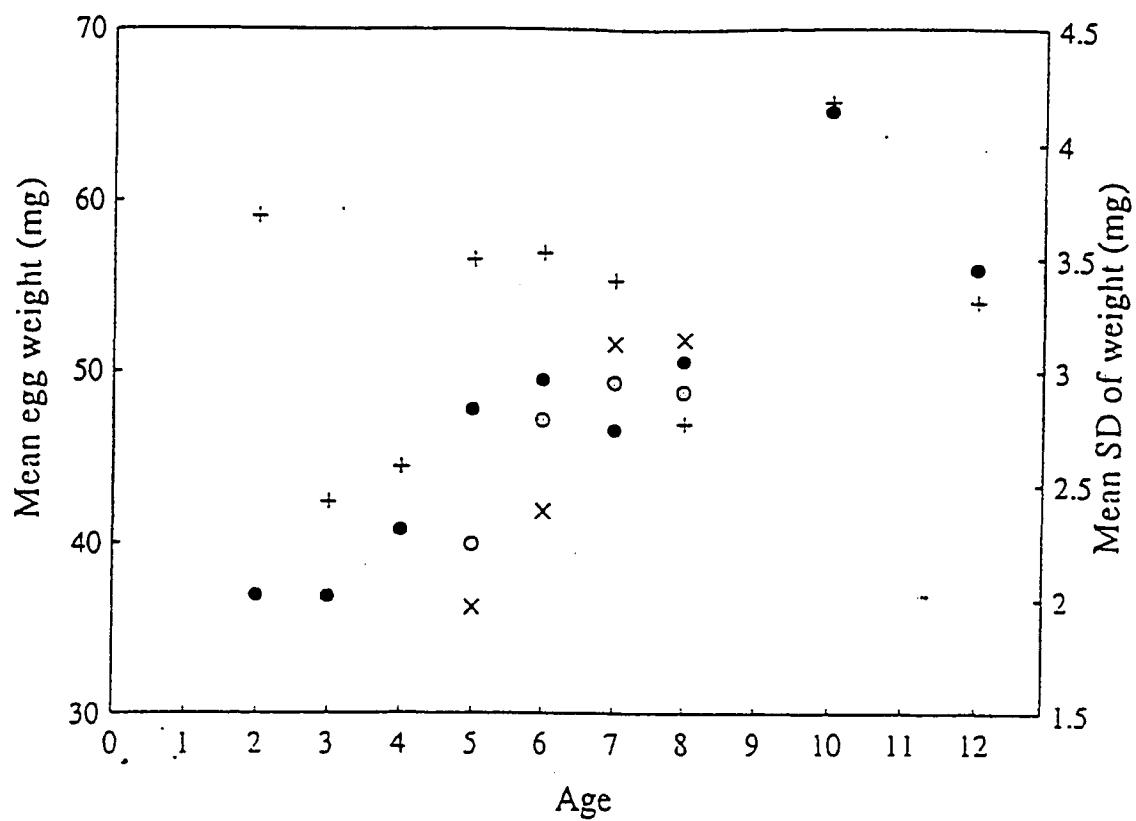Figure 2.8 Egg weight (mg) in relation to age (years). Brown morph (●) and Silver morph (O) (± 1 SD Brown morph = +, and Silver morph = x).

the brown morph appears to have relatively larger eggs than the silver morph when egg size is standardized for fish length ($F_{1,97} = 7.851$, p = 0.006).

There are significant differences in gonadal investment between the brown and silver morph (Fig. 2.9), the mean GSI of females in maturity stages 5-6 are 20.2 and 13.6 respectively ($F_{1,81} = 25.564$, p<0.001). No significant correlation is observed between GSI and age or length of either morph (p>0.05).

The brown morph (n= 19) has significantly higher condition factor, 0.92 than the silver morph (n=22), 0.82 (t = 3.452, p = 0.006). The same is evident for liversomatic index (LSI), which averages 1.09 and 0.77 respectively (t = 4.556, p<0.001). The liversomatic index is an indicator of short term energy storage. However, no significant differences are found in the % dry weight of the morphs, brown morph 21.8%, and the silver morph 20.9% (t = 1.633, p>0.05).

Fin damage during spawning is more common among silver females than brown females. Of 28 postspawning silver females observed, 7 have fin damage, but none of the 19 brown females examined had damage.

