Ecological diversity in the polymorphic fish Arctic charr (*Salvelinus alpinus*)

Pamela J. Woods

Ecological diversity in the polymorphic fish Arctic charr (*Salvelinus alpinus*)

Pamela J. Woods

Dissertation submitted in partial fulfilment of a *Philosophiae Doctor* degree in Biology

Supervisor

Professor Sigurður Snorrason

PhD Committee

Dr. Skúli Skúlason
Dr. Thomas P. Quinn
Dr. Daniel E. Schindler

Faculty of Life and Environmental Sciences
School of Engineering and Natural Sciences
University of Iceland
Reykjavík, December 2011

Ecological diversity in the polymorphic fish Arctic charr (*Salvelinus alpinus*)

Dissertation submitted in partial fulfilment of a *Philosophiae Doctor* degree in Biology

Faculty of Life and Environmental Sciences
School of Engineering and Natural Sciences
University of Iceland
ASKJA, Sturlugata 7
101 Reykjavík
Iceland
Tel: +354 525 4000

Bibliographic information:

Woods, 2011, *Ecological diversity in the polymorphic fish Arctic charr (*Salvelinus alpinus*)*, PhD dissertation, Faculty of Life and Environmental Sciences, University of Iceland, 236 pp.

ISBN 978-9935-9064-3-4

Printing: Háskólaprent
Reykjavik, Iceland, December 2011

Abstract

The Arctic charr *Salvelinus alpinus* is extremely diverse and its differentiation may indicate ecological speciation. This dissertation aims to compare trends in ecological diversity across broad geographical regions and place it within an ecosystem context by comparing study systems in Iceland and Alaska. In the first chapter, gut contents of Arctic charr across ~50 lakes in Iceland were analyzed to form 6 habitat-associated prey categories. Consumption of zooplankton was related to high silicon dioxide and low nutrient concentrations in the lake. Snail, tadpole shrimp, pea clam, and fish consumption were related to lake altitude, depth, and brown trout abundance. In the second chapter, the relationship between morphology and consumption within each prey category is analyzed. In the third chapter, methods are developed to detect polymorphism through the presence of multiple growth curves within populations using mixture models. Random forest models indicated that polymorphism was more likely to occur in lakes with low brown trout abundance, high altitude, and conditions with high zooplankton and fish consumption. The fourth chapter analyzes morphological variation in 4 lakes in southwestern Alaska. Two forms were found to coexist in Lower Tazimina Lake. Finally, food webs are analyzed in the fifth chapter using stable isotope ratios of fish fauna across 11 lakes in Iceland and 4 lakes in Alaska. Limnetic carbon use and piscivory appears dependent on morphological differentiation and the presence of competitors.

Útdráttur

Bleikja *Salvelinus alpinus* er fjölbreytt tegund þar sem stofnaaðskilnaður getur bent til vistfræðilegrar tegundamyndunar. Markmið ritgerðarinnar var að skoða tilhneigingar í vistfræðilegum fjölbreytileika í tengslum við vistkerfi. Þetta var gert á stóru landsvæði með samanburði milli Íslands og Alaska. Í fyrsta kafla var fæða bleikju úr u.þ.b. 50 vötnum skoðuð. Fengust 6 fæðuhópar sem tengja mátti búsvæðum. Fæðunámi á svifdýrum tengdist auknu magni silikon dioxíðs og litlu næringarefnaframboðiu. Át á sniglum, skötuormum, ertuskel og fiskum tengdist hæð yfir sjávarmáli, dýpi og þéttleika urriða. Í öðrum kafla var borið saman útlit og át úr hverjum fæðuhópi. Í þriðja kaflanum voru þróaðar aðferðir til að greina fjölbrigðni. Notuð voru blönduð módel og mismunandi vaxtarkúrfur innan stofna skoðaðar. Tilviljunarkennd skógarmódel (Randon forest models) bentu til þess að fjölbrigðni væri líklegri í vötnum hátt yfir sjávarmáli, urriði sjaldgæfur og mikið étið af svifdýrum og fiski. Í fjórða kaflanum var skoðaður útlitsbreytileiki í fjórum vötnum í suð-vestur Alaska. Í Lower Tazimina Lake fundust tvær gerðir bleikju. Í fimta kaflanum voru rannsakaðir fæðuvefir með því að rannsaka hlutfall stöðugra samsætna í fiskifánu ellefu vatna á Íslandi og fjögura vatna í Alaska. Sviflæg notkun á kolefni og fiskiát virtist vera háð útlitsaðskilnaði og samkeppni.

For my parents

Acknowledgements

The work presented in this dissertation is the result of collaborative oversight by faculty members at the University of Iceland and the University of Washington. The dissertation is submitted to each institution in partial fulfilment of the degree requirements. In addition to my committee members, I would like to thank my many collaborators, especially Dr. Bjarni K. Kristjánsson, Dr. Hilmar Malmquist, Finnur Ingimarsson, Dr. Ulf Dieckmann, Dr. Åke Brännström, and Dr. Dan Young. Thanks also to Dr. Gunnar Stefánsson and Dr. James Thorson for statistical advice. This research has been supported by the European Marie Curie Research Training Network Fish ACE (Fisheries-induced Adaptive Changes in Exploited Stocks), funded through the European Community's Sixth Framework Programme (Contract MRTN-CT-2004-005578), and a research grant provided by the Icelandic Ministry of Fisheries and the University of Washington Graduate School Fund for Excellence and Innovation. The ESIL project was funded with grants from the Icelandic Research Council, the Ministry of the Environment, the Ministry of Agriculture, and the Icelandic Fisheries Research Fund. Special thanks are given to those who participated in the Ecological Survey of Icelandic lakes, especially the Icelandic Institute of Freshwater Fisheries and Natural History Museum of Kópavogur. I would also like to thank the Leifur Eiríksson Foundation for a generous grant that enabled the field studies and analysis of Icelandic lakes. Finally, I would like to thank my friends and family that have been extremely supportive in this endeavor. I would not have been able to do it alone.

Table of Contents

List of Figures

List of Tables

Introduction

Conservation of biological diversity is commonly justified by reasons ranging from enhancement of ecosystem function (Cardinale et al. 2006) to aesthetic value (Jepson and Canney 2003). However, little emphasis is traditionally placed on the importance of intraspecific diversity. One exception is that of salmonid fish conservation, potentially due to their combined commercial value and propensity toward local adaptation (Adams et al. 2007, Waples and Hendry 2008). This dissertation explores diversification in a resident salmonid species from a broad ecological perspective, by inquiring both how this intraspecific diversity may have arisen from local ecological factors and what reciprocal consequences it could have on local ecosystem properties.

Resource polymorphism is a form of intraspecific diversity that results in discrete groups within a population that differ in morphological traits related to resource consumption (Skúlason and Smith 1995). Some species and regions, such as northern temperate freshwater fishes, are particularly prone to resource polymorphism (Robinson and Wilson 1994, Smith and Skúlason 1996). This kind of differentiation is thought to develop through frequency-dependent mechanisms. When conditions are favorable for high intraspecific competition over a given resource, individuals benefits less from specializing on that resource than they would from switching to a more abundant resource. As a result, disruptive selection may develop when it becomes more beneficial to specialize on other resources as they become relatively more abundant, resulting in two (or more) phenotypic peaks of resource use (Dieckmann et al. 2004).

However, differences in resource acquisition clearly cannot be the only driver of divergence in the development of resource polymorphism. Resource polymorphism can also be associated with differences in growth rates, age at maturity, spawn timing and egg size (Skúlason et al. 1989, Skúlason et al., 1992), and may or may not be associated with genetic divergence (Smith and Skúlason 1996). The relationship of size and/or morphology to predict diet can therefore be complex, reflecting differences in morphology and ecology that overlap spatially and yield

multiple peaks of resource use at different sizes or morphologies (i.e., multimodal relationships, Griffiths 1994). These conditions appear to be associated with lower species diversity, reflecting lower interspecific competition (Robinson and Wilson 1994, Smith and Skúlason 1996, Skúlason et al. 1999). Therefore, freshwater ecosystem processes in species depauperate regions may be predisposed to ecological effects of this intraspecific variation on the local environment. If this is the case, then polymorphic species in these regions may have disproportionate effects on ecosystem processes when viewed from a larger geographic scale. This should be an important consideration in the study of cold northern regions, which are both low in species diversity and sensitive to anthropogenic impacts (Schindler and Smol 2006).

As in many salmonids, variability in life history and morphology within Arctic char (*Salvelinus alpinus*) is extreme, as seen by the presence of both migratory and land-locked morphs, dwarf morphs that may or may not co-inhabit a lake with larger morphs, and sympatric divergence of up to four morphs within a lake (Sandlund et al. 1992, Snorrason and Skúlason 2004). However, intraspecific ecological variation, such as resource polymorphism, is rarely considered in ecosystem studies (but see Harmon et al. 2009). This study therefore had two main focuses. First, it analyzed patterns in ecological diversity of Arctic char across large geographic scales to better understand the ecological conditions under which this condition develops. Second, it placed polymorphism within an ecosystem context by analyzing how the role of Arctic charr changes among food webs. This is a first step toward understanding how a polymorphic species interacts with its landscape.

Iceland and Alaska yield a particularly interesting comparison for two main reasons. First, both locations are at similar latitudes, yielding similar seasonality and growing conditions and recent deglaciation, but Iceland has a more geologically active landscape and a much lower overall diversity due to its remote location. The wide range in geological age of bedrock directly affects water origin, productivity, and habitat complexity of freshwater systems (Malmquist 2000, Karst-Riddoch et al. 2009), whereas recent deglaciation and remote geographic location has slowed colonization of salt-intolerant fish species, thereby allowing Arctic char populations to diversify into many available ecological roles (Jónasson et al. 1998, Smith and Skúlason 1996, Snorrason and Skúlason 2004). Second, Arctic charr in Iceland exhibit an extreme

range of ecological variation but little is known about Arctic charr in Alaska.

Because foraging is an important way by which organisms interact with their surrounding ecosystem, the first chapter of this dissertation analyzed dietary habits of Arctic charr. Two goals are accomplished in this study. First, a cluster analysis of prey items in gut contents is used to form prey categories that distinguish habitat-related feeding behaviors commonly found across Arctic charr from widely different ecological scenarios. Because Iceland is a hotspot of geological activity, creating a wide variety of physical habitat within freshwater systems, these feeding behaviors were expected to be related to biotic and abiotic lake characteristics. Therefore, consumption of prey categories was compared with environmental trends in a redundancy analysis to determine how the ecological role of Arctic charr changed with ecosystem characteristics.

The second chapter defined resource polymorphism in Icelandic Arctic char as a complex relationship of morphology and size to predict diet by fitting higher order polynomial generalized linear models to morphological and diet data from Iceland. Consumption of prey categories defined in the first chapter was used as dependent diet variables. An optimal transformation method was presented as useful when the exact nature of a predictor is unknown, as was the case for morphology in this study. By using this technique, one can both define complex polynomial relationships of morphology to predict diet while maintaining a univariate statistical framework. A method for graphically removing regions of low confidence to more easily interpret results was also described. Hypotheses of greater consumption of certain prey by fish with certain morphologies, as observed in past studies, were tested. This initial definition was necessary as a baseline to understand how morphological patterns in Icelandic Arctic charr vary across lakes.

The third chapter presented a method for using mixture models to detect polymorphism in lakes across Iceland using common metrics to facilitate cross-system comparisons. In each lake, models with one, two, or three growth curves were compared to determine whether growth differentiation could be detected. Likewise, models containing one or two morphological distributions were compared to detect morphological differentiation. Results were then compared to ecological variation among lakes to test long-standing hypotheses of whether resource

polymorphism occurs more frequently under conditions of 1) high intraspecific competition, 2) high niche availability, or 3) predator avoidance.

The fourth chapter explored ecological variation in Arctic charr from four lakes in southwestern Alaska. It used the methods developed in Chapter 3 to detect the presence of polymorphism and degree of differentiation in Arctic charr populations from lakes that differed greatly in size, elevation, and fish diversity. Following this, lakes characterized as polymorphic were explored further for differences in diet, meristic counts of gill rakers and pyloric caecae, and gonad size relative to body size. Trends in morphology with diet were also compared within monomorphic groups to determine whether a continuous relationship between morphology and diet could be detected.

The fifth chapter focused on understanding how resource polymorphism affects lake food webs. It was a comparison of food webs from 10 lakes in Icelandic and 4 lakes in Alaskan lakes that varied in the presence of prey fish or competitors. In particular, hypotheses were addressed regarding whether polymorphism or the presence of prey fish increased variability in trophic position or the breadth of carbon used from the limnetic and benthic food chains. In addition, environmental variables were also compared to these characteristics to determine how food web structure varied with the physical environment.

References cited are given after each section of the dissertation, but a bibliography is given at the end to include additional references that were useful through the course of this study.

References cited

Adams, C.E., Bean, C.W., Fraser, D., Maitland, P.S. 2007. Conservation and management of the Arctic charr: a forward view. Ecol. Freshwater Fish 16: 2 – 5.

Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M., Jouseau, C. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature *443:* 989 –992.

Dieckmann, U., Metz, J.A.J., Doebeli, M., and Tautz, D. 2004. Introduction. In: Adaptive Speciation. Cambridge University Press, Cambridge. 460 pp.

Griffiths, D. 1994. The size structure of lacustrine Arctic charr (Pisces: Salmonidae) populations. Biol. J. Linn. Soc. 51: 337 – 357.

Harmon, L.J., Matthews, B., Des Roches, S., Chase, J.M., Shurin, J.B., and Schluter, D. 2009. Evolutionary diversification in stickleback affects ecosystem functioning. Nature 458: 1167 – 1170.

Jepson, P., and Canney, S. 2003. Values-led conservation. Glob. Ecol. Biogeog. 12: 271 – 274.

Jónasson P.M., Jónsson, B., and Sandlund, O.T. 1998. Continental rifting and habitat formation: Arena for resource polymorphism in Arctic charr. Ambio 27: 162-169.

Karst-Riddoch, T.L., Malmquist H.J., and Smol, J.P. 2009. Relationships between freshwater sedimentary diatoms and environmental variables in Subarctic Icelandic lakes. Fund. Appl. Limnol. 175: 1 – 28.

Malmquist, H.J. et al. 2000. Biodiversity of macroinvertebrates on rocky substrate in the surf zone of Icelandic lakes. – Verh. Internat. Verein. Limnol. 27: 121 – 127.

Robinson, B.W., and Wilson, D.S. 1994. Character release and displacement in fishes: a neglected literature. Am. Nat. 144: 596 – 627.

Sandlund, O.T., Gunnarson, K., Jónasson, P.M., Jónsson, B., Lindem, T., Magnusson, K.P., Malmquist, H.J., Sigurjónsdóttir, H., Skúlason, S., and Snorrason, S.S. 1992. The Arctic charr *Salvelinus alpinus* in Thingvallavatn. Oikos *64:* 305 – 351.

Schindler, D.W., and Smol, J.P., 2006. Cumulative effects of climate warming and other human activities on freshwaters of Arctic and subarctic North America. Ambio 35: 160 – 168.

Skúlason, S., and Smith, T.B. 1995. Resource polymorphisms in vertebrates. Trends Ecol. Evol. *10:* 366 – 370.

Skúlason, S., Antonsson, T., Guðbergsson, G., Malmquist, H.J., and Snorrason, S.S. 1992. Variability in Icelandic Arctic charr. Icel. Atr. Sci. 6: 143-153.

Skúlason, S., Snorrason, S.S., and Jónsson, B. 1999. Sympatric morphs, populations and speciation in freshwater fish with emphasis on arctic charr. pp. 70 – 92 In Evolution of Biological Diversity, eds. A.E. Magurran & R.M. May.

Skúlason, S., Snorrason, S.S., Noakes, D.L.G., Ferguson, M.M., and Malmquist, H.J. 1989. Segregation in spawning and early life-history among polymorphic Arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. J. Fish Biol. *35:* 225 – 232.

Smith, T.B., and Skúlason, S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. Ann. Rev. Ecol. System. 27: 111 – 133.

Snorrason, S.S. and Skúlason, S. 2004. Adaptive Speciation in northern freshwater fishes. – In: Dieckmann, U. et al. (eds), Adaptive Speciation, Cambridge Univ. Press, pp. 210 – 228.

Waples, R.S., and Hendry, A.P. 2008. Special issue: Evolutionary perspectives on salmonid conservations and management. Evol. Appl. 1: 183 – 188.

1 Variability in functional role of the consumer Arctic charr *Salvelinus alpinus* as it relates to lake ecosystem characteristics.