The location of ripe and spawning arctic charr was monitored in the lake and in the inlets and the outlet on a weekly basis. Spatial and temporal differences in spawning were observed. Ripe silver morph were mostly found at high density, in the inlets and the outlet of the lake. Few ripe silver morph were caught in the lake itself. Ripe brown morph were most common in the lake, but some were also found in the inlets and the outlet of the lake. The spawning period of the brown morph started in mid-August and was over by the beginning of September. The spawning of the silver morph took longer, started in the beginning of September and lasted into October in the inlets. The brown morph spawned at higher temperatures, 6- 12 °C, than the silver morph 0-8 °C. Silver males arrived at the spawning grounds before the spawning of the brown females was over. Further, some ripe brown males remained on the spawning grounds when the silver females were beginning to spawn. Males of both morphs arrived at the spawning sites at the beginning of spawning and stayed there throughout the spawning of a corresponding female morph. Females did not arrive
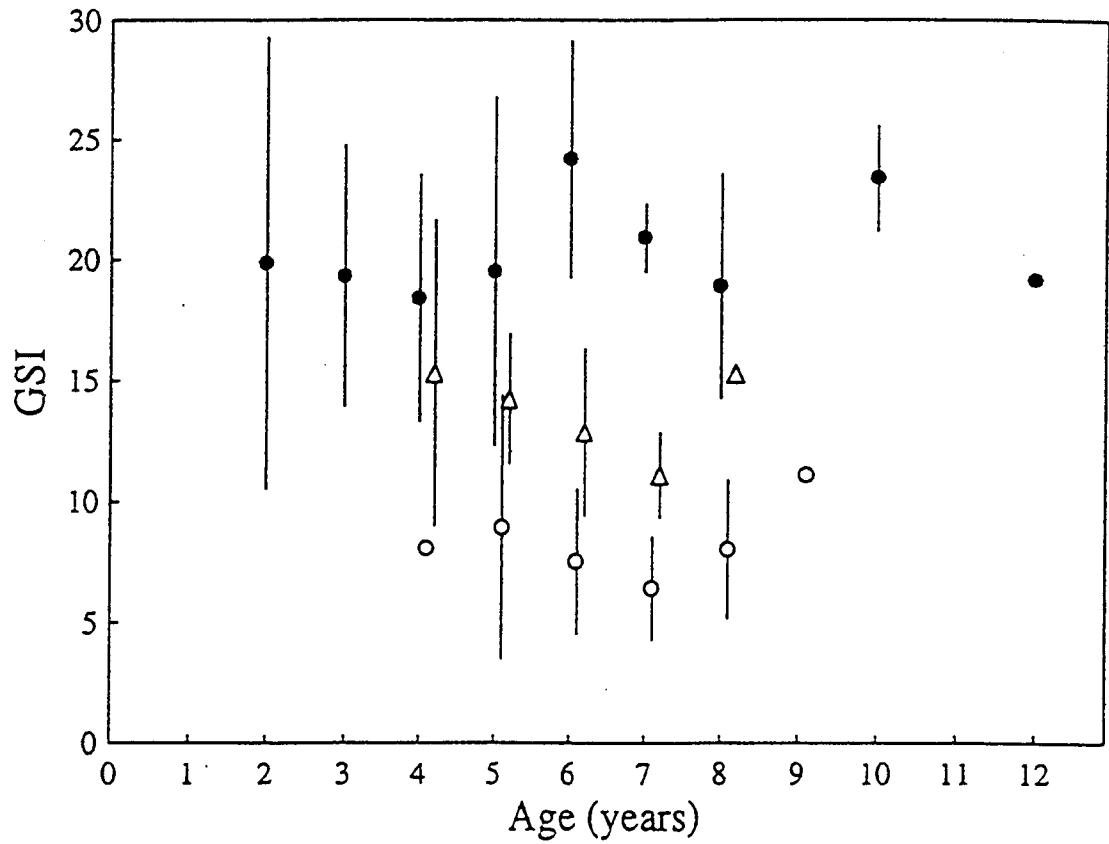
Figure 2.9 The gonadosomatic index (GSI) of females in relation to age. Brown females shaded symbols and Silver females open symbols. Shaded symbols and triangles represent females close to spawning (maturity stages 5-6), circles females caught on August 16. 1996.

until they were almost ripe, spawned, and left the spawning ground shortly after. Spent fish were occasionally found to be feeding on fish eggs.

Discussion

Diet

Both morphs are benthic feeders during summer with little zooplankton in the diet. The morphs have similar diets, but the brown morph appears to be more specialized (Table 2.1), foraging almost exclusively on Eurycercus spp., while the silver morph includes various other prey in its diet, most importantly the mollusc Pisidium (Fig. 2.1). Differences in diet are not explained by size difference between the morphs. There is a trend for large silver morph to forage more than small silver morph on Eurycercus spp. (Fig. 2.2). Cannibalism is rare and does not explain size differences between the charr morphs. Cannibalism is frequently found in other lakes where arctic charr is the only fish, usually at high latitudes where food availability is low (Griffiths 1994, Reist et al. 1995). Lake Vantshlidarvatn is shallow and very productive, which might explain the absence of cannibalism.

Parasites

Parasites are a good indicators of long-term feeding habits of salmonids. Fish become infected by the parasites Eubotrium salvelini, Philoneme oncorhynchi, and Diphyllobotrium spp. when feeding on small crustacean zooplankton or fish that consume it (Curtis 1995). The absence of these parasites from both morphs suggests that these food organisms are of minor importance in the diet of both morphs. Fish become infected by the kidney fluke, Phyllodistomum conostomum when eating Lymnea and Pisidium (Curtis 1995). Low level of infection indicates that few fish feed

mainly on molluscs, although Pisidium appears to be important in the diet of the silver

morph when Eurycercus spp. is at low abundance (Fig. 2.1). Significant differences

between morphs are found in the occurrence of Salmonicola edwardsii. From the eggs

of these crustaceans come free swimming larvae that settle down on fish gills where

they complete their life-cycle. Different susceptibility of the morphs to this parasite

points to differences in physiological state, habitat use, or behavior between the

morphs.

Growth and Sexual Maturation

Sex ratios do not indicate that one sex is more likely to display one morphotype

rather than the other, and the presence of two growth forms of arctic charr in

Vatnshlidarvatn is confirmed (Fig. 2.3). Two alternative maturation strategies are

evidently present among the arctic charr; the brown morph become sexually mature at

young age and small size, the silver morph mature at older age and larger size (Fig. 1.4

chapter 1).

Arctic charr is known to skip years of spawning to regain their energy reserves

before spawning again (Dutil 1986). The silver morph experiences greater variability

in age at sexual maturation than the brown morph that has more predictable maturation

pattern, maturing every year (Fig. 1.4 chapter 1). This might be due to larger size and

longer recovery time, or less stable energy reserves for reproduction, of the former.

Thus, postspawning condition of silver females is relatively poor, they have lower

values for condition factor and LSI (liversomatic index) than that of brown females.

Reproductive Characteristics

When compared directly, both morphs have the same egg size, with egg size

connected to age rather than fish size (Fig. 2.7 and 2.8). Other studies on sympatric

morphs of arctic charr have indicated that larger morphs have larger eggs than small sized morphs (Jonsson and Hindar 1982, Skúlason 1983). Fecundity of both morphs is a function of fish size rather than age (Fig. 2.4 and 2.5). Greater gonadal investment (Fig. 2.9) of the brown females compared to the silver females is thus accomplished by relatively larger egg size of the former (the brown morph has larger egg size than the silver morph after standardizing for size differences between the morphs). It has been suggested that an evolutionary increase in egg size is an adaptation to high juvenile mortality (Wallace and Aasjord 1984, Sargent et al. 1987).

Some studies on sympatric morphs of arctic charr have indicated that larger morphs, due to their growth advantage, have higher fitness than smaller morphs (Jonsson and Hindar 1982, Hindar and Jonsson 1993, Griffiths 1994). My study does not support this conclusion. The brown morph has longer reproductive lifespan (Fig. 1.4 chapter 1), and far higher lifetime fecundity of females than the silver morph (Table 2.2) indicating equal or higher fitness of the former.

Plasticity and Segregation

Previously unidentified mode of phenotypic segregation in a salmonid species is suggested from the current results. Resource polymorphism in the Salmonidae is commonly explained in connection with piscivory/cannibalism, anadromy or the presence of discrete benthic and pelagic habitats in lakes (Skúlason and Smith 1995). None of this seems to explain the polymorphism encountered among arctic charr in Vatnshlidarvatn. The situation in the lake is special. Vatnshlidarvatn is very productive, providing abundant food resources for fish, while interspecific competition is absent. The phenotypic plasticity of arctic charr enables it to utilize variety of habitat and food types. Resource polymorphism in arctic charr can thus be brought about by utilization of empty niches that are not generally available due to competition or interaction with other fish species.

The lake is small, shallow, and geographically simple and both arctic charr morphs are confined to the benthic habitats where they appear to maintain their segregation by different feeding strategies. The presence of one abundant food resource, Eurycercus spp. and lack of interspecific competition may provide the opportunity for the evolution of one feeding specialist, the brown morph. The various other food items available may then be utilized by a second morph, the silver morph, that has more generalized feeding habits. Both morphs converge on feeding on Eurycercus spp. when it is superabundant (August sample), and segregation is only important when that food resource is scarce (July sample) and competition between morphs presumably high (Liem and Kaufman 1984). Coexistence is then made possible by adaptive switching behavior of the generalist, which in turn decreases temporal variation in habitat availability experienced by the specialist (Wilson and Yoshimura 1994).

The segregation between the arctic charr morphs is relatively well developed in morphology and reproductive strategies, but the conditions prevailing in the lake may favor overlap in resource use to the extent that it maximizes use of available resources. This is in agreement with Liem (1984) who emphasized the great versatility of teleost fish enabled them to sustain considerable overlap in resource use.

More variable diet possibly relates to greater behavioral plasticity of the silver morph than the brown morph, which could also clarify why the silver morph is more variable in reproductive characteristics than the brown morph. Day et al. (1994) found that variable diet of a limnetic threespined stickleback morph was related to relatively high morphological plasticity, compared to a sympatric benthic morph with more diet specialization. Griffiths (1994) reviewed the literature on bimodal size distribution among arctic charr populations. His data indicate that the existence of larger morphs is based on more variable food selection than exhibited by the coexisting smaller morph. This is in agreement with my results. Differences in behavior and behavioral plasticity can thus initiate and explain the different life history trajectories (Metcalfe 1993, Skúlason and Smith 1995) (Fig. 2.10).
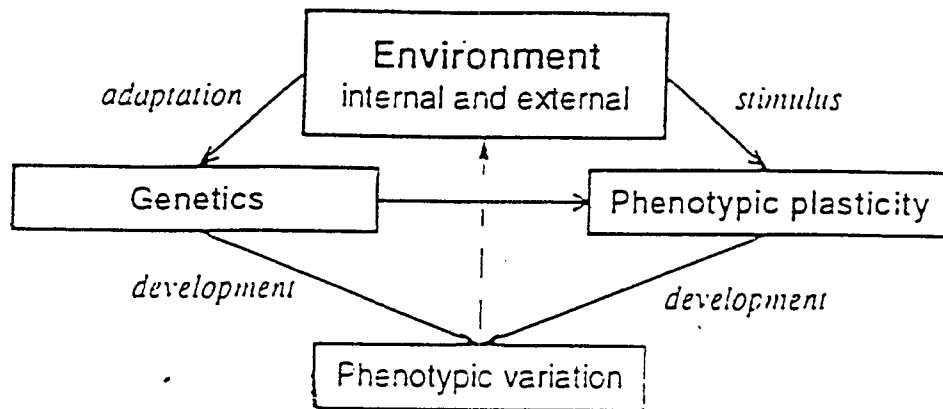
Figure 2.10 Schematic of the relationship between environment (internal and external), genetics, and phenotypic plasticity in the development of a phenotype. Phenotypic plasticity is affeced by genetic adaptation.

Spatial and temporal differences in spawning suggest some assortative mating of the two morphs. Other studies of sympatric arctic charr have indicated a gradient in isolating mechanisms, from partial isolation in Vangsvatnet, Norway (Jonsson and Hindar 1982), Stora Rösjön Sweden (Svedäng 1992), to being more pronounced like in Thingvallavatn Iceland (Skúlason et al. 1989a). Studies on other salmonid species like whitefish (Kirkpatrick and Selander 1978, Bodaly et al. 1992), atlantic salmon (Salmo salar) (Verspoor and Cole 1989, Birt et al. 1991), and sockeye salmon and kokanee (Oncorhynchus nerka) (Wood and Foote 1996), show that reproductive isolation can be accomplished in sympatry through assortative mating of co-occurring morphs on the spawning grounds.

Polymorphism can be maintained by disruptive selection (Smith 1993), or frequency- dependent natural selection (without reproductive isolation) (Gross 1991, Pfennig 1992, Hori 1993). Factors that lead to reproductive isolation can be correlated with factors responsible for maintenance of ecological segregation. The process of speciation thus can be brought about despite gene flow, by divergent selection, sampling drift, and sexual selection (Rice and Hostert 1993).

Although there is considerable evidence for the presence of two arctic charr morphs with different life histories and morphology in Vatnshlidarvatn, further research is needed to clarify its species status. The results, though, warrant the two morphs being treated as two separate species for conservation, biological, and management purposes.

References

Adalsteinsson, H. 1979. Zooplankton and its relation to available food in Lake Mývatn. *Oikos* **32**: 162 - 194.

Barber WA, and McFarlane GA. 1987. Evaluation of three techniques to age Arctic char from Alaskan and Canadian waters. *Transactions into the American Fisheries Society* **116**: 874 - 881.

Birt TP, Green JM, and Davidson WS. 1991. Midochondrial DNA variation reveals genetically distinct sympatric populations of anadromous and nonanadromous Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences* **48**: 577 - 582.