1.0 Abstract

This study investigated how dietary habits vary with the ecological landscape in a species that exhibits extreme morphological and ecological variability, the Arctic charr *Salvelinus alpinus*. Iceland is a hotspot of geological activity, so its freshwater ecosystems vary greatly in physical and chemical attributes. Natural associations of dietary items within guts were used to form prey categories that reflect prey habitats and feeding behavior associated with them. Six prey categories were defined: snails (*Radix peregra*), tadpole shrimp (*Lepidurus arcticus*), pea clam (*Pisidium* spp.), the cladoceran *Bosmina* sp., chironomid pupae, and fish (*Gasterosteus aculeatus*). Removal of individual variation by summing diets over lakes obscured habitat associations, indicating that individuals co-occurring in the same lake exhibited different habitat-specific feeding. Zooplanktivory and piscivory co-occurred with consumption from off-shore and littoral benthic habitats, respectively, supporting the idea that benthic foods supplement pelagic diets. Consumption within defined prey categories was analyzed in relation to geography and environmental lake characteristics to determine how diet changed with abiotic and biotic factors. Redundancy analyses showed that variation in diet was related to characteristics on the scale of the prey's environment: piscivory depended on brown trout abundance and mean lake depth, zooplanktivory was linked to latitude

and chemical conditions, and benthic resource consumption was associated with mean lake depth and altitude. This study shows that trends previously observed across fish species were supported at the intraspecific level, indicating that a single species with flexible dietary habits fill functional roles expected of multiple species in more diverse food webs. Consequences of this diet variation on variation in food webs and ecosystem processes are discussed.

1.1 Introduction

Although species are considered singular units of biological diversity, considerable ecological variability occurs within species, especially in diet and feeding behavior, morphology, life history, and reproductive characteristics. This intraspecific variation can have important consequences on population structure and evolutionary dynamics (Bolnick et al., 2003; Knudsen et al., 2010), as well as the species' role within its encompassing ecosystem (Harmon et al., 2009). The goal of this study is to characterize dietary trends across a broad geographical scale to gain a better grasp of how the functional role of a consumer varies with the environment.

Feeding is the main route by which fish can affect ecosystem properties. Through different dietary habits, they can structure carbon flow and change energy transfer pathways through food webs by causing trophic cascades (Schindler et al., 1997; Hulot et al., 2000; Jeppesen et al., 2003; Taylor et al., 2006), add trophic levels (Post et al., 2000; Vander Zanden & Fetzer, 2007), or utilize allochthonous energy subsidies (Cole et al., 2006). In addition, fish can affect nutrient cycling by either recycling nutrients within water columns or transferring digested nutrients from benthic prey to the water column during excretion, thereby supporting nutrient availability within the water column (Schindler & Scheurell, 2002; Vanni 2002).

The realized effects that fish have on an ecosystem depends on the prey taxa consumed, which represents a complex interaction of feeding behavior, functional morphology, and environmental factors. Morphological specialization may or may not reflect behavioral constraints, since fish with a specialized morphology can have diverse feeding capabilities (Liem 1980). Diverse feeding within a species is accomplished through behavioral flexibility or switching, leading to "generalist" feeding, "omnivory" (i.e., feeding a different trophic

levels), or "resource polymorphism" (Post et al., 2000; Schaus et al., 2002; Vander Zanden & Vadeboncoeur, 2002; McCann et al., 2005). Past studies have focused mainly on the role of temporal ecological changes in diverse feeding, but spatial variation may also be apparent across ecosystems (McCann et al., 2005; Verant et al., 2007). For example, shoreline complexity affects relative use of the littoral area by piscivores (Dolson et al., 2008), ecosystem size affects the development of high trophic positions (Post et al., 2000; Vander Zanden & Fetzer, 2007), and the presence of submerged structures affects prey species abundances based on habitat availability (Okun et al., 2005). Furthermore, biotic interactions influence relative consumption of prey taxa through competition (Hesthagen et al., 1997; Forseth et al., 2003) or predation risk that affects habitat use (Okun et al., 2005).

This study investigated how dietary habits vary with the abiotic and biotic ecosystem characteristics in a species that exhibits extensive morphological and ecological variability, the Arctic charr *Salvelinus alpinus*. Arctic charr dietary habits are diverse ontogenetically (Byström & Andersson, 2005), across lakes and populations (Skúlason et al., 1992; Jonsson & Jonsson, 2001; Gantner et al., 2010; Alekseyev et al., 2002; Klemetsen, 2010), and seasonally or annually (Saskgård & Hesthagen, 2004, Amundsen et al., 2008, Corrigan et al., 2011). In addition, they reflect resource polymorphism, in which phenotypic variation yields a functional advantage to consume certain prey within certain habitats (Malmquist 1992; Malmquist et al., 1992; Adams and Huntingford 2002; Andersson 2003; Snorrason & Skúlason, 2004; Knudsen et al., 2010). The availability of Arctic charr diet data from the project Ecological Survey of Icelandic Lakes (ESIL, Malmquist et al., 2000; Karts-Riddoch et al., 2009) yields a unique opportunity to study diet variation at the novel scale of an intraspecific study across locations that show extreme physical diversity due to their various geological ages (Jónasson et al., 1998).

This study analyzed patterns of prey taxa eaten by Arctic charr across Iceland to lay groundwork for an understanding of how diet variation in an ecologically diverse species is related to the ecosystem, and can therefore systematically affect the ecosystem. To do this, this study addressed 1) how associations of prey taxa within individual guts reflected habitat associations and feeding strategies, 2) whether associations among prey taxa based on co-occurrence within individual guts were lost when individual variation is removed by aggregating on

the scale of whole lakes, and 3) how dietary variation was related to lake environment. For the first analysis, we expected that prey taxa co-occur in guts due to similarities in habitat. Therefore, similarities in habitat were first defined in a preliminary analysis indicating how prey taxa abundances varied by habitat. For the second analysis, we compared patterns in prey co-occurrence based on variation among individual guts with patterns based on variation among lakes. Finally, our hypotheses regarding expected correlations with environment in the third analysis were based on results from interspecific studies or past studies of Arctic charr diets:

1. Because benthivory supports the consumption of less stable limnetic resources and higher trophic levels at the interspecific level (Schindler & Scheurell, 2002; Vander Zanden & Vadeboncoeur, 2002; Vander Zanden et al., 2005), we expected to detect an association between limnetic feeding or piscivory and the consumption of some benthic prey. However, it is unknown which benthic prey will hold the closest associations.
2. Because food chains are thought to be longer in larger ecosystems (Post et al., 2000; Vander Zanden & Fetzer, 2007), we expected to find greater piscivory in larger lakes.
3. Deeper lakes have a greater ratio of volume to benthic area than do shallower lakes, and therefore more pelagic habitat (Schindler & Scheurell; 2002). Shallower lakes have greater benthic production due to higher water temperatures, greater benthic sunlight availability, lesser nutrient dilution, and greater nutrient resuspension from wind turbulence (Hanson & Leggett, 1982; Schindler & Scheurell, 2002; Jeppesen et al., 2003). Therefore, through physical arguments, Arctic charr were expected to consume more zooplankton in deep lakes and more benthic invertebrates in shallow lakes. However, because fish density is also greater in smaller volumes of water (Jeppesen et al., 2003), greater zooplanktivory may also occur in shallow water when Arctic charr abundance is high.
4. The presence of brown trout (*Salmo trutta*) is thought to displace Arctic charr away from shallow benthic habitat due to a superior competitive status and/or different feeding behaviors (e.g., Hesthagen et al., 1997; Jansen et al., 2002; Forseth et al., 2003). Therefore, greater consumption of

zooplankton was expected to occur when brown trout were abundant.

5. In general, greater consumption of all resources was expected at higher densities of that resource. For zooplankton, high abundances are also expected to occur when phytoplankton density is high, which may be driven by high nutrient concentrations in the water column (Jeppesen et al., 2003). Under these conditions, a positive correlation between zooplanktivory and nutrient concentrations (in addition to a correlation between zooplanktivory and zooplankton abundance) was expected. However, because large phytoplankton blooms may also remove nutrients from the water column, a negative correlation of nutrient concentration with zooplanktivory was also possible (Siwertsson et al., 2011).

1.2 Methods

1.2.1 Data acquisition

Data from 62 lakes were used for this study; however, different subsets of lakes were used for each analysis depending on data availability (Table 1). For all lakes analyzed except Thingvallavatn, data were derived from the database of Ecological Survey of Icelandic Lakes, which took place in August – September each year during 1992 – 2004. Data at each lake were collected at a single sampling event, so temporal variation (within or between years) may confound spatial effects. However, samples were all obtained within the same 2-month period, and the large number of lakes, variables measured, and contrasting environmental factors should provide enough power to detect spatial patterns. Data included morphometry, hydrology, and physicochemical factors of the lake environment, information on benthic invertebrate abundances from the shallow (0.2 – 0.5 m) rocky littoral habitat and the off-shore fine-grained sediment habitat, zooplankton abundances from the limnetic habitat, and abundances of Arctic charr, brown trout, and Atlantic salmon (Salmo salar) from benthic gill nets.

Zoobenthos from littoral habitats were sampled from 4 – 6 stations spread around the lakeshore, at which 5 10 – 15 cm stones from 20 – 50 cm depth were taken and sampled for invertebrates (Malmquist et al., 2000). For off-shore benthic habitats, 5 Kajak core samples were taken

at each of 2 – 4 stations along a transect in the middle of each lake, and fine-grained sediment was sieved to sample invertebrates. Zooplankton were collected by tow net (125 μm mesh) at the same transect stations, where 3 vertical hauls (max. 15 m) were taken beginning 30 – 50 cm from the bottom. Samples were fixed in ~1% Lugol's solution, stored in dark-brown glass bottles, identified, and counted. Density for stone and off-shore samples were measured m-2, and volumetric zooplankton densities were converted to this by multiplying values m-3 by mean depth (m). All variables were scaled to a mean of 0 and standard deviation 1.

To catch salmonids, 11 (22 for lakes > 10 km2) single-mesh, single-strand nylon gill nets (Lundgren series) were set in the littoral zone perpendicular to shore, from ca. 2 m depth out- and downwards and then left overnight for 12 hours. The gill nets were 25 m long and 1.5 m high with mesh sizes 10, 12.5, 15.5, 19.5, 21.5, 24.0, 29.0, 35.0, 43.0, 55.0, and 60.0 mm (knot to knot). Threespine stickleback *Gasterosteus aculeatus* were caught with minnow traps (see Malmquist et al., 2000, and Karst-Riddoch et al., 2009 for details).

Wet weight (to the nearest 1.0 g) was measured for every Arctic charr, and stomachs were removed for diet analysis from a subsample of up to100 individuals. Stomach fullness was visually estimated and rated as 0 (empty), 1 (trace, < 1/3 full), 2 (half, 1/3 – 2/3 full), or 3 (entire, > 2/3 full). Food items were identified and counted, and individuals with empty stomachs were excluded, resulting in gut content data from 57 lakes (Table 1).

Prey taxa were identified mostly as taxonomic groups, but in some cases they were more general (Table 2). Invertebrate survey data were aggregated into the same groups. "Small fish" were almost entirely the threespine stickleback, although small Arctic charr were included in rare cases (< 1% guts). "Fish eggs" were most likely *Salvelinus* eggs, but were also rare (< 1% guts). "Other flies" included adult stoneflies, dagger flies (Empididae), heather flies (Bibio pomonae), or blowflies (Calliphora spp.). "Copepoda" included unidentified copepods, and was the only group to taxonomically overlap with other groups, i.e., *Diaptomus* spp. and *Cyclops* spp. These copepod groups were not aggregated because they may have different habitat affinities, which could be most easily detected if left separate. In all cases, dietary items were only placed in a single category.

Data on Arctic charr from Thingvallavatn were derived from sampling in July and late September – October 1997. Sampling followed the protocol of the ESIL project in major details, except that chironomids were only identified to family. These data were only used in generalized linear models and cluster analysis of lakes (see last section in Methods), so they have no effect on any other analysis, including correspondence, cluster, or redundancy analyses.

All environmental variables were taken or calculated from the ESIL database, including abiotic (physicochemical) and biotic variables. Abiotic variables included mean depth (MD), volume (VOL), July-August mean precipitation (PR), altitude (ALT), July-August mean air temperature (AT), lake surface temperature (ST), conductivity (COND), total phosphorous (TP), total nitrogen (TN), total organic carbon (TOC), silicon dioxide (SiO2), calcium (CA), and iron (FE). To correct for skewness, these variables were all transformed by log(x) or log(x+1) if the variable ranged < 1, except for SiO_2 which was square-root transformed and AT which needed no transformation. Biotic variables included brown trout and Arctic charr abundances, estimated as catch per unit effort and transformed by log(x+1) (BTA, ACA), and stickleback presence as a binary factor (SP1 / SP0).

Table 1.1. The presence/absence (1/0) or non-empty Arctic charr gut sample size (N) is indicated for each analysis below. Only lakes with invertebrate survey data were included in the habit cluster analysis, only those with diet data were included in DCAs, only individuals with weight and diet data were included in GLMs, and only lakes with environmental data were included in RDAs. The lake number, year sampled, geographic position, general region (cardinal direction or West Fjords "WF"), and assigned cluster (Fig. 1.3) are also given.

Lake	Year	Lat. (N)	Long. (W)	Region	Lake #	Hab. Clust.	DCA N	GLM N	RDA	Clust.
Thingvallavatn	1997	64º10´	21º08´	SW	0	0	0	97	0	10
Apavatn	1993	64º10´	20º38´	S	1	1	40	36	1	9
Elliðavatn	1993	64º05´	21º48´	SW	2	1	40	27	1	4
Eyrarvatn	1992	64º25´	21º36´	W	3	1	40	37	1	8
Galtaból	1992	65º15´	19º43´	W	4	1	40	22	1	2
Geitabergsvatn	1992	64º27´	21º31´	W	5	1	40	0	0	-
Glammastaðavatn	1992	64º26´	21º35´	W	6	1	40	40	1	8
Hraunhafnarvatn	1993	66º31´	16º02´	NE	7	1	40	37	1	9
Hvítárvatn	1994	64º36´	19º52´	S	8	1	40	25	1	6
Kötluvatn	1993	66º30´	16º30´	NE	9	1	60	57	1	6
Langavatn	1993	64º07´	18º49´	S	10	1	40	39	1	4
Mjóavatn	1992	65º15´	19º48´	NW	11	1	40	37	1	6
Nýjavatn	1993	64º06´	18º53´	S	12	1	0	0	0	11
Selvatn	1992	65º57´	20º03´	NW	13	1	40	30	1	10
Sigurðurstaðavatn	1993	66º29´	16º18´	NE	14	1	48	36	1	1
Skálavatn	1993	64º05´	18º48´	S	15	1	3	2	1	-
Stóra Fossvatn	1993	64º09´	18º46´	S	16	1	0	0	0	-
Stóra Viðarvatn	1993	66º14´	15º50´	NE	17	1	60	57	1	6
Svartárvatn	1993	65º20´	17º14´	NE	18	1	4	0	0	-
Svínavatn	1993	65º32´	20º06´	NW	19	1	63	60	1	5
Úlfljótsvatn	1993	64º06´	21º02´	S	20	1	81	68	1	6
Vatnshlíðarvatn	1992	65º31´	19º38´	NW	21	1	61	24	1	11
Vestar Friðmundarvatn	1992	65º18´	14º41´	NW	22	1	40	32	1	6
Ytra Deildarvatn	1993	66º24´	15º58´	NE	23	1	36	35	1	9
Ölvesvatn	1992	65º58´	20º05´	NW	24	1	40	31	1	4
Hólmavatn/Hrútafj.	1992	65º09´	20º56´	NW	25	1	0	0	0	-
Baulárvallavatn	1994	64º54´	22º55´	W	27	1	0	0	0	-
Haukadalsvatn	1994	65º35´	21º37´	W	28	1	50	47	1	6
Hítarvatn	1994	64º53´	21º55´	W	29	1	50	44	1	8
Oddastaðavatn	1994	64º54	22º13´	W	30	1	40	24	1	7

(Continued)

Table 1.1 (Continued). The presence/absence (1/0) or non-empty Arctic charr gut sample size (N) is indicated for each analysis below. Only lakes with invertebrate survey data were included in the habit cluster analysis, only those with diet data were included in DCAs, only individuals with weight and diet data were included in GLMs, and only lakes with environmental data were included in RDAs. The lake number, year sampled, geographic position, general region (cardinal direction or West Fjords "WF"), and assigned cluster (Fig. 1.3) are also given