Bodaly RA, Clayton JW, Lindsey CC, and Vuorinen J. 1992. Evolution of Lake whitefish (*Coregonus clupeaformis*) in North America during the Pleistocene: Genetic differentiation between sympatric populations. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 769 - 779.

Curtis M. 1995. The ecological parasitology of Charrs: Relationships between parasites and food web structure in Northern lakes. *Nordic Journal of Freshwater Research* **71**: 92 - 101.

Dahl K. 1917. *Studier and forsök over örret og örretvand.* Kristiania: Centraltrykkeriet.(Studies on trout and trout-lakes). [In Norwegian.]

Day T, Pritchard J, and Schluter D. 1994. A comparison of two sticklebacks. *Evolution* **48**: 1723 - 1734.

Dutil JD. 1986. Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). *Copeia* : 945 - 955.

Everhart WH, and Youngs WD. 1981. *Principles of Fishery Science.* 2ed. Ithaca: Comstock Publications Associates.

Gardner AS, Walker AF, and Greer RB. 1988. Morphometric analysis of two ecologically distinct forms of Arctic charr, *Salvelinus alpinus* (L.), in Loch Rannoch, Scotland. *Journal of Fish Biology* **32**: 901 - 910.

Gotelli NJ. 1995. *A primer of Ecology.* Sunderland: Sinauer.

Griffiths D. 1994. The size structure of lacustrine Arctic charr (Pisces: Salmonidae) populations. *Biological Journal of the Linnean Society* **51**: 337- 357.

Gross MR. 1991. Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. *Philosophical Transactions Royal Society of London* **332**: 59 - 66.

Hindar K, and Jonsson B. 1993. Ecological polymorphism in Arctic charr. *Biological Journal of the Linnean Society* **48**: 63 - 74.

Hindar K, Ryman N, and Ståhl G. 1986. Genetic differentiation among local populations and morphotypes of Arctic charr, *Salvelinus alpinus*. *Biological Journal of the Linnean Society* **27**: 269 - 285.

Hori M. 1993. Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. *Science* **260**: 216 - 219.

Johnson L. 1980. The arctic charr, *Salvelinus alpinus*. In E. K. Balon [ed.] *Charrs. Salmonid Fishes of the genus Salvelinus*. The Hague: Dr W. Junk. pp 15 - 98.

Johnson L. 1983. Homeostatic characteristics of single species fish stocks in arctic lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 987 - 1024.

Jonsson B, and Hindar K. 1982. Reproductive strategy of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet lake Western Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **39**: 1404 - 1413.

Jonsson B, Skúlason S, Snorrason SS, Sandlund OT, Malmquist HJ, Jónasson PM, Gydemo R, Lindem T. 1988. Life history variation of polymorphic Arctic charr (*Salvelinus alpinus*) in Thingvallavatn, Iceland. *Canadian Journal of Fisheries and Aquatic Sciences* **45**: 1537 - 1547.

Kirkpatrick M, and Selander RK. 1978. Genetics of speciation in lake whitefishes in the Allegash Basin. *Evolution* **33**: 478 - 485.

Liem KF. 1984. Functional versatility, speciation, and niche overlap: are fishes different? In: Meyers DG, Strickler JR. eds. *Trophic interactions within aquatic ecosystems.* Westview Press, 269 - 305.

Liem KF, and Kaufman LS. 1984. Intraspecific macroevolution: functional biology of the polymorphic cichlid species *Cichlasoma minckleyi*. In Echelle A A, and Kornfield I. eds. *Evolution of fish species flocks*. Orono: University of Maine press, 203 - 215.

Ludwig JA, and Reynolds JF. 1988. *Statistical ecology. A primer on methods and computing*. John Wiley and Sons, New York, New York, USA.

Malmquist HJ, Snorrason SS, Skúlason S, Jonsson B, Sandlund OT, Jónasson PM. 1992. Diet differentiation in polymorphic Arctic charr in Thingvallavatn Iceland. *Journal of Animal Ecology* **61**: 21 - 34.

Metcalfe NB. 1993. Behavioural causes and consequences of life history variation in fish. *Marine Behavioral Physiology* **23**: 205 -217.

Nordeng H. 1983. Solution to the "char problem" based on Arctic char (*Salvelinus alpinus*) in Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 1372 - 1387.

Pfennig DW. 1992. Polyphenism in spadefoot toad tatpoles as a logally adjusted evolutionarily stable strategy. *Evolution* **46**: 1408 - 1420.

Reist JD, Gyselman E, Babaluk JA, Johnson JD, Wissink R. 1995. Evidence for two morphotypes of Arctic char (*Salvelinus alpinus* (L.)) from Lake Hazen, Ellesmere Island, Northwest Territories, Canada. *Nordic Journal of Freshwater Research* **71**: 396-410.

Rice WR, and Hostert EE. 1993. Laboratory experiments on speciation: what have we learned in 40 years?. *Evolution* **47**: 1637 - 1653.

Robinson BW, and Wilson DS. 1994. Character release and displacement in fishes: A neglected literature. *The American Naturalist* **144**: 596 - 627.

Robinson BW, Wilson DS, Margosian AS, and Lotito PT. 1993. Ecological and morphological differentiation of pumpkinseed sunfish in lakes without bluegill sunfish. *Evolutionary Ecology* **7**: 451 - 464.

Sargent RC, Taylor PD, and Gross MR. 1987. Parental care and the evolution of egg size in fishes. *The American Naturalist* **129**: 32 - 46.

Schluter D. 1988. Character displacement and the adaptive divergence of finches on islands and continents. *The American Naturalist* **131**: 799 - 824.

Schluter D, and McPhail JD. 1992. Ecological character displacement and speciation in sticklebacks. *The American Naturalist* **140**: 85 - 108.

Skúlason S. 1983. *Útlit, vöxtur og aexlunarlíffraedi mismunandi gerda bleikjunnar,* Salvelinus alpinus (L.) *i Thingvallavatni.* (Morphology, growth and reproductive characteristics of different morphs of arctic charr, *Salvelinus alpinus* (L.) in Thingvallavatn, Iceland.) Unpublished Post-graduate Thesis, University of Iceland. [In Icelandic with English abstract.]

Skúlason S, Antonsson T, Gudbergsson G, Malmquist HJ, and Snorrason SS. 1992. Variability in Icelandic Arctic charr. *Icelandic Agricultural Sciences* : 143 - 153.

Skúlason S, Noakes DLG, and Snorrason SS. 1989a. Ontogeny of trophic morphology in four sympatric morphs of arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. *Biological Journal of the Linnean Society* **38**: 281 - 301.

Skúlason S, and Smith TB. 1995. Resource polymorphism in vertebrates. *Tree* **10**: 347 -388.

Skúlason S, Snorrason SS, Noakes DLG, Ferguson MM, and Malmquist HJ. 1989b. Segregation in spawning and early life history among polymorphic Arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. *Journal of Fish Biology* **35** (Supplement A): 225 - 232.

Skúlason S, Snorrason SS, and Noakes DLG. 1996. Genetic basis for life history variation in polymorphic Arctic charr, *Salvelinus alpinus*. In press *Canadian Journal of Fisheries and Aquatic Sciences*.

Smith TB. 1993. Disruptive selection and the genetic basis of bill size polymorphism in the African finch Pyrenestes. *Nature* **363**: 618 - 620.

Smith TB, and Skúlason S. 1996. Evolutionary significance of resource polymorphisms in fishes amphibians and birds. In press *Annual Review of Ecology and Systematics*.

Snorrason SS, Skúlason S, Jonsson B, Malmquist HJ, Jónasson PM, Sandlund OT, and Lindem T. 1994. Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces; Salmonidae): morphological divergence and ontogenetic niche shifts. 1994. *Biological Journal of the Linnean Society* **52**: 1 - 18.

Sparholt H. 1985. The population, survival, growth, reproduction and food of arctic charr, *Salvelinus alpinus* (L.), in four unexploited lakes in Greenland. *Journal of Fish Biology* **26**: 313 - 330.

Svedäng H. 1990. Genetic basis of life-history variation of dwarf and normal Arctic charr, *Salvelinus alpinus* (L.), in Stora Rösjön, central Sweden. *Journal of Fish Biology* **36**: 917 - 932.

Svedäng H. 1992. Observations on interbreeding between dwarf and normal arctic charr, *Salvelinus alpinus*, from Stora Rösjön, central Sweden. *Environmental Biology of Fishes* **33**: 293 - 298.

Tómasson T. 1987, *unpublished.* The connection between growth and size at sexual maturity in Icelandic arctic charr (*Salvelinus alpinus*). A paper prepared for the International conference on alternative life history styles of fishes and other organisms. Grahamstown, South Africa.

Verspoor E, and Cole LJ. 1989. Genetically distinct sympatric populations of resident and anadromous Atlantic salmon, *Salmo salar*. *Canadian Journal of Zoology* **67**: 1453 - 1461.

Wallace JC, and Aasjord D. 1984. An investigation of the consequences of egg size for the culture of Arctic charr, *Salvelinus alpinus* (L.). *Journal of Fish Biology* **24**: 427 - 435.

Wilson DS, and Yoshimura J. 1994. On the coexistence of specialists and generalists. *The American Naturalist* **144**: 692 - 707.

Wood CC, and Foote CJ. 1996. Evidence for sympatric genetic divergence of anadromous and non-anadromous morphs of Sockeye salmon (*Oncorhynchus nerka*). *Evolution* **50**: 1256 - 1279.

SUMMARY

The study supports the hypothesis that arctic charr in Vatnshlidarvatn constitute two different morphs. The morphs differ in growth and age at sexual maturation, they differ in body shape, and gill raker number, in feeding and reproduction.

BIBLIOGRAPHY

Adalsteinsson H. 1979. Zooplankton and its relation to available food in Lake Mývatn. *Oikos* **32**: 162 - 194.

Barber WA, McFarlane GA. 1987. Evaluation of three techniques to age Arctic char from Alaskan and Canadian waters. *Transactions into the American Fisheries Society* **116**: 874-881.

Birt TP, Green JM, Davidson WS. 1986. Midochondrial DNA variation reveals genetically distinct sympatric populations of anadromous and nonanadromous Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences* **48**: 577-582.

Bodaly RA, Clayton JW, Lindsey CC, and Vuorinen J. 1992. Evolution of Lake whitefish (*Coregonus clupeaformis*) in North America during the Pleistocene: Genetic differentiation between sympatric populations. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 769 - 779.

Curtis M. 1995. The ecological parasitology of Charrs: Relationships between parasites and food web structure in Northern lakes. *Nordic Journal of Freshwater Research* **71**: 92 - 101.

Dahl K. 1917. Studier and forsök over örret og örretvand. Kristiania: Centraltrykkeriet.(Studies on trout and trout-lakes). [In Norwegian.]

Damsgård B. 1991. Smolting characters in anadromous and resident Arctic charr, Salvelinus alpinus (L.). *Journal of Fish Biology* **39**: 765-774.

Day T, Pritchard J, and Schluter D. 1994. A comparison of two sticklebacks. *Evolution* **48**: 1723 - 1734.

Dutil JD. 1986. Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). *Copeia*. 945 - 955.

Echelle AA, Kornfield I, eds. 1984. *Evolution of Fish Species Flocks*. Orono: University of Maine Press.

Everhart WH, and Youngs WD. 1981. *Principles of Fishery Science.* 2ed. Ithaca: Comstock Publications Associates.

Gardner AS, Walker AF, Greer RB. 1988. Morphometric analysis of two ecologically distinct forms of Arctic charr, *Salvelinus alpinus* (L.), in Loch Rannoch, Scotland. *Journal of Fish Biology* **32**: 901-910.

Gotelli NJ. 1995. *A primer of Ecology* Sunderland: Sinauer.

Griffiths D. 1994. The size structure of lacustrine Arctic charr (Pisces: Salmonidae) populations. *Biological Journal of the Linnean Society* **51**: 337-357.

Gross MR. 1991. Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. *Philosophical Transactions Royal Society of London* **332**: 59 - 66.

Harvey PH, Pagel MD. 1993. *The Comparative Method in Evolutionary Biology.* Oxford: Oxford University Press.