Vatnsholtsvatn	1994	64º49´	23º16´	W	31	0	50	46	1	3
Ánavatn	1994	65º13´	15º31´	NE	32	1	40	29	1	6
Sænautavatn	1994	65º16´	15º31´	NE	33	1	40	33	1	3
Eiðavatn	1994	65º24´	14º21´	NE	34	1	25	15	1	5
Urriðavatn	1994	65º17´	19º51´	NE	35	1	40	32	1	6
Thiðriksvallavatn	1995	65º41´	21º46´	WF	36	1	62	33	1	6
Högnavatn	1995	65º48´	22º10´	WF	37	1	80	77	1	6
Unnamed	1995	65º42´	22º06´	WF	38	1	15	0	0	-
Ásbjarnarvatn Syðra	1996	65º03´	18º48´	NW	39	0	80	69	1	8
Hópið	1996	65º31´	20º30´	NW	41	1	40	37	1	6
Vesturhópsvatn	1996	65º28´	20º39´	NW	42	1	40	33	1	6
Langavatn	1996	65º49´	17º17´	NE	43	0	40	32	1	10
Reyðarvatn	1996	65º06´	18º32´	NW	44	0	45	45	1	11
Másvatn	1996	65º38´	17º14´	NE	46	0	7	7	1	5
Fljótsbotn	1997	63º52´	18º54´	S	47	1	80	70	1	8
Frostastaðavatn	1997	64º01´	19º03´	S	48	0	40	29	1	6
Eystra Gíslholtsvatn	1997	63º57´	20º29´	S	49	0	60	29	1	7
Hestvatn	1997	64º01´	20º42´	S	50	0	66	66	1	6
Hlíðarvatn	1997	63º52´	21º43´	SW	51	0	53	44	1	10
Hólmavatn/Tungukoll.	1997	65º02´	20º33´	NE	52	0	12	10	1	11
Arnarvatn Stóra	1997	64º57´	20º19´	NW	53	0	32	20	1	4
Úlfsvatn	1997	64º53´	20º35´	NW	54	0	28	27	1	10
Langisjór	1998	64º10´	18º17´	S	57	1	20	20	1	8
Skorradalsvatn	1998	64º27´	21º09´	W	58	1	97	95	1	10
Lagarfljót	1998	65º10´	14º38´	NE	59	1	40	39	1	10
Thuríðarvatn	1998	65º36´	15º10´	NE	60	0	40	40	1	10
Heiðarvatn	1998	65º14´	14º10´	E	61	0	40	28	1	5
Skriðuvatn	1998	64º57´	14º38´	NE	62	0	76	55	1	5
Sandvatn	1998	65º18´	14º41´	NE	64	0	50	43	1	10
Thríhyrningsvatn	1998	65º10´	15º46´	NE	65	1	65	46	1	8
Vífilsstaðavatn	1998	64º04´	21º52´	SW	66	1	60	0	0	-
Hafravatn	1998	64º07´	21º44´	SW	67	1	12	11	1	8

1.2.2. Habitat associations of prey taxa

This preliminary analysis was used to form a hypothesis of expected prey associations in the gut by indicating how prey taxa were associated based on habitat alone. If Arctic charr feed within a single habitat at a time, it is reasonable to expect that associations among prey taxa in gut contents will reflect prey-habitat associations. Invertebrate abundance data from these habitats in the 45 lakes with invertebrate survey data were included in this analysis. In this first hierarchical cluster analysis, sample methods (i.e., plankton hauls, Kajak cores, and littoral stone collections) were assumed to generally indicate limnetic, benthic off-shore, and benthic littoral habitats respectively. Counts for each individual prey taxon were summed across lakes within each habitat, and this sum was divided by the sum across all three habitats to yield a habitat frequency across lakes for each taxon. These frequencies were analyzed in a hierarchical cluster analysis using Euclidean distance and McQuitty linkage.

1.2.3. Forming prey categories

To compare consumption within prey categories with lake characteristics, a measure of consumption within prey categories among lakes first needed to be defined. This was accomplished by predicting consumption of each prey category based on the categorical predictor Lake in generalized linear models (GLMs). Estimated lake coefficients from these models were used to reflect consumption of a prey category relative to other lakes. Because all prey categories were consumed within Thingvallavatn, it was used as the baseline and given coefficients = 0. Second, coefficient values were analyzed in a third hierarchical cluster analysis to group lakes by similarities in dietary habits using Euclidean distance and McQuitty linkage. and trends of increasing latitude or longitude within clusters were analyzed. Third, to test for trends outlined as hypotheses, redundancy analyses (RDAs) were used to form correlations between consumption coefficients and a matrix of lake-specific environmental conditions.

Table 1.2. Biomass indicator conversion factors for prey taxa are given along with the expected capture habitat based on invertebrate surveys (from Fig. 1.1, top), and prey categories (from Fig. 1.1, bottom). Capture habitats include stone (S), fine-grained sediment (mud: M), or water column (W); prey included snail (S), tadpole shrimp (T), pea clam (P), Bosmina *(B), chironomid pupae (C), and fish (F) categories; and exclusions are indicated (0). Capture habitats are listed in order of importance, with backslashes indicating similar frequencies (20% – 80%). Parentheses indicate that general knowledge was used to fill information for taxa absent in invertebrate surveys.*

Dietary taxa	Common name	Biomass (mg)	Capture Habitat	Prey Cat.
Chydorus sp.	cladoceran	0.001	W/M	0
Fish eggs	fish eggs	1	(S)	0
Gammurus sp.	amphipod	1	S	0
Limnephilus spp. L	caddisfly larvae	1	M/S	S
Apatania zonella L	caddisfly larvae	1	M/S	S
Radix peregra	snail	1	M/S	S
Daphnia spp.	cladoceran	0.01	W, M	T
Cyclops spp.	copepod	0.01	M, W	T
Ostracoda	ostracod	0.001	M, W	T
Macrothrix sp.	cladoceran	0.01	M, W	T
Alona spp.	cladoceran	0.001	M, W	T
Lepidurus arcticus	tadpole shrimp	10	M, W	T
Coleoptera	beetle	1	S	T
Other flies	other flies	0.1	S	T
Eurycercus sp.	cladoceran	0.1	M, W	M
Polyphemus sp.	cladoceran	0.001	(M, W)	M
Simocephalus vetulus	cladoceran	0.001	M, W	M
Chironomidae L	fly larvae	0.1	M/S	M
Pisidium casertanum	pea clam	1	M, W	M
Annelida	worm	0.1	M, W	M
Diaptomus spp.	copepod	0.01	W, M	B
Bosmina sp.	cladoceran	0.01	W, M	B
Copepoda	copepod	0.01	(W/M)	B
Trichoptera A	caddisfly	0.1	(S)	C
Chironomidae A	fly	0.1	S	C
Hemiptera	true bug	0.1	(WC/M)	C
Hydracarina sp.	water mite	0.1	WC/M	C
Chironomidae P	fly pupae	0.1	M/S	C
Small fish	small fish	10	M/S	F

In the estimation of lake coefficients, 2 types of GLMs were used, following the delta-gamma method for fitting a model to overdispersed abundance data (Stefánsson, 1996). The first GLM used presence/absence data to predict probability of the prey category

occurrence within individual guts with a logit link function and Bernoulli errors. The second GLM used biomass indicator data to predict biomass with a log link function and gamma-distributed error, but only using the subset of individuals with that prey category present since gamma distributions contain no 0s. This delta-gamma model is useful because results may be extrapolated to all individuals by multiplying the two predictions to yield the joint probability of biomass given its presence.

In the prediction of consumption within each prey category, the biomass of prey within any category may differ by several orders of magnitude. Therefore, summed counts across taxa within prey categories are less comparable than would be summed biomass. Approximate biomasses within dietary categories were first calculated by multiplying the counts of each prey taxon by an appropriate order of magnitude in mg (i.e., 0.001, 0.01, 0.1, 1, or 10), as indicated by wet weights found in literature and local expert knowledge (Table 2), and then summing within categories. This method does not calculate a true biomass, but scales prey taxa by a rough relative biomass.

Larger fish should consume more biomass of all prey categories simply due to stomach size constraints, and fewer of all prey should be consumed when stomachs are not full. To control for this less meaningful variation, prey category biomasses were 1) corrected for body weight and adjusted for stomach fullness before being predicted by GLMs and 2) diagnostically tested to ensure that gamma errors were appropriate. To accomplish the first task, non-linear models were used to determine whether a linear or power function better fit prey category prediction by body weight*stomach fullness adjustment (i.e., 1/3 for rating 1, 2/3 for 2, and 1 for 3). This comparison was made because metabolism generally scales to body weight with an exponent = 0.75 (Brown et al., 2004), so we expected that food intake rates may do the same. Model fits were compared using an F-test, which indicated that including a third exponential parameter in a power function yielded a better fit over the 2 parameters in a linear function ($F_{1,2101} = 8.145$, $P = 0.004$). Parameter estimates (parameter ± S.E., t-value, P-value: intercept = -15.416 ± 11.175, -1.379, 0.168; slope = 2.137 ± 1.240, 1.724, 0.085; exponent = 0.783 ± 0.08862, 8.839, < 0.0001) were used to remove this variation by dividing dietary categories by (body weight*stomach fullness adjustment)^exponent, yielding a measure used in GLMs of g prey category / g body weight that was no longer

dependent on body weight or stomach fullness. Only the 54 lakes with both gut content and body weight data were included in GLMs.

To accomplish the second task, a linear relationship between log mean and log variance were fit to the subset of prey category biomass > 0 (Stefánsson, 1996). Gamma errors were deemed appropriate because slopes (β) were not significantly different from 2 (B1: $\beta = 1.782 \pm 0.418$ SE, $F_{1,2} = 18.20$, $P = 0.051$; B2: $\beta = 2.058 \pm 0.134$ SE, $F_{1,2} = 235.1$, $P = 0.004$; B3: $\beta = 2.016 \pm 0.199$ SE, $F_{1,3} = 102.9$, $P = 0.002$; Z1: $\beta = 1.948 \pm 0.105$ SE, $F_{1,1} = 341.5$, $P = 0.034$; Z2: $\beta = 2.182 \pm 0.296$ SE, $F_{1,2} = 54.39$, $P = 0.018$; and F: $\beta = 2.261 \pm 0.842$ SE, $F_{1,4} = 7.217$, $P = 0.055$).

All environmental variables were included in RDAs, which were done separately for abiotic and biotic variables to minimize restrictions due to missing data, yielding 53 lakes for the abiotic analysis and 42 for biotic analysis (11 lacked invertebrate survey data, Table 1). The availability of each prey category was also included as a biotic variable by treating survey counts m-2 the same as dietary counts: they were multiplied by respective indicator biomasses (Table 1) and then summed within the same defined prey categories. Benthic off-shore data for lakes 31, 39, 61, 62, and 64 were lacking, so these were replaced with mean counts of benthic off-shore taxa calculated over all other lakes. Forward and backward stepwise algorithms were used to select models by minimum AIC. RDAs were implemented using the "vegan" package (Oksanen et al., 2009).

1.3 Results

1.3.1. Habitat associations of prey taxa

The cluster analysis of invertebrate sample frequencies within habitats (benthic littoral, benthic off-shore, or limnetic) yielded hypotheses for prey associations in guts. Limnetic zooplankton species (i.e., *Diaptomus* spp., *Bosmina* sp., and *Daphnia* spp.) were mostly found in plankton tows, indicating a strong presence in the water column (Fig. 1.1, top). *Chydorus* sp., *Hydracarina* sp., *Cyclops* spp., Alona spp., and more distinctly benthic crustacean species (i.e., *Eurycercus* sp., *Simocephalus vetulus*, *Macrothrix* sp., and ostracods) were partially found in the water column, but were also frequently sampled in fine-grained sediments

(mud, M) with infauna such as pea clams and annelids. Snails, caddisfly larvae, and chironomid larvae and pupae were found commonly in both fine-grained sediment and stone samples. *Gammarus* sp., Coleoptera, chironomid adults, and other flies were found only in stone samples (Fig. 1.1, Table 2).

1.3.2. Forming prey categories

The by-individual DCA ordination and first cluster analysis yielded prey categories with strong habitat associations, indicating 6 feeding strategies (Fig. 1.1, bottom). The first four axes (DCA1 - DCA4) of this by-individual DCA yielded eigenvalues of 0.8556, 0.7824, 0.7417, and 0.7840, and axis lengths were 4.8103, 3.8628, 5.4610, and 4.6952. Starting left in Fig. 1.2, the first category indicated limnetic feeding within the water column (*Bosmina* sp., *Diaptomus* spp., and Copepoda). The second category was defined as including only fish, although fish clustered closely with snails and caddisflies. This division was meant to reflect behavioral modifications, since not all Arctic charr individuals or populations have the same tendency to become piscivorous, despite availability of fish prey (Malmquist et al.,1992). The third category indicated feeding on zoobenthos (i.e., caddisflies and snails) in the stony littoral zone. The fourth indicated a mixture of limnetic and benthic feeding on non-sedentary crustaceans and aquatic and terrestrial insects that are sometimes found in the water column, possibly in patchy near-shore habitats (i.e., *Lepidurus arcticus*, *Daphnia* spp., *Cyclops* spp., *Macrothrix* sp., *Alona* spp., Ostracoda, Coleoptera, and other flies). The placement of *Daphnia* with species less frequently found in the water column likely reflects either 1) our inability to distinguish species within this genus with differing habitat preferences or 2) a difference in limnetic feeding habits of Arctic charr between lakes dominated by *Daphnia* spp. rather than *Bosmina* spp. The fifth category indicated feeding on prey that live in or on fine-grained sediment that settles further off shore (i.e., pea clams *Pisidium* spp., annelids, chironomid larvae, *Polyphemus* sp., *Eurycercus* sp., and *Simocephalus vetulus*). Finally, the sixth category indicated a combination of limnetic and benthic feeding, but may also reflect surface feeding since the surface was not sampled in invertebrate surveys (chironomid pupae and adults, *Hydracarina* sp., Hemiptera, and trichopteran adults). Fish eggs, *Chydorus* sp., and *Gammarus* sp. were found in few lakes and lacked

strong affinities, so they were excluded from prey categories. Category names were based on the common name of the dominant prey, as defined by the greatest total indicator biomass of all constituent prey taxa: snail (S), tadpole shrimp (T), pea clam (P, although chironomid larvae were a close second), *Bosmina* (B), chironomid pupae (C), and fish (F).

The by-lake DCA indicated that habitat-related consumption patterns observable within individual guts are lost for most prey categories when aggregated within lakes (Fig. 1.2). This DCA of gut contents summed by lake yielded the first four axes with eigenvalues 0.6501, 0.5665, 0.5339 and 0.4357, and axis lengths of 4.8970, 2.7513, 3.0650, and 2.7497. Affinities within prey categories of the by-individual DCA, indicated by lines drawn around prey category constituents (left, Fig. 1.2), showed a benthic-limnetic trend along the first axis, whereas the second axis distinguished mainly other categories. In the by-lake DCA, the same style of line was drawn around the same prey constituents (Fig. 1.2, right). *Bosmina* category constituents were mixed with constituents of the chironomid pupae and pea clam categories, indicating that lakes with individual *Bosmina*-consumers also contained chironomid-pupae- and pea-clam-consumers. Lepidurus sp. became singularly positioned on the far right, likely reflecting high consumption of tadpole shrimp only in certain lakes, whereas other constituents of the tadpole shrimp category were mixed with other species. High overlap was also apparent among zoobenthos categories. This greater mixture of prey from various habitats indicated that analyzing associations among prey within individual guts, rather than across lakes, was necessary for the detection of habitat-associated feeding patterns. The by-lake DCAs, on the other hand, show that consumption of certain categories is rare among lakes, but composes substantial portion of the diet when present (e.g., tadpole shrimp). This analysis also indicates that certain prey categories were commonly consumed by different but co-occurring fish within the same lake (e.g., *Bosmina* and chironomid pupae or pea clam categories, various zoobenthos categories).

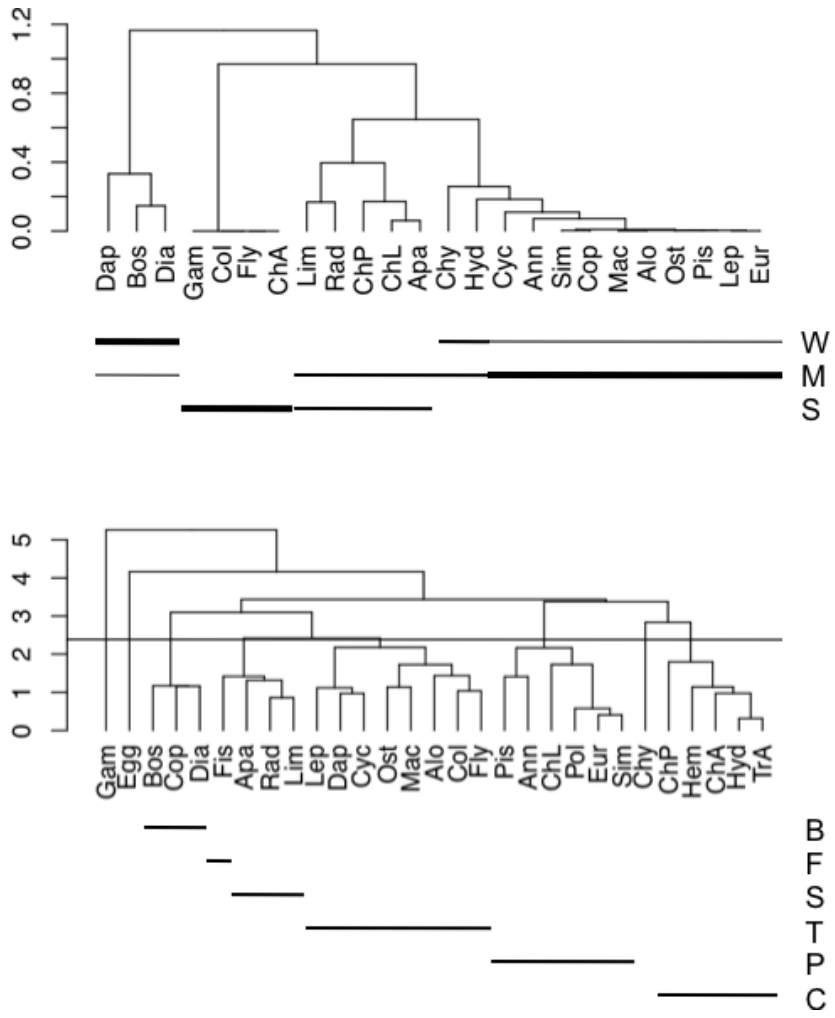


Figure 1.1. Hierarchical cluster analysis of prey taxa frequencies (top) found within stone (S), fine-grained sediment (mud: M), or water column (W) habitats in invertebrate surveys. Lines indicate frequency: thick > 80%, light < 20%, or medium ~50%. Hierarchical cluster analysis of by-individual DCA scores (bottom) yielded prey categories with habitat associations under the horizontal cut-off line: snail (S), tadpole shrimp (T), pea clam (P), Bosmina *(B), chironomid pupae (C), and fish (F). Prey taxa include: Alo =* Alona *spp.; Ann = Annelida; Apa =* Apatania zonella*; Bos =* Bosmina *sp.; ChA = chironomid adults; ChL = chironomid larvae; ChP = chironomid pupae; Chy =* Chydorus *sp.; Col = Coleoptera; Cop = Copepoda; Cyc =* Cyclops *sp.; Dap =* Daphnia *spp.; Dia =* Diaptomus *spp.; Egg = fish eggs; Eur =* Eurycercus *sp.; Fis = fish; Fly = other flies; Gam =* Gammarus *sp.; Hem = Hemiptera; Hyd =* Hydracarina *sp.; Lep =* Lepidurus arcticus*; Lim =* Limnephilus *spp.; Rad =* Radix peregra*; Mac =* Macrothrix *sp.; Ost = Ostracoda; Pis =* Pisidium *spp.; Pol =* Polyphemus *sp.; Sim =* Simocephalus vetulus*; TrA = Trichopteran adults.*

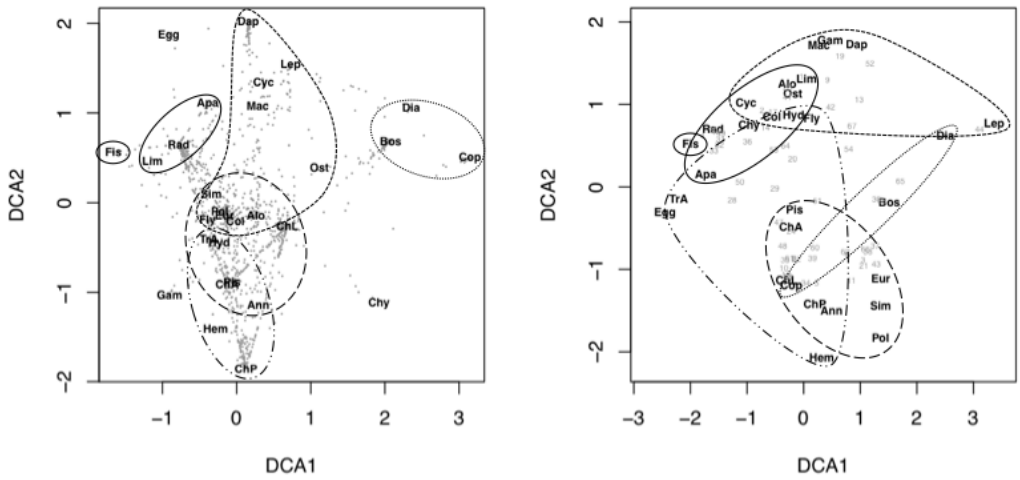


Figure 1.2. DCA ordinations of prey item counts for individuals guts (left) and guts summed by lake (right). Affinities within prey categories, indicated by surrounding lines (left), are degraded when individual variation is removed (right). Line types match the same category in each panel. Weighted average values for each taxon are indicated by text: Alo = Alona *spp.; Ann = Annelida; Apa =* Apatania *sp.; Bos =* Bosmina *sp.; ChA = chironomid adults; ChL = chironomid larvae; ChP = chironomid pupae; Chy =* Chydorus *sp.; Col = Coleoptera; Cop = Copepoda; Cyc =* Cyclops *spp.; Dap =* Daphnia *spp.; Dia =* Diaptomus *spp.; Egg = fish eggs; Eur =* Eurycercus *sp.; Fis = fish; Fly = other flying insects; Gam =* Gammarus *sp.; Hem = Hemiptera; Hyd =* Hydracarina *sp.; Lep =* Lepidurus arcticus*; Lim =* Limnephilus *spp.; Rad =* Radix peregra*; Mac =* Macrothrix *sp.; Ost = Ostracoda; Pis =* Pisidium *spp.; Pol =* Polyphemus *sp.; Sim =* Simocephalus vetulus*; TrA = Trichopteran adults*

1.3.3. Comparisons of diet with geographic and environmental trends

Lake of origin significantly predicted prey consumption in GLMs and accounted for a substantial proportion of variation in the data (Table 3, for coefficient estimates see Appendix 1, Tables A1 and A2). Therefore, coefficients gained from these models were informative in reflecting differences in prey use among lakes, although the causes for these differences among lakes remain unknown. Where lakes had Arctic charr that consumed none of a given prey category, these lakes were excluded from the GLMs that predict indicator biomass, and consequently lacked coefficients. We therefore replaced these missing values with a number that was lower than all estimated coefficients to scale this lack of consumption as a minimum. As long as the value was a minimum, it had no effect on analyses and was arbitrarily chosen as the minimum

estimated coefficient across lakes, rounded to the next lowest integer (S: -5, T: -12, P: -5, B: -9, C: -5, F: -2).

Table 1.3. Results of GLMs to predict presence/absence and biomass indicator using a categorical Lake predictor for each prey category: snail (S), tadpole shrimp (T), pea clam (P), Bosmina *(B), chironomid pupae (C), and fish (F).*

Model	Prey Cat.	N	Residual Deviance	Null Deviance	Residual df	Variance Explained
Presence/ Absence	S	2104	1989.80	2731.30	2050	27.15%
	T	2104	1929.00	2807.20	2050	31.28%
	P	2104	2009.00	2913.60	2050	31.05%
	B	2104	757.60	1262.10	2050	39.97%
	C	2104	2026.40	2829.10	2050	28.37%
	F	2104	978.47	1452.11	2050	32.62%
Biomass Indicator	S	742	912.81	1224.02	692	25.43%
	T	813	2676.70	6341.60	765	57.79%
	P	1011	2166.20	3314.60	961	34.65%
	B	187	542.56	879.01	162	38.28%
	C	838	1426.30	2018.70	795	29.35%
	F	230	139.70	345.28	200	59.54%

The cluster analysis of lake coefficients showed similarities among lakes in resource use (Fig. 1.3). The first split distinguished lakes with no consumption of prey in the *Bosmina* category (Clusters 1 – 6) from those where these were consumed (Clusters 7 – 11). In Clusters 1 – 3, fish had similar extreme dietary habits: in cluster 1 fish only ate snail category prey, whereas in cluster 2 they consumed only snail and fish categories, and in 3 consumed these and minimal amounts in the pea clam and chironomid pupae categories. Lakes in Clusters 4 – 6 were similar in showing some consumption of prey in the tadpole shrimp category, but differed as Arctic charr in Cluster 4 lakes consumed no chironomid pupae, and Arctic charr in Cluster 5 lakes consumed no fish. Cluster 4 was spread across the western half of Iceland, but Clusters 5 and 6 had a strong presence in the north and northeast regions, where cooler climates and older basaltic bedrock are common. For lakes with some consumption within the *Bosmina* category, Clusters 7 – 8 split from 9 – 11 by Arctic charr consuming low frequencies of prey from the pea clam category and high biomass of prey from the *Bosmina* category.

Except for two valley lakes (3 and 6 in the same river system), these lakes were located within or had inflows from young bedrock areas (< 0.7 myr of age). In addition, 6 of the 8 lakes in Cluster 8 were located in the southwestern region of the country. Because of apparent latitudinal trends in consumption of the *Bosmina* category within clusters 5 – 8 (i.e., 30 lakes), linear models were fit and indicated negative relationships between latitude and both the *Bosmina* coefficient sets (biomass: $F_{1,28} = 7.478$, $P = 0.011$; presence / absence: $F_{1,28} = 9.239$, $P = 0.005$). Lakes in Cluster 10 differ from lakes in Cluster 11 by Arctic charr consuming fish and large quantities in the chironomid pupae category, as opposed to consuming high frequencies of all prey categories except fish and snails (Cluster 11).

The abiotic RDA indicated that consumption of prey categories was related to mean depth, pH, and SiO2, altitude, and total nitrogen : total phosphorous ratio (TNTP), all of which were retained in the final model. Altitude was selected only during forward model selection, and TNTP was selected only during backward selection, so both were retained in the final model to indicate their similar importance. Permutation tests indicated that this final model was significant ($F_{5,47} = 2.580$, $P = 0.005$ with 199 permutations). The constrained portion accounted for 21.5% of the variation, whereas 78.5% was unconstrained. Of the constrained portion, the first axis (RDA1) accounted for 41.9% and the second axis (RDA2) accounted for 33.2%. Weighted average positions of GLM coefficients for a given model and prey category were labeled beginning with the prey category (S, T, P, B, C, F) followed by the model code (presence / absence = D; gamma-distributed biomass = G, Fig. 1.4). In general, correlations with environmental variables indicated that more fish were consumed in lakes with higher pH and higher TNTP but less SiO2. Prey category coefficients SD and SG, and to a lesser extent FG, FD, CG, and CD, were positioned away from the TNTP arrow, indicating that they were consumed more when TNTP was lower. The position of FD, FG, SD, SG, CD, and CG in the direction of MD and opposite ALT indicated that Arctic charr in lakes at lower altitudes and deeper lakes had greater tendency to consume fish and invertebrates in the snail and chironomid pupae categories, whereas Arctic charr in low altitude and shallow lakes predominantly consumed prey in the tadpole shrimp or pea clam categories. The placement of BD, BG, CD, and CG near the SiO2 arrow

indicated that higher SiO2 concentrations were associated with consumption of prey from the *Bosmina* and chironomid categories.

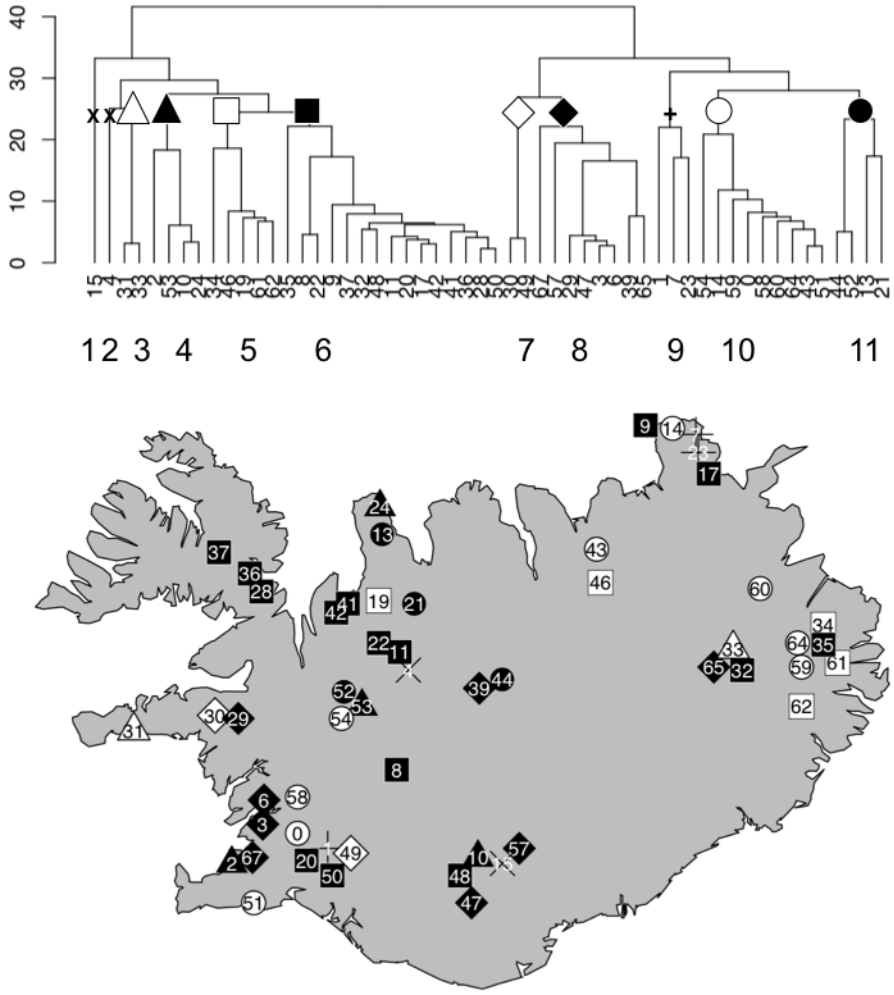


Figure 1.3. The hierarchical cluster analysis of lake coefficient values (top) estimated from GLMs and geographic spread of the Cluster assignments (1 – 11) are illustrated in the map (bottom), with lake numbers referenced in Table 1.1. The symbols at the base of each cluster in the dendrogram (top) indicate the cluster to which the lake number belongs in the map (bottom). These symbols correspond left to right with Clusters 1 – 11 (labeled below the dendrogram).

The biotic RDA showed that consumption of prey categories was related to brown trout abundance, stickleback presence, and abundance of prey in the snail and chironomid pupae categories. The best model

was the same using forward and backward model selection, and permutation tests showed it to be significant ($F_{4,37} = 4.430$, $P = 0.005$ with 199 permutations). The constrained portion accounted for 32.3% of the variance, whereas the unconstrained portion accounted for 67.6%. Of the constrained portion, the first axis (RDA1) accounted for 43.0% of the variance, and the second axis (RDA2) accounted for 34.4%. The BTA arrow pointed away from FD and FG (Fig. 1.4), indicating that piscivory among Arctic charr was negatively associated with brown trout abundance (BTA) and high consumption within the snail category, but positively associated with the presence of stickleback. The S arrow pointed toward SD and SG, indicating that consumption within the snail category was closely related to abundance within its own prey category. In contrast, the C arrow pointed toward BD and BG, indicating that consumption within the *Bosmina* category was related to the abundance of prey in the chironomid pupae category.