Hindar K, Jonsson B. 1982. Habitat and food segregation of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet lake, Western Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **39**: 1030-1045.

Hindar K, Jonsson B. 1993. Ecological polymorphism in Arctic charr. *Biological Journal of the Linnean Society* **48**: 63-74.

Hindar K, Ryman N, Ståhl G. 1986. Genetic differentiation among local populations and morphotypes of Arctic charr, *Salvelinus alpinus*. *Biological Journal of the Linnean Society* **27**: 269-285.

Hori M. 1993. Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. *Science* **260**: 216 - 219.

Johnson L. 1980. The arctic charr, *Salvelinus alpinus*. In E. K. Balon [ed.] Charrs. Salmonid Fishes of the genus Salvelinus. The Hague: Dr W. Junk. pp 15 - 98.

Johnson L. 1983. Homeostatic characteristics of single species fish stocks in arctic lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 987-1024.

Jolicoeur P. 1963. The multivariate generalization of the allometry equation. *Biometrics* **19**: 497-499.

Jonsson B, Hindar K. 1982. Reproductive strategy of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet lake Western Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **39**: 1404-1413.

Jonsson B, Skúlason S, Snorrason SS, Sandlund OT, Malmquist HJ, Jónasson PM, Gydemo R, Lindem T. 1988. Life history variation of polymorphic Arctic charr (*Salvelinus alpinus*) in Thingvallavatn, Iceland. *Canadian Journal of Fisheries and Aquatic Sciences* **45**: 1537 - 1547.

Kirkpatrick M, and Selander RK. 1978. Genetics of speciation in lake whitefishes in the Allegash Basin. *Evolution* **33**: 478 - 485.

Kuhry B, Marcus LF. 1977. Bivariate linear models in biometry. *Systematic Zoology* **26**: 201-209.

Liem KF 1984. Functional versatility, speciation, and niche overlap: are fishes different? In: Meyers DG, Strickler JR, eds.*Trophic interactions within aquatic ecosystems*. Westview Press, 269-305.

Liem KF, and Kaufman LS. 1984. Intraspecific macroevolution: functional biology of the polymorphic cichlid species *Cichlasoma minckleyi*. In Echelle, A. A., and Kornfield, I, eds. *Evolution of fish species flocks*. Orono: University of Maine press, 203 - 215.

Ludwig JA, and Reynolds JF. 1988. Statistical ecology. A primer on methods and computing. John Wiley and Sons, New York, New York, USA.

Malmquist HJ, Snorrason SS, Skúlason S, Jonsson B, Sandlund OT, Jónasson PM. 1992. Diet differentiation in polymorphic Arctic charr in Thingvallavatn Iceland. *Journal of Animal Ecology* **61**: 21 - 34.

Marcus LF. 1988. Traditional morphometrics. In: Rohlf FJ, Bookstein FL, eds. *Proceedings of the Michigan morphometrics workshop.*77-122.

Metcalfe NB. 1993. Behavioural causes and consequences of life history variation in fish. *Marine Behavioral Physiology* **23**: 205 -217.

Meyer A. 1990. Morphometrics and allometry in the trophically polymorphic cichlid fish, *Cichlasoma citrinellum*: Alternative adaptations and ontogenetic changes in shape. *Journal of Zoology London* **221**: 237-260.

Nordeng H. 1983. Solution to the "char problem" based on Arctic char (*Salvelinus alpinus*) in Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 1372-1387.

Nyman L, Hammar J, Gydemo R. 1981. The systematics and biology of landlocked populations of Arctic char from Northern Europe. Institute of Freshwater Research Drottningholm. Report No. 59: 128-41.

Pfennig DW. 1992. Polyphenism in spadefoot toad tatpoles as a logally adjusted evolutionarily stable strategy. *Evolution* **46**: 1408 - 1420.

Pimentel RA. 1979. *Morphometrics*. Iowa: Kendal/Hunt Publishing Company.

Reist JD. 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. *Canadian Journal of Zoology* **63**: 1429-1439.

Reist JD, Gyselman E, Babaluk JA, Johnson JD, Wissink R. 1995. Evidence for two morphotypes of Arctic char (*Salvelinus alpinus* (L.)) from Lake Hazen, Ellesmere Island, Northwest Territories, Canada. *Nordic Journal of Freshwater Research* **71**: 396-410.

Rencher AC. 1988. On the use of correlations to interpret canonical functions. *Biometrika* **75**: 363-365.

Rice WR, and Hostert EE. 1993. Laboratory experiments on speciation: what have we learned in 40 years?. *Evolution* **47**: 1637 - 1653.

Robinson BW, and Wilson DS. 1994. Character release and displacement in fishes: A neglected literature. *The American Naturalist* **144**: 596 - 627.

Robinson BW, Wilson DS, Margosian AS, and Lotito PT. 1993. Ecological and morphological differentiation of pumpkinseed sunfish in lakes without bluegill sunfish. *Evolutionary Ecology* **7**: 451 - 464.

Sargent RC, Taylor PD, and Gross MR. 1987. Parental care and the evolution of egg size in fishes. *The American Naturalist* **129**: 32 - 46.

Schluter D. 1988. Character displacement and the adaptive divergence of finches on islands and continents. *The American Naturalist* **131**: 799 - 824.

Schluter D, and McPhail JD. 1992. Ecological character displacement and speciation in sticklebacks. *The American Naturalist* **140**: 85 - 108.

Schmitz M. 1992. Annual variations in rheotactic behavior and seawater adaptability in landlocked Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 448-452.

Shea BT. 1985. Bivariate and multivariate growth allometry: statistical and biological considerations. *Journal of Zoology London* (A) **206**: 367-390.

Skúlason S. 1983. *Útlit, vöxtur og aexlunarlíffraedi mismunandi gerda bleikjunnar,* Salvelinus alpinus (L.) *i Thingvallavatni.* (Morphology, growth and reproductive characteristics of different morphs of arctic charr, *Salvelinus alpinus* (L.) in Thingvallavatn, Iceland.) Unpublished Post-graduate Thesis, University of Iceland. [In Icelandic with English abstract.]

Skúlason S, Antonsson T, Gudbergsson G, Malmquist H J, Snorrason SS. 1992. Variability in Icelandic Arctic charr. *Icelandic Agricultural Sciences* : 143-153.