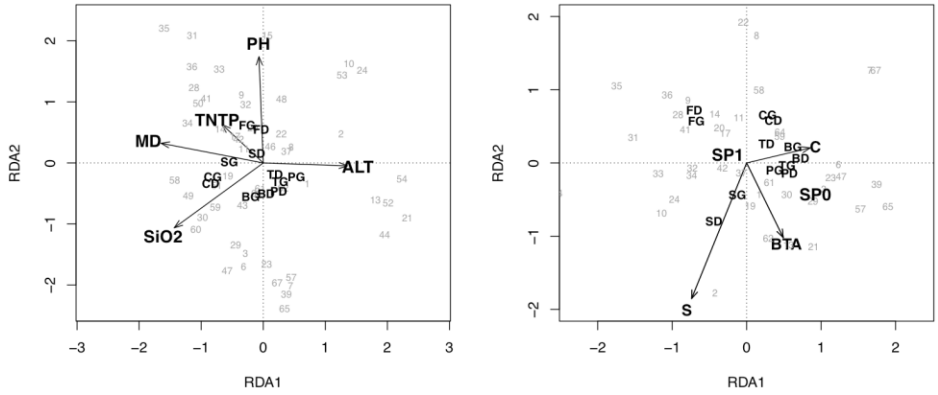


Figure 1.4. Redundancy analysis ordinations show how diet was correlated with abiotic (left) and biotic (right) variables. Positions of numbered lakes (Table 1.1) reflect axis scores. SD, TD, PD, BD, CD, and FD represent the weighted average scores of lake coefficients, scaled relative to axis eigenvalues, from models predicting presence/absence of the snail, tadpole shrimp, pea clam, Bosmina*, chironomid pupae, and fish prey categories respectively. SG, TG, PG, BG, CG, and FG represent the same but from models predicting indicator biomass. Vector direction and length reflect value and strength of correlations. Environmental variables include mean depth (MD), altitude (ALT), total nitrogen : total phosphorous (TNTP), silicon dioxide (SiO2), pH (PH), snail category abundance (S), chironomid pupae category abundance (C), brown trout abundance (BTA), threespine stickleback presence (SP1) or absence (SP0) indicated by weighted average positions.*

1.4 Discussion

This study focused on characterizing dietary trends in Arctic charr at a broad geographical scale, across many ecologically diverse lakes within Iceland, in order to gain a better grasp of how the functional role of Arctic charr as a consumer varies with the environment. By doing so, it resulted in a number of important conclusions regarding variability in Arctic charr diet across Iceland. First, prey categories were defined from gut content data and reflected similarities in prey habitat, so that consumption within these categories can be interpreted as habitat-associated feeding strategies. However, there was enough variability among individuals within a lake to obscure this pattern. Second, geographical analyses were used to indicate whether any climatic or latitudinal variation could be observed in how Arctic charr diets vary. This study showed that prey consumption in the *Bosmina* category was generally more prevalent in the south, indicating either that a limnetic feeding strategy is less common in the north or that the season during which it occurs is shorter or shifted in timing, so that our late summer and fall sampling period missed it. Finally, we found that feeding was related to both biotic and abiotic conditions within the lake environment (i.e., depth, altitude, total nitrogen to phosphorous ratio, pH, silicon dioxide, brown trout abundance, stickleback presence, snail abundance, and chironomid pupae abundance). The strongest trends occurred on the scale of the prey's environment. For example, piscivory was most related to fish community (i.e., brown trout abundance and the presence of stickleback), zooplanktivory was related to nutrient availability (i.e, total nitrogen to phosphorous ratio and silicon dioxide concentrations), and benthivory (although common) was related to physical characteristics (i.e., mean depth and altitude).

By comparing these environmental trends to past studies regarding comparisons of diet and among and within species, we found support for a number of hypotheses. First, although limnetic feeding strategies were apparent on the scale of analyzing individual guts, a comparison with the by-lake DCA showed that other individuals co-occurring in the same lake consumed from prey categories found in fine-grained sediment (mud). Fish consumption was also closely associated with snail consumption in DCA and cluster analyses. These associations are further supported by similarities in position of prey categories in RDAs. Therefore, our results support the idea that benthic feeding supports

limnetic and piscivorous feeding strategies (1: Schindler & Scheurell, 2002, Vander Zanden & Vadeboncoeur, 2002, Vander Zanden et al., 2005), and further suggests a difference in the zoobenthos habitat being utilized. Limnetic feeders appear to utilize supplemental zoobenthos from off-shore lake habitats where fine-grained sediment accumulates whereas piscivores supplemented their diets with common littoral prey in stone habitats. Snails and caddisflies may therefore be a subsidy for more piscivorous Arctic charr diets, as it can be consumed as a stable resource when prey fish are scarce.

This likely also occurs when brown trout are instead the dominant piscivore to Arctic charr, since brown trout likewise consume fish and zoobenthos in littoral areas (Hesthagen et al., 1997) and in our study, reduce fish consumption in Arctic charr. The RDA with biotic variables, greater brown trout abundance was not found to correspond with greater zooplanktivory, as has been found before (4: Hesthagen et al., 1997; Jansen et al., 2002; Forseth et al., 2003), but was instead related to lower piscivory. Prey fish availability was a prerequisite for piscivory in Arctic charr, but piscivory was reduced by greater brown trout densities. This trend is likely a result of habitat displacement of Arctic charr in the presence of brown trout away from littoral zones (Langeland et al., 1991), where stickleback were consumed alongside the snail category in this study. In our study, this apparently resulted in greater off-shore benthic consumption. However, the lack of our detection of a relationship between brown trout abundance and zooplankton consumption may also be due to other factors not accounted for in our study, such as temperature, ice cover, and productivity that may influence Arctic charr / brown trout interactions (Finstad et al., 2010; Helland et al., 2011).

Although we did not find a relationship with lake volume, lake depth was positively correlated with greater piscivory in the RDA with abiotic variables. This yields partial support for the idea that food chains are longer in larger lakes (2: Post et al., 2000; Vander Zanden & Fetzer, 2007). However, the mechanism behind this food-chain lengthening is unclear. For example, deeper lakes yield may yield 1) greater fish prey diversity or abundance facilitated through greater habitat heterogeneity or prey refugia (Post et al., 2000), or 2) reduced omnivory in Arctic charr due to reduced habitat proximity or greater cascading effects (Vander Zanden & Vadeboncoeur, 2002; McCann et al., 2005). Food chain length has long been thought of as a fundamental property of

ecosystems that reflects the number of energy transfers through the food web and links species diversity to ecosystem function (Post et al., 2000; Vander Zanden & Fetzer, 2007). This study showed that variability in Arctic charr diet increased food chain length, as indicated by piscivory, even when fish species diversity was low. Further studies including stables isotope samples would further clarify this relationship.

Although depth was not well associated with consumption of limnetic, yielding no support for greater consumption of zooplankton under greater availability of limnetic volume (3: Schindler & Scheurell, 2002), further explorations (not shown) indicated that this resulted from the presence of a many deep lakes with no zooplankton consumption in our dataset, possibly indicating an interaction with nutrient availability. When excluding lakes with no zooplankton consumption, a positive trend was observed that was not detectable using our multivariate analyses. Therefore, Hypothesis 3 should not be completely discounted. We also found support for greater consumption of zoobenthos in shallow lakes (3: Hanson & Leggett, 1982; Schindler & Scheurell, 2002; Jeppesen et al., 2003), but only for those associated with off-shore habitats rather than stony littoral habitats. Also, we found no support for greater zooplanktivory in shallow lakes, since neither zooplanktivory nor greater Arctic charr abundance was notably correlated with depth (3: Jeppesen et al., 2003). Zooplanktivory was instead related to nutrient availability through a negative correlation with the total nitrogen to phosphorous ratio and positive correlation with silicon dioxide in the RDA with abiotic variables. This indicated that nitrogen is likely being taken out of the water column by large phytoplankton blooms, and that high availability of silicon dioxide facilitated diatom blooms. Therefore, our results support the idea greater consumption of zooplankton was due to its greater availability, but this could not be detected through direct correlations with zooplankton abundance (5). Instead, low nutrient levels were associated with zooplankton consumption, as has been detected in similar systems (Siwertsson et al., 2011), indicating a potential for dynamical effects of zooplankton consumption that lead to trophic cascades. In addition, the negative latitudinal gradient indicated either a climatic or seasonal effect on zooplanktivory. Of the other prey categories, only snail abundance was directly related to their consumption.

Trophic cascades have traditionally been studied as linkages through the limnetic food chain that ultimately affect the trophic status

and nutrient cycling within lakes (Schindler et al., 1997; Hulot et al., 2000). This may explain the correlation between greater zooplankton consumption under low nutrient availability by indicating that high predation pressure on zooplankton may allow phytoplankton populations to remain high enough for nutrient levels to be depressed. However, our results generally agree with those of Jeppesen et al. (2003) in that predation pressure on zooplankton appears stronger under nutrient-poor conditions, although a variety of factors my contribute to this pattern. They include such explanations as longer pre-reproductive vulnerability of cladocerans due to colder waters, higher visual acuity of predators due to clearer water, or higher benthic production due to further light penetrance that may alternately sustain fish populations. This can be achieved through switching to benthic feeding during spells of low zooplankton density or by utilizing benthic insect pupae as they ascend to the surface prior to emerging as adults. Our data support this idea through the above-mentioned co-occurrence of zooplanktivory and consumption of benthic off-shore prey.

Arguments have been made both for and against the case of stronger trophic cascades in nutrient-poor lakes. A broad empirical study indicated that despite heavier predation pressure on zooplankton in nutrient-poor lakes, this pressure only translated into stronger cascades in eutrophic systems (Jeppesen et al., 2003). We cannot directly detect trophic cascades with our data, but the generally high dependence of Arctic charr on zoobenthos in our study also leaves the possibility for littoral trophic cascades to occur. Although rarely studied, littoral cascades can affect prey abundances and benthic algal production (Brönmark, 1994), and have been described under similar subarctic conditions through the consumption of snails (Hershey et al., 1999). In our study, the trend of greater snail consumption with snail abundance may indicate that consumption by Arctic charr may actually be causing reductions in snail populations.

We therefore conclude that intraspecific diet variation allows Arctic charr in Icelandic freshwater systems to fill many functional roles normally expected from multiple species in regions with greater fish diversity. Although dietary variation may be extreme within a species, how it affects ecosystem processes will depend strongly on whether diet variation was temporally stable, possibly as an adapted trait (Bolnick et al., 2003; Knudsen et al., 2010), or whether individual variation simply reflected mobility, which integrates spatial linkages into food webs

(McCann et al., 2005). In either case, our study is novel in that it presents a rare case in which enough detailed and standardized data were available to yield a geographically broad analysis of how a species functional role can vary with the environment and potentially affect ecosystem characteristics. First, we found that benthic prey appeared to be an important subsidy for both zooplanktivores and piscivores, but the type of benthic prey associated with each differed by habitat. Therefore, although piscivory is traditionally studied as a component of the limnetic food chain (Vander Zanden et al., 2005), in this case perhaps it would be more appropriately studied within a littoral benthic food chain, which may furthermore be separated from a benthic off-shore food chain. In addition, given the relatively nutrient-poor status of most lakes and fast erosion of andic soils in Iceland (Karst-Riddoch et al., 2009) and the high dependence of zooplanktivory on nutrient availability in our study, nutrient availability may be especially important for the limnetic food chain. Therefore, variation among lakes either in the transfer of nutrients to the water column through the consumption of benthic prey or in nutrient loading due to variation in surrounding terrestrial vegetation are likely important factors explaining nutrient cycles in Icelandic lakes (Schindler & Scheurell, 2002; Jeppesen et al., 2003). The presence of only one notable latitudinal gradient was not surprising given that subarctic latitudinal gradients are weaker in Iceland, which has a maritime climate (Karst-Riddoch et al., 2009). Recognizing the importance of this intraspecific diversity in regions of low species diversity may be an important consideration in management of these freshwater systems. Further work would especially benefit by the inclusion of temporal population dynamics, such as density effects, as well as ontogenetic shifts in diet to more fully understand these systems.

1.5 References cited

Adams, C. E. & Huntingford, F. A. (2002) The functional significance of inherited differences in feeding morphology in a sympatric polymorphic population of Arctic charr. Evolutionary Ecology, 16, 15-25.

Alekseyev, S. S., Samusenok, V. P., Matveev, A. N. & Pichugin, M. Y. (2002) Diversification, sympatric speciation, and trophic polymorphism of Arctic charr *Salvelinus alpinus* complex, in Transbaikalia. Environmental Biology of Fishes, 64, 97-114.

Amundsen, P., Knudsen, R. & Klemetsen, A. (2008) Seasonal and ontogenetic variations in resource use by two sympatric Arctic charr morphs. Environmental Biology of Fishes, 83, 45-55.

Andersson, J. (2003) Effects of diet-induced resource polymorphism on performance in Arctic char (*Salvelinus alpinus*). Evolutionary Ecology Research, 5, 213-228.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. et al. (2003) The ecology of individuals: incidence and implications of individual specialization. American Naturalist, 161, 1-28.

Brönmark, C. (1994) Effects of Tench and Perch on interactions in a freshwater, benthic food chain. Ecology, 75, 1818-1828.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. (2004) Toward a metabolic theory of ecology. Ecology, 85, 1771-1789.

Byström, P. & Andersson, J. (2005) Size-dependent foraging capacities and intercohort competition in an ontogenetic omnivore (Arctic char). Oikos, 110, 523-536.

Cole, J. J., Carpenter, S. R., Pace, M. L., Van de Bogert, M. C., Kitchell, J. L. & Hodgson, J. R. (2006) Differential support of lake food webs by three types of terrestrial organic carbon. Ecology Letters, 9, 558-568.

Corrigan, L. J., Winfield, I. J., Hoelzel, A. R. & Lucas, M. C. (2011) Dietary plasticity in Arctic charr (*Salvelinus alpinus*) in response to long-term environmental change. Ecology of Freshwater Fish, 20, 5-13.

Dolson, R., McCann, K., Rooney, N. & Ridgway, M. (2009) Lake morphometry predicts the degree of habitat coupling by a mobile predator. Oikos, 118, 1230-1238.

Finstad, A. G., Forseth, T., Jonsson, B., Bellier, E., Hesthagen, T., Jensen, A. J. et al. (2011) Competitive exclusion along climate

gradients: energy efficiency influences the distribution of two salmonid fishes. Global Change Biology, 17, 1703-1711.

Forseth, T. Ugedal, O., Jonsson, B. & Fleming, I. A. (2003) Selection on Arctic charr generated by competition from brown trout. Oikos, 101, 467-478.

Gantner, N., Muir, D. C., Power, M., Iqaluk, D., Reist, J. D., Babluk, J. A. et al. (2010) Mercury concentrations in landlocked Arctic char (*Salvelinus alpinus*) from the Canadian Arctic. Part I : Insights from the trophic relationships in 18 lakes. Environmental Toxicology and Chemistry, 29, 621-632.

Hanson, J. M. & Leggett, W. C. (1982) Empirical prediction of fish biomass and yield. Canadian Journal of Fisheries and Aquatic Sciences, 39, 257-263.

Harmon, L. J., Matthews, B., Des Roches, S. D., Chase, J. M., Shurin, J. B. & Schluter, D. (2009) Evolutionary diversification in stickleback affects ecosystem functioning. Nature, 458, 1167-1170.

Helland, I. P., Finstad, A. G., Forseth, T., Hesthagen, T. & Ugedal, O. (2011) Ice-cover effects on competitive interactions between two fish species. Journal of Animal Ecology, 80, 539-547.

Hershey, A. E., Gettel, G. M., McDonald, M. E., Miller, M. C., Mooers, H., O'Brien, J. et al. (1999) A geomorphic-trophic model for landscape control of Arctic lake food webs. BioScience, 49, 887-897.

Hesthagen, T., Jonsson, B., Ugedal, O. & Forseth, T. (1997) Habitat use and life history of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) in some low acidity lakes in central Norway. Hydrobiologia, 348, 113-126.

Hulot, F. D., Lacroiz, G., Lescher-Moutoué, F. & Loreau, M. (2000) Functional diversity governs ecosystem response to nutrient enrichment. Nature, 405, 340-344.

Jansen, P. A., Slettvold, H., Finstad, A. G. & Langeland, A. (2002) Niche segregation between Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*): an experimental study of mechanisms. Canadian Journal of Fisheries and Aquatic Sciences, 59, 6-12.

Jeppesen, E., Jensen, J. P., Jensen, C., Faafeng, B., Hessen, D. O., Søndergaard, M. et al. (2003) The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: a study of 466 lakes from the temperate zone to the arctic. Ecosystems, 6, 313-325.

Jónasson, P. M., Jonsson, B. & Sandlund, O. T. (1998) Continental rifting and habitat formation: Arena for resource polymorphism in Arctic charr. Ambio 27, 162-169.