Skúlason S, Noakes DLG, Snorrason, SS. 1989a. Ontogeny of trophic morphology in four sympatric morphs of arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. *Biological Journal of the Linnean Society* **38**: 281-301.

Skúlason S, Smith TB. 1995. Resource polymorphism in vertebrates. *Tree* **10**: 347-388.

Skúlason S, Snorrason SS, Noakes DLG, Ferguson MM, and Malmquist HJ. 1989b. Segregation in spawning and early life history among polymorphic Arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. *Journal of Fish Biology* **35** (Supplement A): 225 - 232.

Skúlason S, Snorrason SS, and Noakes DLG. 1996, *in press.* Genetic basis for life history variation in polymorphic Arctic charr, *Salvelinus alpinus.* In press *Canadian Journal of Fisheries and Aquatic Sciences.*

Smith TB. 1993. Disruptive selection and the genetic basis of bill size polymorphism in the African finch Pyrenestes. *Nature* **363**: 618 - 620.

Smith TB, Skúlason S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. In press *Annual Review of Ecology and Systematics Journal of the Linnean Society* **52**: 1-18.

Snorrason SS, Skúlason S, Jonsson B, Malmquist HJ, Jónasson PM, Sandlund OT, and Lindem T. 1994. Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces; Salmonidae): morphological divergence and ontogenetic niche shifts. 1994. *Biological Journal of the Linnean Society* **52**: 1 - 18.

Sokal RR, Rohlf FJ. 1981. *Biometry*. New York: W.H. Freeman and Co.

Sparholt H. 1985. The population, survival, growth, reproduction and food of arctic charr, *Salvelinus alpinus* (L.), in four unexploited lakes in Greenland. *Journal of Fish Biology* **26**: 313-330.

Staurnes M, Sigholt T, Lysfjord G, Gulseth OA. 1992. Difference in the seawater tolerance of anadromous and landlocked populations of Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 443-447.

Stoner AW, Livingston RJ. 1984. Ontogenetic patterns in diet and feeding morphology in sympatric sparid fishes from seagrass meadows. *Copeia*: 174-187.

Strauss RE. 1990. Heterochronic variation in the developmental timing of cranial ossifications in pociliid fishes (Cyprinodontiformes). *Evolution* **44**: 1558-1567.

Strauss RE, Fuiman LA. 1985. Quantitative comparisons of body form and allometry in larval and adult pacific sculpins (Teleostei: Cottidae). *Canadian Journal of Zoology* **63**: 1582-1589.

Svedäng H. 1990. Genetic basis of life-history variation of dwarf and normal Arctic charr, *Salvelinus alpinus* (L.), in Stora Rösjön, central Sweden. *Journal of Fish Biology* **36**: 917-932.

Svedäng H. 1992. Observations on interbreeding between dwarf and normal arctic charr, *Salvelinus alpinus*, from Stora Rösjön, central Sweden. *Environmental Biology of Fishes* **33**: 293 - 298.

Taylor EB, Foote CJ. 1991. Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). *Journal of Fish Biology* **38**: 407-419.

Toline CA, Baker AJ. 1993. Foraging tactic as a potential selection pressure influencing geographic differences in body shape among populations of dace (*Phoxinus eos*). *Canadian Journal of Zoology* **71**: 2178-2184.

Tómasson T. 1987, *unpublished.* The connection between growth and size at sexual maturity in Icelandic arctic charr (*Salvelinus alpinus*). A paper prepared for the International conference on alternative life history styles of fishes and other organisms. Grahamstown, South Africa.

Verspoor E, and Cole LJ. 1989. Genetically distinct sympatric populations of resident and anadromous Atlantic salmon, *Salmo salar. Canadian Journal of Zoology* **67**: 1453 - 1461.

Wallace JC, and Aasjord D. 1984. An investigation of the consequences of egg size for the culture of Arctic charr, *Salvelinus alpinus* (L.). *Journal of Fish Biology* **24**: 427 - 435.

Wilson DS, and Yoshimura J. 1994. On the coexistence of specialists and generalists. *The American Naturalist* **144**: 692 - 707.

Wood CC, and Foote CJ. 1996. Evidence for sympatric genetic divergence of anadromous and non-anadromous morphs of Sockeye salmon (*Oncorhynchus nerka*). Evolution **50**: 1265 - 1279.

APPENDICES

Appendix 1. Statistical Considerations

All the morphometric methods used; univariate analysis, PCA, and CDA, are successful in segregating between the two morphs. The use of the pooled within-class standardized canonical coefficients over total canonical structure is emphasized. The total canonical structure seems to be a direct function of the univariate F's for the separate variables (table 1.1 and 1.2), indicating that it does not provide additional multivariate information. Such correlation's have been noticed previously by Rencher (1988), who used the pooled-within sample variability in computing the canonical correlation's. I calculate the correlation's in my study using the total variability. My results concur with Marcus (1988), who suspected that Renchers results hold for other methods in calculating the correlation's as well.

This study reveals the limitations of the regression method in estimating allometric slopes when forms compared have low or unequal correlation's between morphometric variables. As the correlation deviates more from 1.0, greater underestimation of the true slopes occur (table 1.3, and appendix 2). The low correlation's between characters of the brown morph cause the regression method to greatly underestimate allometric coefficients, while high correlation's between characters of the silver morph result in relatively accurate estimates compared to other methods employed (table 1.3). These results underline that the regression method should not be employed if an accurate estimate of the true slope is pursued (see Harvey and Pagel 1993). The covariance method (Kuhry and Marcus 1977) has the important property of being independent of the true error λ and its use for calculating bivariate slopes is recommended.

There is a good coherence between the allometric coefficients calculated from the covariance ratio and the multivariate allometric coefficients (table 1.1). Again indicating that both methods give accurate results.

Appendix 2. Bivariate Correlations

Correlations (r) used in calculating covariances for estimation of bivariate allometric slopes, by the covarinance-ratio method. Correlations are between 16 mensural characters on arctic charr from Vatnshlidarvatn, Iceland, against standard length (STL), and head length (HL).