Jonsson, B. & Jonsson N. (2001) Polymorphism and speciation in Arctic charr. Journal of Fish Biology, 58, 605-638.

Karst-Riddoch, T. L., Malmquist, H. J. & Smol, J. P. (2009) Relationships between freshwater sedimentary diatoms and environmental variables in Subarctic Icelandic lakes. Fundamental and Applied Limnology, 175, 1-28.

Klemetsen, A. (2010) The char problem revisited: exceptional phenotypic plasticity promotes ecological speciation in postglacial lakes. Freshwater Reviews, 3, 49-74.

Knudsen, R., Primicerio, R., Amundsen, P. A. & Klemetsen, A. (2010) Temporal stability of individual feeding specialization may promote speciation. Journal of Animal Ecology, 79, 161-168.

Langeland A., L'Abée-Lund, J. H., Jonsson, B. & Jonsson, N. (1991) Resource partitioning and niche shift in Arctic char *Salvelinus alpinus* and Brown trout *Salmo trutta*. Journal of Animal Ecology, 60, 895-912.

Liem, K. F. (1980) Adaptive significance of intraspecific and interspecific differences in the feeding repertoires of cichlid fishes. American Zoologist, 20, 295-314.

Malmquist, H. J. (1992) Phenotype-specific feeding behaviour of two arctic charr *Salvelinus alpinus* morphs. Oecologia (Berlin), 3, 354-361.

Malmquist, H. J., Antonsson, T., Guðbergsson, G., Skúlason, S. & Snorrason, S. S. (2000) Biodiversity of macroinvertebrates on rocky substrate in the surf zone of Icelandic lakes. Verhandlungen des Internationalen Verein Limnologie, 27, 1-7.

Malmquist, H. J., Snorrason, S. S., Skúlason, S., Jónsson, B., Sandlund, O. T. & Jónasson, P. M. (1992) Diet differentiation in polymorphic Arctic charr In Thingvallavatn, Iceland. Journal of Animal Ecology 61: 21-35.

McCann, K. S., Rasmussen, J. B. & Umbanhower, J. (2005) The dynamics of spatially coupled food webs. Ecology Letters, 8, 513-523.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minhin, P. R., O'Hara, R. B. et al. (2009) Vegan: Community Ecology Package. R package version 1.15-4. http://CRAN.R-project.org/package=vegan

Okun, N., Lewin, W. C. & Mehner, T. (2005) Top-down and bottom-up impacts of juvenile fish in a littoral reed stand. Freshwater Biology, 50, 798-812.

Post, D. M., Pace, M. L. & Hairston, N. G., Jr. (2000) Ecosystem size determines food chain length in lakes. Nature, 405, 1047-1049.

R Development Core Team. (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Saskgård, R. & Hesthagen, T. (2004) A 14-yr study of habitat use and diet of Brown trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*) in Lake Atnsjoen, a subalpine Norwegian lake. Hydrobiologia, 521, 187-199.

Schaus, M. H., Vanni, M.J., & Wissing, T. E. (2002) Biomass-dependent diet shifts in omnivorous gizzard shad: implications for growth, food web, and ecosystem effects. Transactions of the American Fisheries Society, 131, 40-54.

Schindler, D. E., Carpenter, S. R., Cole, J. J., Kitchell, J. F. & Pace, M. (1997) Influence of food web structure on carbon exchange between lakes and the atmosphere. Science, 277, 248-250.

Schindler, D.E. & Scheurell, M.D. (2002) Habitat coupling in lake ecosystems. Oikos, 98, 177-189.

Siwertsson, A., Knudsen, R., Kahilainen, K. K., Praebel, K., Primicerio, R. & Amundsen, P. A. (2010) Sympatric diversification as influenced by ecological opportunity and historical contingency in a young species lineage of whitefish. Evolutionary Ecology Research, 12, 929-947.

Skúlason, S., Antonsson, T., Guðbergsson, G., Malmquist, H. J. & Snorrason, S. S. (1992) Variability in Icelandic Arctic charr. Icelandic Agricultural Science, 6, 143-153.

Snorrason, S. S. & Skúlason, S. (2004) Adaptive Speciation in northern freshwater fishes. In: Adaptive Speciation (Eds U. Dieckmann, M. Doebeli, J.A.J. Metz & D. Tautz), pp. 210 – 228. Cambridge University Press, Cambridge.

Stefánsson, G. (1996) Analysis of groundfish survey abundance data: Combining the GLM and delta approaches. International Council for the Exploration of the Seas Journal of Marine Science, 53, 577-588.

Taylor, B. W., Flecker, A. S. & Hall, R. O., Jr. (2006) Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. Science, 313, 833-836.

Vander Zanden, M. J. & Fetzer, W. W. (2007) Global patterns of aquatic food chain length. Oikos, 116, 1378-1388.

Vander Zanden, M. J. & Vadeboncoeur, Y. (2002) Fishes as integrators of benthic and pelagic food webs in lakes. Ecology, 83, 2152-2161.

Vander Zanden, M. J., Essington, T. & Vadeboncour, Y. (2005) Is pelagic top-down control in lakes augmented by benthic energy pathways? Canadian Journal of Fisheries and Aquatic Sciences, 62, 1422-1431.

Vanni, M. J. (2002) Nutrient cycling by animals in freshwater ecosystems. Annual Review of Ecology and Systematics, 33, 341-370.

Verant, M. L., Konsti, M. L., Zimmer, K. D. & Deans, C. A. (2007) Factors influencing nitrogen and phosphorous excretion rates of fish in a shallow lake. Freshwater Biology, **52**, 1968-1981.

.

2 Choosing the best morphology to predict complex resource use based on morphology and body size across populations of Arctic charr (*Salvelinus alpinus*) in Iceland

2.0 Abstract

Organisms exhibiting resource polymorphism are characterized by extensive ecological diversity, as shown by correlations between morphological and ecological characteristics that reflect their diet and habitat. Yet, studies of resource polymorphism are usually constrained to only a few locations exposing the most extreme variation in those characteristics. These ecological patterns may be non-linear and complex, both within localities harboring extreme cases of morphological divergence as well as across larger spatial scales. By using data from 50 Icelandic lakes taken from an extensive database resulting from the Ecological Survey of Icelandic Lakes, we aim to predict the relative quantities of 6 dietary categories consumed based on morphology and size by fitting higher order polynomial generalized linear models in a delta-gamma framework. These results will then be used to analyze whether patterns of specialization and allometry are similar to patterns from single-lake studies of resource polymorphism in Icelandic Arctic charr, especially those from Thingvallavatn. To do this, an optimal transformation method is presented that is useful when the exact nature of a predictor is unknown, as was the case for morphology in this study. This was furthermore done both under the condition that the optimal predictor of morphology may differ between dietary

categories, and that the optimal predictor must be the same among dietary categories. This study is novel in that it 1) uses a wide array of ecologically diverse lakes to study polymorphism within a species, 2) presents a method for optimizing a predictor variable when the best predictor is unknown while using higher order polynomial models, and 3) graphically removes regions of low confidence of predictions (i.e., high variance or low data density) for ease of interpretation. Results indicate that some, although not all, of the expected patterns in specialization can be detected across lakes. In addition, dietary studies should focus on higher resolution categories rather than "zoobenthos" or "zooplankton" if interpretations of morphological or size effects are to be comparable across studies and interpretable in an ecosystem context.

2.1 Introduction

Dietary habits result from a complex interaction of the species behavior, functional morphology, and environmental constraints. Therefore, characterizing the full range of dietary habits of species that exhibits intraspecific morphological and ecological variation, such as those that exhibit resource polymorphism (Skúlason and Smith 1995), can be difficult. This is because resource polymorphism is a form of intraspecific diversity that results in divergence of morphology, body size, and a variety of other ecological or physiological characteristics as they are associated with differences in diet and/or habitat (Skúlason and Smith 1995), yielding high rates of resource use at different sizes or morphologies (i.e., multimodal relationships, Griffiths 1994).

Despite this difficulty, feeding habits of variable species may are important for understanding how food webs vary spatially and temporally, since variable feeding behavior is highly responsive to varying environmental conditions and strongly effects food web structure (Loueille 2010). For example, adaptive foraging behavior, in which changes in relative resource use yield fitness benefits (e.g., energy acquisition or expenditure benefits, predator or competition avoidance), can have strong stabilizing or structural effects on food webs (Kondoh and Ninomiya 2009, Loueille 2010). In addition, body size may be the single most important trait for understanding proximal mechanisms of food web structure, since it constrains attack rates as well as trophic interaction strength among species (Neubert et al. 2000, Hjelm and Persson 2001, Emerson and Rafaelli 2004. Loueille 2010).

Like in many salmonids, variability in life history and morphology within Arctic charr (*Salvelinus alpinus*) is extreme, as seen by the presence of both migratory and land-locked morphs, dwarf morphs that may or may not co-inhabit a lake with larger morphs, and sympatric divergence of up to four morphs within a lake (Sandlund et al. 1992, Snorrason and Skúlason 2004, Kristjánsson 2008, Kapralova et al. 2010). Arctic charr found within Iceland are particularly amenable for studies of intraspecific variation because they exhibit the most extreme range of ecological variation known in the species, most likely as a result of high physical diversity found within Iceland's volcanic landscape, a short evolutionary history due to recent deglaciation, and low colonization rates due to Iceland's great distance from continental mainlands. For these reasons, Arctic charr has been an exemplary model system in studies of the evolutionary mechanisms that lead to ecological speciation (Schluter 1996), with many studies focusing on the functional importance and heritability of behavioral and morphological differences among morphs related to food acquisition (Snorrason et al. 1994, Skúlason and Smith 1996, Andersson 2003, Andersson et al. 2005, Andersson and Persson 2005, Byström and Andersson 2005, Sigursteinsdóttir and Kristjánsson 2005, Parsons 2008). However, many past studies focus on individual study systems that may differ in morphological characteristics under study and their importance for defining resource polymorphism.

By using data from 50 Icelandic lakes resulting from the Ecological Survey of Icelandic Lakes (e.g. Malmquist et al. 2000, and Karst-Riddoch et al. 2009), the first goal of this study is to use morphology and body size to predict resource use of 6 prey categories consumed by Arctic charr on a geographically broad scale. Although behavioral experiments are a more direct way to quantify relative foraging effort on different prey, they are time- and resource- intensive, and have inherent problems in extrapolation of results to natural settings (Calisi and Bentley 2009). Our study instead attempts to analyze dietary trends across a broad geographical scale to detect a common pattern in how size and morphology relate to diet after accounting for lake-specific environmental effects, such as density-dependence or resource availability. We therefore still expect to see certain trends based on smaller scale studies. First, because the original colonizers of Icelandic Arctic charr were most likely anadromous, it is thought that the ancestral phenotype must resemble the present anadromous form with more stream-lined bodies and with terminal mouths. Flexible

generalists, piscivores and pelagic forms are thought to be most morphologically similar to the ancestral form. Second, piscivores are expected to be constrained as only large Arctic charr since individuals in many charr populations become facultative piscivores and in some cases cannibalistic only after attaining a minimum size (Andersson et al. 2007). Third, despite the seasonal instability of zooplankton abundances, some pelagic forms can be described as planktivorous morphs (e.g. "murta" in Thingvallavatn) that have undergone an almost irreversible ontogenetic shift to planktivory (Malmquist et al. 1992). These are thought to have more delicate head features in some cases (Johnson 1980, Adams et al. 1998, Adams and Huntingford 2002a) in addition to being stream-lined. However, morphs that consume large quantities of zooplankton must to some degree also rely on benthic invertebrates. Third, specialist benthivores are expected to show a more derived morphology. Benthic forms may be either large or stunted, and usually have sub-terminal mouths (Jonsson and Jonsson 2001, Snorrason and Skúlason 2004, Kristjánsson 2008). Fourth, we expect to observe high benthic invertebrate consumption by a small benthic form. This form is also paedomorphic, retaining a juvenile morphology at maturity that includes parr marks and a blunt snout (Snorrason and Skúlason 2004).

Prey categories were defined by a hierarchical cluster analysis of gut contents in another study (Woods et al. 2011); however, it remains unknown 1) what morphological characteristics best predict diet over all lakes included, and 2) how complex are the relationships that relate diet to morphology. For example, bimodal relationships referenced above would require fitting a fourth-order polynomial equation to these data. Therefore, the second goal of this study is to account for both model complexity and predictor uncertainty by presenting a method for choosing an optimal predictor variable, dubbed "optimal morphology" for the purposes of this study, by combining morphological variables via a spherical transformation. Therefore, this study is not only novel in that it approaches the idea of resource polymorphism from a geographically broad perspective, but because novel methodological approaches will be presented.

2.2 Methods

2.2.1. Data collection and treatment

Digital images, size measurements, and dietary item counts on Arctic charr from as well as lake environment data and invertebrate

abundances from benthic stone habitats, benthic mud habitats using Kajak cores, and pelagic samples using 125 µ plankton tow-net were derived from the Ecological Survey of Icelandic Lakes (ESIL), which took place in August – September each year from 1992 – 2004 (see Malmquist et al. 2000, Karst-Riddoch et al. 2009, and Woods et al. 2011 for details). Arctic charr data from Thingvallavatn were collected July and October 1997 were provided by Finnur Ingimarsson at the Natural History Museum of Kópavogur, Iceland. The sampling protocol for Thingvallavatn followed similar methods as those followed for the ESIL project. Although timing of the Thingvallavatn collection slightly differed, samples were retained to ensure that the greatest diversity of morphs possible were included in this analysis (Snorrason and Skúlason 2004). Immature fish were excluded to reduce confounding effects of ontogeny on body size, and individuals with empty stomachs were excluded in the analysis, resulting in fish from 50 lakes (Chapter 1).

Morphological variables were derived from digital images using a geometric morphometric approach in TPS software (TPSDig V. 2.1, TPSUtil V. 1.40, TPSRel V. 2.4, Rohlf, 2004, life.bio.sunysb.edumorph). Eighteen landmarks and 6 sliding landmarks were placed at homologous locations on images of each fish. The landmark positions chosen reflect either a central position (e.g., eye) or the transition between two tissues that can be defined in both and x and y direction. Sliding landmarks are only defined in one direction and are allowed to slide in the other direction between the two adjacent landmarks (Fig. 2.1). These landmark configurations were then unbent, aligned, rotated, and scaled to form a generalized orthogonal least-squares Procrustes average configuration. This average configuration serves as the basis for formation of the thin-plate spline interpolating function. Partial warp scores for each individual were then formed by comparing the relative departure in configuration of individuals from the average configuration, and these served as morphological data. These data were analyzed with a relative warp analysis, which is analogous to a principal component analysis and results in scores on orthogonal relative warps for each individual (for further details, see Bookstein 1991 and Rohlf et al. 2004). The first three relative warps, which contributed the largest percentages of the total variation, were used as morphological variables in following analyses. Although centroid size (i.e., square root of the sum of squared distances from each landmark to the configuration centroid) is the only size variable not

correlated with landmark configurations (Bookstein 1991), fork length was used in following analyses because it is more easily comparable to other ecological studies, it is easily comprehended, and fish length is highly correlated with centroid size (results not shown).

Six dietary categories served as dependent variables and were formed in a previous study to reflect habitat-associated feeding strategies of Arctic charr across Iceland (Sandlund et al. 1992, Malmquist et al. 2000, Snorrason and Skúlason 2004, Woods et al. 2011). Counts were summed within groups after first multiplying them with an indicator of relative biomass taken from literary sources and rounded to the closest order of magnitude (Chapter 1). This study also indicated body weight, adjusted by a visually estimated stomach fullness rating, was related to total stomach weight via a power function with exponent = 0.783 (Woods et al. 2011). Therefore, dietary category weights were corrected by dividing by body weight*stomach fullness adjustment raised to the exponent 0.783, where 1/3, 2/3, and 1 were the stomach fullness adjustments respectively for ratings 1 (trace, <1/3 full), 2 (half, 1/3–2/3 full), or 3 (entire, >2/3 full).

2.2.2. Optimal predictor transformation

The main goal of this analysis is to address two problems common when using morphological data: 1) choosing the morphological variable with the greatest predictive ability and 2) fitting higher-order polynomial models to reflect non-linear relationships. For the first problem, a method for rotating relative warp axes was employed to systematically define a variety of composite morphological axes, from which the one with the most predictive ability could be chosen in a grid search. For the second problem, we varied the degree (i.e., complexity) of the polynomial model used in the first step as 1, 2, 3, or 4 and performed a heuristic search over the grid and over all full polynomial models. In all models, a lake categorical factor with 50 levels, reflecting the lake of origin for individual fish, was estimated to account for lake differences. Thingvallavatn was used as a baseline for this factor, so that all coefficients reflect differences in consumption of prey categories in relation to Thingvallavatn.

To perform the rotation in the first problem, the first three orthogonal relative warps from the geometric morphometric analysis were combined into a single composite morphological variable using a

spherical rotation. Cartesian coordinates used as coefficients were constrained to lie on a sphere with radius $r = 1$ (Eq. 1 – 4), in which φ represents the angle of the composite morphological variable away from the x-axis, and θ represents the angle of the composite morphological variable away from the y-axis. The composite variable m was formed by standardizing relative warp 1 (m_1), relative warp 2 (m_2), and relative warp 3 (m_3), and then combining them in proportions determined by their respective rotation coefficients c_1, c_2, and c_3:

$$m' = c_1 m_1 + c_2 m_2 + c_3 m_3 \quad \text{Eq. 1}$$

$$c_1 = \cos(\theta)\cos(\phi) \quad \text{Eq. 2}$$

$$c_2 = \sin(\theta)\cos(\phi) \quad \text{Eq. 3}$$

$$c_3 = \sin(\phi) \quad \text{Eq. 4}$$

$$c_1^2 + c_2^2 + c_3^2 = 1 \quad \text{Eq. 5}$$

This composite variable can be envisioned as a vector beginning at the origin of a sphere with $r = 1$ and ending at the point on a sphere that corresponds with the three coefficient values (c_1, c_2, and c_3), with the vector direction determined by the angles φ and θ. A composite morphological variable composed entirely of the first relative warp (i.e., $m = m_1$) would be found lying along the *x*-axis, as described by the angle values $\varphi = \pm \pi$ or 0, and $\theta = \pm \pi/2$, and which results in $c_1 = \pm 1$, $c_2 = 0$, and $c_3 = 0$. Likewise, a composite morphological variable composed entirely of relative warp 2 (i.e., $m = m_2$) would have angles $\varphi = \pm \pi/2$ and $\theta = \pm \pi/2$, resulting in $c_1 = 0$, $c_2 = \pm 1$, and $c_3 = 0$ and lying along the *y*-axis, and a composite morphological variable composed entirely of relative warp 3 (i.e., $m = m_3$) would have the angle $\varphi = \{-\pi, \pi\}$ and $\theta = \pm \pi$ or 0, resulting in $c_1 = 0$, $c_2 = 0$, and $c_3 = 1$ and lying along the *z*-axis. The constraint to form coordinates along a sphere with radius = 1 (Eq. 5) ensures that the scale of any calculated m will not change relative to others (i.e., m always has the same length $r = 1$). A grid of possible composite morphological predictors was then formed by varying c_1 and c_2 in intervals of $\pi/100$ and calculating c_3 as $1 - c_1 - c_2$ (Eq. 5). This grid was then used in the next step to evaluate models at each possible morphological predictor in a global, heuristic search for the composite morphological variable that yields the best predictive ability (m').

To vary model complexity in the second step, each composite morphological predictor in the above grid was evaluated with 4 generalized linear models (GLMs), each full polynomials of degree 1 – 4 respectively for both predictor variables size (*s*) and composite morphology (*m*) to predict diet (*d*). If default starting values for the model coefficients were not sufficient for model convergence in GLMs, the best-fit coefficients from converged models were used as starting values. Model results, including Aikaike's Information Criteria (AIC), were compiled for each possible composite morphological variable. All GLMs were performed in R statistical software R V. 2.9.2 (R Development Team, 2009) with iteratively reweighted least squares estimation and 100 maximum iterations, and graphs were made using Mathematica V. 7.01.0.

Results from the grid-based search were then used as a starting point for *c* coefficient optimization and model reduction. The grid-based heuristic search yielded a model with the minimum AIC at a given composite variable (defined by the *c* values) and a given polynomial degree. First, the polynomial degree was held constant in a full model, while c_1 and c_2 were optimized using negative log likelihood minimization using a limited-memory, quasi-Newton algorithm (Byrd et al. 1995), and the third was calculated from the constraint (Eq. 5). Bounds were obtained as the minimum and maximum c_1 and c_2 values from the subset models that fell within a range of the minimum AIC + 2 during the heuristic search, thereby representing a subset of equivalent models (Bolker et al. 2008), although these bounds were relaxed if necessary.

Second, the composite morphological variable resulting from this first optimization was held constant while the model was reduced by removing terms that did not decrease the model AIC by more than 2 when included in the model. However, uninformative main effects were not removed if interactions including that main effect remained in the model. In this case, the main effect and interactions were removed only if their joint inclusion did not yield a drop in AIC greater than 2*# terms being tested. Third, a second optimization of the composite morphological variable was then performed following the same methods as the first optimization to obtain the final optimal morphology (*m'*) corresponding with final model results.

For comparison, another search for a morphological variable that simultaneously best predicts consumption in all prey categories was also implemented. A procedure similar to that described above for individual models was performed, except that each point in the global heuristic search was evaluated by finding the minimum sum of the negative log likelihoods from models across all prey categories. This sum is not itself a likelihood, but could be expected to find the best predictor across models, given that the models are weighted equally. Other objective functions could be used, depending on the interests of the evaluator. For simplicity, the initial grid-based search was constrained to contain only fourth degree polynomial equations for all models. The *c* values were then held constant at the value chosen by the grid-based search, and models were reduced separately by removing terms from each model if their inclusion did not yield a drop in AIC of at least 2 (under the constraints on main effects listed above). Last, a joint optimization of c_1 and c_2 was performed as described above by minimizing the sum of the likelihoods across models.

2.2.3. Model combination and interpretation

To model the quantity consumed for each dietary category, the delta-gamma modeling framework was employed, which has been previously been used in the analysis of diet and fisheries trawl data (Stefánsson1996, Stefánsson1997, Brynjarsdóttir and Stefánsson 2004). This approach splits the data set into two processes that are first modeled separately. The first model fits presence/absence data using binomial errors and a logit link function, which predicts the probability that the dietary item *k* is present in the stomach based on morphology and size ($D_k(m_{kd}, s)$). The second model is fit to the subset of biomass data in which the dietary category was present, using gamma distributed errors and a log link function, thereby predicting biomass of a dietary item k based on morphology and size, given that it is present in the stomach ($G_k(m_{kg}, s)$. These two models will be referred to as "logistic" and "log" models respectively. The optimal morphology procedure described above was first run separately for all models, yielding 12 reduced generalized linear models (i.e., 1 logistic and 1 log model for each dietary category for GLMs). Therefore, each logistic and log model has a corresponding optimal morphology *m'*, that depends on both the resource (*k*) and model type (*d* / *g*). Predicted values from each model

are then multiplied to yield the joint probability of dietary category biomass. This prediction is dependent on both m_{kd} and m_{kg}, and is applicable to the full range of data, regardless of whether the dietary item was present in an individual's stomach $DG_k(m_{kd}, m_{kg}, s)$ (Stefánsson 1996).

For each of the 12 models three models were fit for comparison: 1) one in which only the lake factor was included as a predictor, 2) one for which a lake factor, size, and morphology predictors were included, with morphology optimized separately for each model, and 3) one for which a lake factor, size, and morphology predictors were included, with morphology being optimized simultaneously across all models. These models were compared using AIC, although the AIC and degrees of freedom were increased by 2 from the GLM output to account for estimation of c_1 and c_2 coefficients.

As with non-linear modeling, fitting complex GLMs may lead to the inclusion of higher order predictors that cause unrealistic predictions when extrapolating beyond the range of data. Therefore, to aid in interpretation, we corrected our delta-gamma GLM predictions ($DG_k(m_d, m_g, s)$) by defining a correction function ($C_k(m_d, m_g, s)$) that reflects our believability in the predicted surfaces as it relates to variance and density of data points. The correction equation was modeled after standard error, so that it resembles a pointwise variance divided by an indicator of sample size expected at that point. This function was then scaled to range{0,1} to be used as a weight.

The pointwise variance of a delta-gamma model is defined as:

$$Var(X) = p\sigma^2 + \mu^2 p(1-p) = \mu^2\left[p\left(1+\frac{1}{r}\right) - p^2\right] \qquad \text{Eq. 6}$$

where p is probability estimated from the logistic model, and μ and r are the mean and shape parameters of the gamma distributions estimated in the log model (Stefánsson 1996). The correction function was then formed for a given resource by first inserting the estimated logistic GLM for p ($D(m_d, s)$), the estimated log GLM for μ ($G(m_g, s)$), and the shape parameter estimated in the log GLM fit for r. Two bivariate probability distribution functions ($P_d(m_d, s)$, $P_g(m_g, s)$) were then estimated from the full dataset, one for each morphology axis, and the geometric mean of these probability distribution functions was used as an indicator of density of data points for a given delta-gamma model.

To resemble the square root of sample size found in the denominator of standard error, the denominator of the correction function consists of the square root of the product of total sample size N = 1239 and the geometric mean of probability distribution functions. Last, this function was converted to range {0, 1} by taking the inverse logit, indicated by the function lt^{-1}, subtracting 0.5 and multiplying by 2:

$$C_k(m_d, m_g, s) = 2\left(lt^{-1}\left(\frac{G_k(m_g,s)^2\left[D_k(m_d,s)\left(1+\frac{1}{r}\right) - D_k(m_d,s)^2\right]}{N\sqrt[4]{P_{kd}(m_d,s)P_{kg}(m_g,s)}}\right) - 0.5\right)$$

Eq. 7

This correction function therefore approaches 1 when either variance around a point is high or its probability of existing in the dataset is low, but approaches 0 in the opposite case. A corrected delta-gamma model was then calculated as the sum of 1) predictions weighted by our belief in them (1- $C_k(m_d, m_g, s)$), and 2) 0 weighted by our non-belief ($C_k(m_d, m_g, s)$). This procedure inherently assumes that none of a resource is consumed outside the range of our data:

$$CDG_k(m_d, m_g, s) = DG_k(m_d, m_g, s)[1 - C_k(m_d, m_g, s)] + 0[C_k(m_d, m_g, s)]$$

Eq. 8

Due to numerical problems associated with extremely high numbers produced by both the estimated log GLM models and corresponding variance functions, these were given a maximum at a value that far exceeded any of the data. A maximum prediction of 272,500 was given for the variance function (Eq. 6), corresponding with a prediction of 500 for $G_k(m_g, s)$ and 0.1 for $D_k(m_d, s)$, and 50 for $DG_k(m_d, m_g, s)$.

2.3 Results

The first relative warp axis (m_1) accounted for 24.2% of the total variation and reflected bending around the abdominal section, as well as variation in head depth and caudal peduncle length (Fig. 2.1). Negative m_1 scores also indicated expansion of the lower head, yielding a more upturned mouth, whereas positive m_1 scores yielded an expansion of the upper head yielding a more downturned mouth. The second relative warp axis (m_2) accounted for 15.6% of the total variation and indicated

individuals with positive scores had relatively larger heads and shorter bodies, especially in the caudal peduncle region. Negative scores indicated individuals with relatively smaller heads and longer bodies and caudal peduncles. The third relative warp (m_3) accounted for 11.8% of the total variation and reflected variation in head length, caudal peduncle length, and body depth. Individuals with negative scores had relatively smaller heads, shorter and deeper caudal peduncles, and deep bodies. Individuals with positive scores had longer heads, longer and narrow bodies, and narrower caudal peduncles (Fig. 2.1).

For the grid-based search, 1250 potential composite morphological variables were formed and used to fit models for each of the 4 polynomial levels analyzed in each of the two model types. Of these 1250, 625 were unique because models were the same when using $\{c_1, c_2, c_3\}$ or $-1*\{c_1, c_2, c_3\}$. However, both cases were retained in case one did not converge. For each composite morphological variable, the final model with minimum AIC was chosen from the set of 8 models (4 polynomial models * 2 cases using either $\{c_1, c_2, c_3\}$ or $-1*\{c_1, c_2, c_3\}$. Although convergence was sometimes not achieved for more complex GLMs, the GLM with the minimum AIC always converged. If more than one polynomial level was included in the subset of AIC + 2 retained from the heuristic search, the more complex model was used to start model reduction.

For the case in which morphologies were optimized separately among models, the optimal morphological axes to predict diet differed in some cases between the logistic and log models, but not widely in most cases (Fig. 2.2, Table 2.1). Because the coefficient sets $\{c_1, c_2, c_3\}$ and $-1*\{c_1, c_2, c_3\}$, which correspond with m' and $-m'$, result in the same model but with reversed coefficients for terms containing m or m^3, the coefficient set reported was that with a positive c_2 value to correspond with graphs of the grid-based search (Fig. 2.2, Table 2.1). However, m was multiplied by -1 for some models (i.e., logistic snail, log tadpole shrimp, and both fish consumption) to align meaningful morphological axes that were more dependent on c_1 and c_3 as positive before the formation of plots for interpretation of model fits. All interpretations below are therefore founded on trends in Fig. 2.3 and Table A2.9, for which the sign of m was flipped from those reported in Tables 2.1 and A2.3 – A2.8 for the four models listed. Changing the sign of m has no effect on GLM fits, so model coefficients reported in Appendix 2 (Tables A2.1 – A2.6) directly match Table 2.1.

The best morphological predictor for both snails and fish was heavily dependent on m_1, as indicated by the high absolute values of c_1, reflecting predictability based on head depth, expansion of opercular regions, caudal peduncle depth, and mouth direction (subterminal / terminal). Although snail consumption occurred in a wide variety of sizes and morphological values, indicating high general consumption per g consumer, there were two clear peaks of snail category consumption at high morphological values and two different sizes. Fish consumption was also highly dependent on m_1, with large quantities mainly being eaten by large Arctic charr (> 20 cm) at negative m_1 values, indicating terminal mouths and deeper heads and caudal peduncles. The large contribution of positive m_2 values also indicated that bodies were generally streamlined, rather than deep, in piscivores, even though morphology was generally quite variable. Large biomass values of fish consumption per gram of consumer also indicate that this resource is eaten in large quantities when consumed. Piscivory steeply increased to high levels over 20 cm, indicating an ontogenetic shift toward piscivory.

Prediction of the tadpole shrimp category consumption was mainly dependent on m_2 and m_3, although these were of different signs only in the log model, which was multiplied by -1 to align m_3 before interpretation (Fig. 2.3). This result indicated that variability in head size and body length, especially in the caudal peduncle region, had the most predictive ability. This category was consumed mostly by Arctic charr with medium sizes, peaking around 20 cm with negative optimal morphology scores, reflecting a combination of negative m_3 and positive m_2 characteristics. The peak therefore reflects slightly downturned mouths with rather deep bodies and large heads, but variation in caudal peduncle length cancels out.