Trait[a]	STL				HL			
	B1	S1	B0	S0	B1	S1	B0	S0
POL	0.928	0.980	0.926	0.963	0.946	0.983	0.943	0.966
OOL	0.839	0.954	0.857	0.872	0.870	0.954	0.892	0.881
HL	0.977	0.993	0.976	0.986	1.000	1.000	1.000	1.000
MXL	0.954	0.990	0.961	0.979	0.970	0.992	0.984	0.987
LJ	0.946	0.989	0.962	0.981	0.963	0.991	0.983	0.988
HDD	0.960	0.975	0.964	0.979	0.970	0.975	0.979	0.982
MXW	0.721	0.964	0.899	0.900	0.722	0.958	0.919	0.895
IOW	0.950	0.989	0.958	0.974	0.971	0.988	0.967	0.978
PCL	0.956	0.987	0.948	0.970	0.967	0.988	0.966	0.971
PVL	0.938	0.981	0.928	0.965	0.955	0.981	0.956	0.970
ANL	0.930	0.981	0.926	0.961	0.940	0.980	0.944	0.960
ANW	0.891	0.966	0.943	0.934	0.908	0.959	0.949	0.925
CPL	0.817	0.956	0.739	0.922	0.763	0.961	0.710	0.895
CPD	0.951	0.983	0.919	0.960	0.951	0.983	0.914	0.958
CFL	0.902	0.985	0.901	0.926	0.922	0.983	0.896	0.927
FLT	0.762	0.900	0.683	0.825	0.796	0.906	0.740	0.831

[a] For key to abbreviations, see legend to Fig. 1.2
B1 = brown males; S1 = silver males; B0 = brown females; S0 = silver females

Appendix 3. Standard Deviations

Standard deviations (SD) used in calculating covariances for estimation of bivariate allometric slopes, by the covariance-ratio method. Standard deviations for 17 mensural characters on arctic charr from Vatnshlidarvatn, Iceland

Trait[a]	SD			
	B1	S1	B0	S0
POL	0.208	0.335	0.211	0.215
OOL	0.117	0.199	0.122	0.122
HL	0.164	0.285	0.153	0.178
MXL	0.204	0.327	0.189	0.201
LJ	0.207	0.339	0.192	0.205
HDD	0.178	0.299	0.175	0.188
MXW	0.231	0.294	0.160	0.182
IOW	0.188	0.315	0.181	0.202
PCL	0.184	0.307	0.173	0.190
PVL	0.191	0.304	0.180	0.187
ANL	0.194	0.303	0.190	0.193
ANW	0.210	0.350	0.188	0.211
CPL	0.215	0.301	0.198	0.189
CPD	0.178	0.306	0.166	0.198
CFL	0.171	0.288	0.136	0.180
FLT	0.190	0.255	0.236	0.230
STL	0.170	0.299	0.171	0.184
Sample size	92	152	74	127

[a] For key to abbreviations, see legend to Fig. 1.2
B1 = brown males; S1 = silver males; B0 = brown females; S0 = silver females

Appendix 4. Raw Coefficients

Raw canonical coefficients (CAN) from canonical discriminant analysis of 16 mensural characters size adjusted by regression technique, computation of residuals from the regression of untransformed morphological variables on standard length (STL). Raw multivariate coefficients from within-group PCAs, of 17 log transformed mensural characters, based on a variance-covariance matrix. Data on arctic charr from Vatnshlidarvatn, Iceland

Trait[a]	Raw CAN	Raw multivariate coefficients			
		B1	S1	B0	S0
POL	0.006	0.199	0.330	0.200	0.207
OOL	0.060	0.101	0.190	0.109	0.108
HL	0.023	0.162	0.284	0.152	0.177
MXL	0.003	0.198	0.325	0.186	0.199
LJ	− 0.166	0.201	0.337	0.188	0.202
HDD	0.052	0.174	0.293	0.171	0.185
MXW	0.018	0.175	0.285	0.149	0.166
IOW	0.311	0.182	0.312	0.175	0.199
PCL	0.330	0.181	0.305	0.169	0.187
PVL	0.009	0.185	0.300	0.173	0.183
ANL	0.166	0.186	0.299	0.182	0.188
ANW	0.000	0.192	0.338	0.181	0.200
CPL	− 0.304	0.168	0.288	0.147	0.173
CPD	− 0.012	0.169	0.301	0.151	0.191
CFL	− 0.145	0.158	0.284	0.124	0.169
FLT	− 0.104	0.158	0.269	0.192	0.203
(STL)		0.167	0.297	0.166	0.182

[a] For key to abbreviations, see legend to Fig. 1.2
B1 = brown males; S1 = silver males; B0 = brown females; S0 = silver females

Appendix 5. Standard Deviations of PCA Scores

Standard deviations (SD) of principal component scores for type, sex, and age groups, from between group PCAs, based on a variance-covariance matrix. Multivariate analysis of 16 mensural characters, size adjusted by regression technique, computation of residuals from the regression of untransformed morphological variables on standard length (STL). Data on arctic charr from Vatnshlidarvatn, Iceland.

| | Brown type | | | | | | | | | | | | Silver type | | | | | | | | | | | |
| | males | | | females | | | males | | | females | | |
Age	SD PC1	SD PC2	n	SD PC1	SD PC2	n	SD PC1	SD PC2	n	SD PC1	SD PC2	n
1+	0.67	0.28	6	–	–	1	0.29	0.43	13	–	–	0
2+	0.52	0.46	53	0.34	0.46	3	0.54	0.75	11	0.69	0.90	4
3+	0.66	0.63	13	1.41	0.72	20	0.54	0.73	40	0.55	0.94	29
4+	0.67	1.08	10	0.60	1.14	8	0.67	0.92	19	0.53	0.39	19
5+	1.44	0.80	7	1.06	0.96	13	0.64	1.19	35	0.62	0.62	32
6+	1.42	0.72	3	0.72	0.99	16	0.98	0.66	17	0.76	1.04	21
7+	–	–	0	0.98	0.50	4	1.25	1.45	14	0.76	0.92	11
8+*	–	–	0	0.82	0.80	9	1.13	0.95	3	1.02	1.35	12

* 8+ and older combined