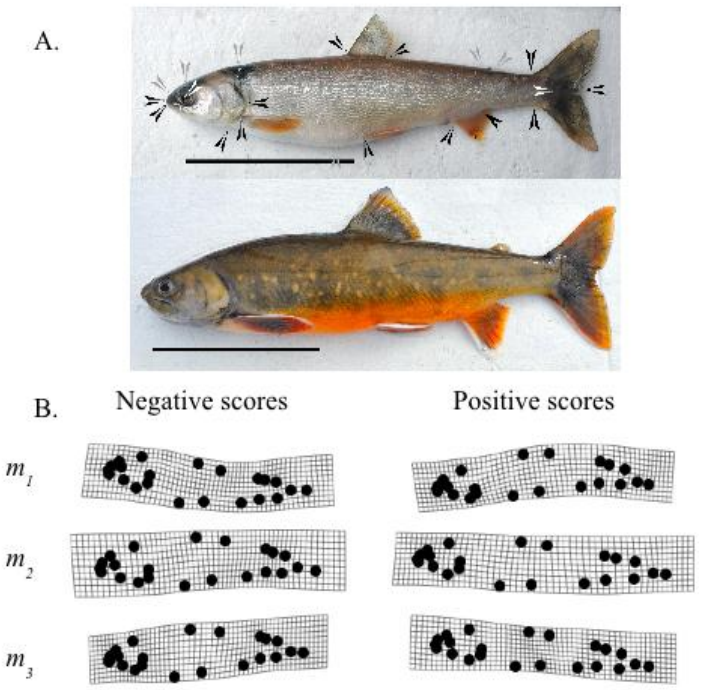


Figure 2.1. A. Arctic charr Salvelinus alpinus *are extremely variable in size at maturity and morphology. The top panel represents a typical limnetic morph, whereas the bottom represents a typical benthic morph. These individuals are from Thingvallavatn, which also contains a piscivorous and small benthic morph (Snorrason and Skúlason 2004). The twelve black and two white arrows in the upper panel represent landmarks at the junction of two tissues or the center of a morphological feature. The six grey arrows indicate sliding landmarks. The black bar is 10 cm length in both panels. B. Results of the relative warp analysis of landmark data yielded three relative warp axes reflecting variation in bending in the abdomen (*m_1*, top), short bodies with large heads (*m_2*, middle left) versus long bodies with large heads (*m_2*, middle left), and deep short bodies with large heads (*m_3*, bottom left) versus small long heads with long thin bodies (*m_3*, bottom left). Points correspond with landmark positions and represent extreme values of relative warps within the range of data.*

Table 2.1. Optimum, minimum, and maximum values for the transformation coefficients of relative warp axes used to form the optimal morphology m' *for the indicated model. Values in bold indicate large contributions of the corresponding relative warp toward* m'. *Deviance, AIC, percent variance explained, and degrees of freedom are also indicated for the final reduced GLMs. All models that included a morphology optimization were corrected in their degrees of freedom by subtracting 2 and in their AIC by adding 2. Percent variance explained is calculated as 1 – Residual Deviance / Null Deviance.*

Generalized Linear Models

Model			c_1	c_2	c_3	AIC	Dev.	% Dev.	df
Snail	Logistic	L only	-	-	-	1338.4	1238.4	0.25	1189
		simult. opt.	-0.3468	**-0.8364**	0.4245	1316.1	1202.1	0.27	1181
		optimum	**-0.8098**	0.5143	0.2823	1292.0	1170.0	0.29	1177
		SE	0.0630	0.0699	-				(1238)
	Log	L only	-	-	-	658.7	586.9	0.28	438
		simult. opt.	-0.3468	**-0.8364**	0.4245	655.7	573.6	0.30	432
		optimum	**0.9191**	0.3841	0.0880	642.3	554.3	0.32	429
		SE	0.0556	0.0916	-				(480)
Tadpole shrimp	Logistic	L only	-	-	-	1195.9	1095.9	0.32	1189
		simult. opt.	-0.3468	**-0.8364**	0.4245	1169.4	1061.4	0.35	1184
		optimum	0.2182	0.3342	**0.9169**	1161.9	1049.9	0.35	1182
		SE	0.1257	0.1282	-				(1238)
	Log	L only	-	-	-	-1239.1	1019.8	0.71	405
		simult. opt.	-0.3468	**-0.8364**	0.4245	-1274.0	940.1	0.73	398
		optimum	0.2363	**0.8378**	-0.4922	-1272.3	939.8	0.73	397
		SE	0.1152	0.0494	-				(448)
Pea clam	Logistic	L only	-	-	-	1269.5	1169.5	0.32	1189
		simult. opt.	-0.3468	**-0.8364**	0.4245	1259.9	1155.9	0.33	1186
		optimum	0.1079	**0.7687**	**0.6304**	1247.5	1139.5	0.34	1184
		SE	0.1187	0.0826	-				(1238)
	Log	L only	-	-	-	-398.3	1186.1	0.39	543
		simult. opt.	-0.3468	**-0.8364**	0.4245	-419.6	1128.4	0.42	534
		optimum	**0.8066**	0.5346	**0.2523**	-426.6	1105.7	0.43	530
		SE	0.0805	0.1194	-				(589)
Cladoceran	Logistic	L only	-	-	-	480.7	380.7	0.38	1189
		simult. opt.	-0.3468	**-0.8364**	0.4245	425.3	309.3	0.50	1180
		optimum	**0.7349**	0.3721	-0.5670	424.9	316.9	0.48	1184
		SE	0.1307	0.1571	-				(1238)
	Log	L only	-	-	-	-78.7	194.5	0.46	62
		simult. opt.	-0.3468	**-0.8364**	0.4245	-85.1	149.1	0.58	50
		optimum	0.1739	**0.9738**	-0.1467	-109.8	115.0	0.68	49
		SE	0.0419	0.0096	-				(83)

(Continued)

Table 2.1 (Continued). Optimum, minimum, and maximum values for the transformation coefficients of relative warp axes used to form the optimal morphology m' *for the indicated model. Values in bold indicate large contributions of the corresponding relative warp toward* m'*. Deviance, AIC, percent variance explained, and degrees of freedom are also indicated for the final reduced GLMs. All models that included a morphology optimization were corrected in their degrees of freedom by subtracting 2 and in their AIC by adding 2. Percent variance explained is calculated as 1 – Residual Deviance / Null Deviance.*

Chironomid pupae	Logistic	L only	-	-	-	1301.6	1201.6	0.29	1189
		simult. opt.	-0.3468	**-0.8364**	0.4245	1278.7	1156.7	0.32	1177
		optimum	0.4968	**0.8172**	-0.2922	1275.7	1151.7	0.32	1176
		SE	0.1112	0.0764	-				(1238)
	Log	L only	-	-	-	-1268.8	861.5	0.32	497
		simult. opt.	-0.3468	**-0.8364**	0.4245	-1338.8	748.3	0.41	485
		optimum	0.3124	**0.9494**	-0.0328	-1342.4	751.1	0.41	488
		SE	0.0000	0.0000	-				(536)
Fish	Logistic	L only	-	-	-	633.1	533.1	0.38	1189
		simult. opt.	-0.3468	**-0.8364**	0.4245	550.1	438.1	0.49	1182
		optimum	-0.4603	**0.8703**	0.1750	534.5	418.5	0.51	1180
		SE	0.1127	0.0678	-				(1238)
	Log	L only	-	-	-	198.6	72.3	0.42	110
		simult. opt.	-0.3468	**-0.8364**	0.4245	169.4	54.5	0.57	103
		optimum	**-0.9762**	0.1802	0.1209	156.6	46.5	0.63	98
		SE	0.0296	0.1335	-				(134)

Figure 2.2 (facing page). Coefficients (c_1 – c_3) resulting from optimization procedure on morphological predictors are illustrated within the global search space for each model (columns) within each dietary category (rows). Colors represent relative contributions of m_1 (red), m_2 (green), and m_3 (blue) based on the magnitude coefficient values. Each black point within the sphere represents a location evaluated with 8 models: 1 for each polynomial degree model evaluated during the global heuristic search (1-4) at the indicated location for both {c_1, c_2, c_3} and {c_1, -c_2, c_3}. Opacity of the black overlay corresponds with the minimum AIC among these 8 models, so that the darkest regions indicate areas in which all models yielded high AIC values. The black polygons indicate regions of models that yielded AIC values during the global search that were within +2 of the minimum AIC. The star indicates the final optimal values of c coefficients after model reductions and corresponds with Table 2.1. These stars may fall slightly outside of the global searches because global searches were based on full polynomials with all interactions included, whereas models with optimal values of c have been reduced.

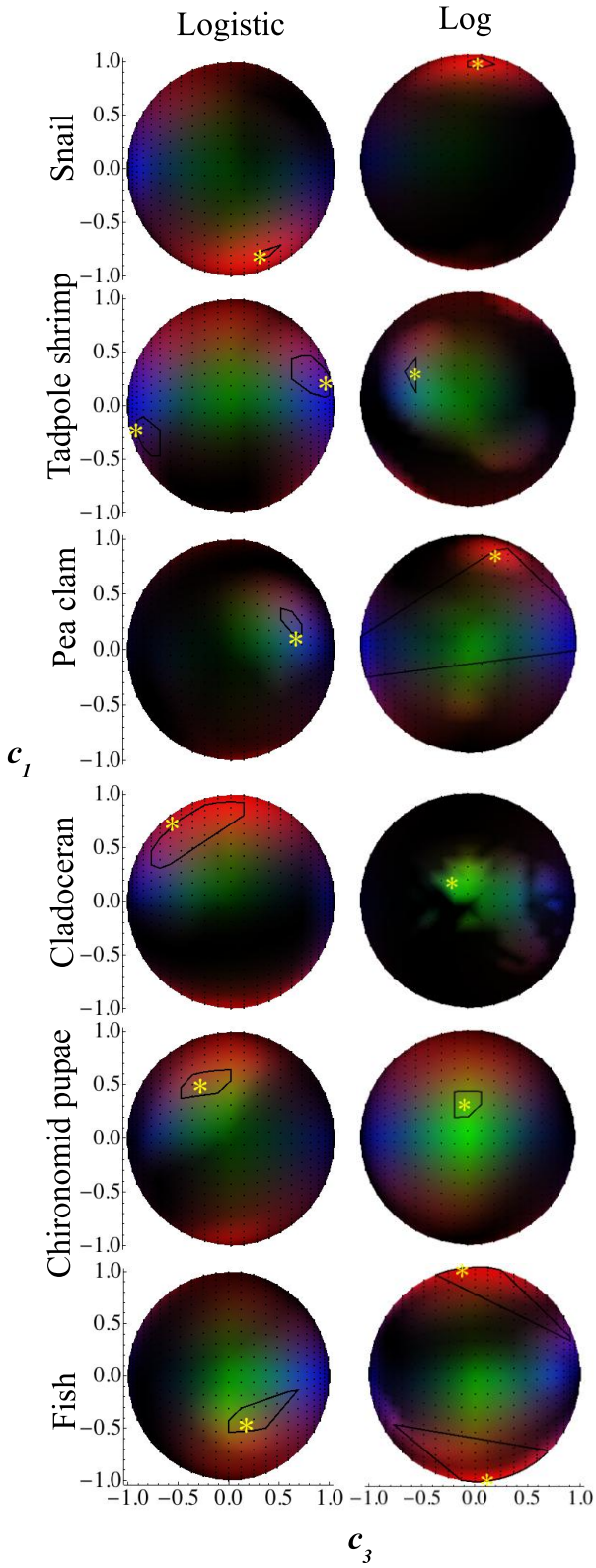
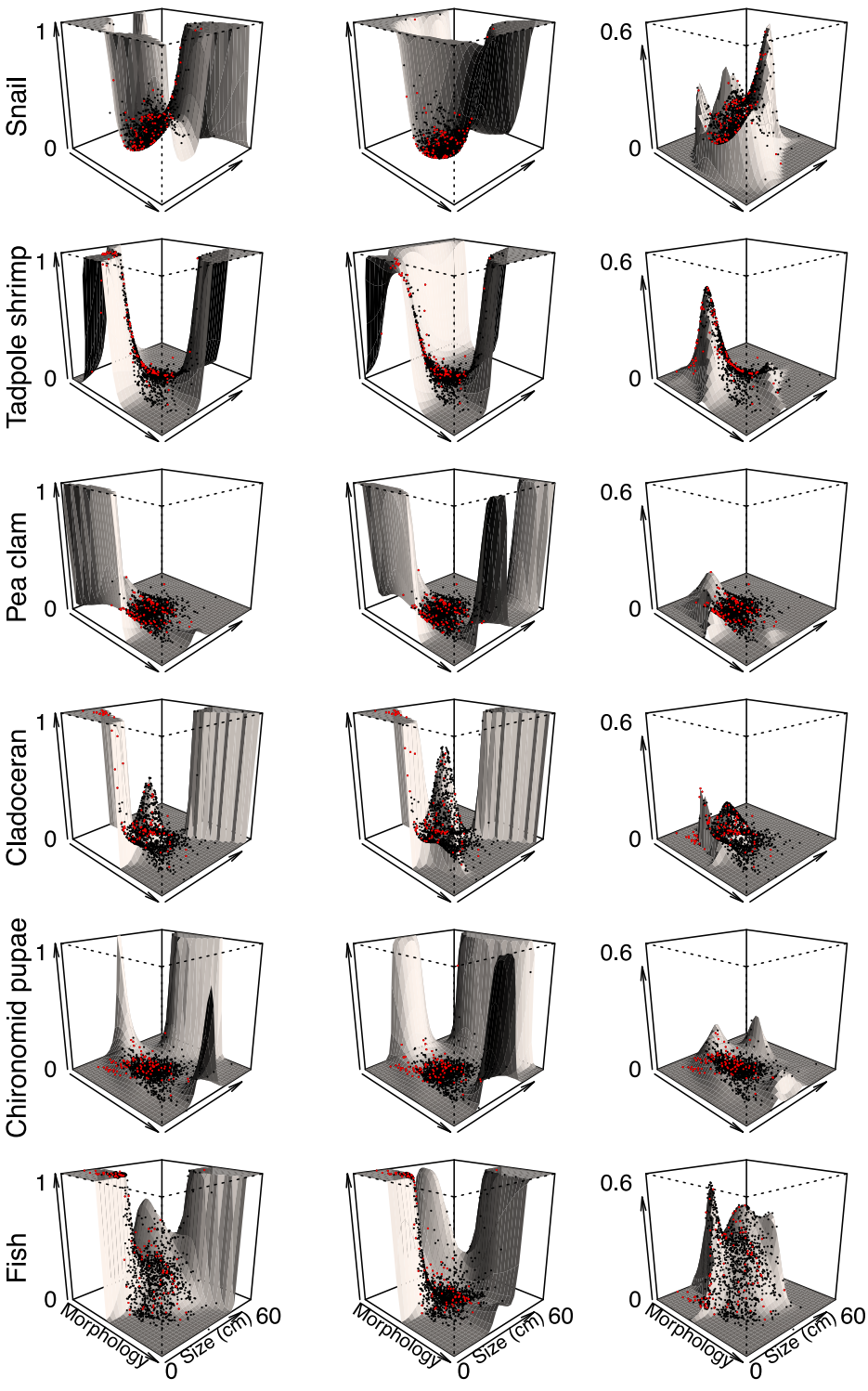

Logistic
Log
Snail
Tadpole shrimp
Pea clam
Cladoceran
Chironomid pupae
Fish
1.0
0.5
0.0
−0.5
−1.0
c_1
c_3

Figure 2.3 (facing page). The left column of panels represents predicted dietary category based on morphology and size of each dietary category after model combination (i.e., $DG_k(m_{kd}, m_{kg}, s)$). Because this function actually depends on three variables, yet 2 variables are the simplest for graphical representation, $m_{kd} = m_{kg}$ in these graphs, even though this may not be the case for individual fish. To ensure that m_{kd} and m_{kg} were aligned and could be interpreted similarly, the sign of m and model coefficients for terms containing m or m^3 were flipped for the logistic snail model, the log tadpole shrimp model, and both fish models (see text for details). Figures below therefore directly correspond with models in Table 2.1, except that optimal c values for these 4 models have been multiplied by -1. Interpretations of how diet varies with morphology will not be affected as long as both m_{kd} and m_{kg} are considered as contributing to the morphological axis; however, exact predictions based on individuals cannot be fully represented by these graphs, and are instead only represented by their m_{kg} values. Black and red points are therefore used to show general patterns of data density, not exact predictions based individual fish. Thingvallavatn is distinguished by red points to contrast patterns in fish that contributed to our original hypotheses. The second column represents corresponding correction functions ($C_k(m_{kd}, m_{kg}, s)$), whereas the third column represents corrected delta-gamma models upon which interpretations are based ($CDG_k(m_{kd}, m_{kg}, s)$).

The prediction of pea clam category consumption, which also contained a large number of chironomid larvae (Woods et al. 2011), was heavily dependent on all three morphological axes. The pea clam category was mainly consumed by small Arctic charr with neutral morphology, or larger Arctic charr with deeper bodies, shorter caudal peduncles, and terminal mouths (Fig. 2.3).


Snail
Tadpole shrimp
Pea clam
Cladoceran
Chironomid pupae
Fish
1
0
0.6
Morphology
Size (cm)
60

For the last two dietary categories, cladoceran and chironomid pupae, optimal morphologies were similar, with a large contribution from m_2, and from m_1 for the cladoceran category. Although m_3 provided the overall lowest contribution to the optimal morphology for both zooplankton categories, it was negative in combination the positive m_1 and m_2 values, thereby differing from all other dietary categories. Therefore, for both categories, higher consumption occurred with lower morphological values, reflecting positive scores for m_1 and m_2 and negative scores for m_3: large heads with terminal mouths and slightly thinner and longer bodies than found in the other categories. This was especially true for the cladoceran category, which had higher contributions from m_1 and m_3, and was consumed at smaller categories.

The simultaneous optimization led to a coefficient set that was similar to the tadpole shrimp log model, cladoceran log model, both chironomid pupae models, and the fish logistic model. However, this was most likely due to convergence problems within the tadpole shrimp and cladoceran log models that restricted the full space of possible models that could be searched. These models performed generally worse than optimizations performed separately, with morphology dropping out completely from one model (Tables A2.1 – A2.6). However, these models still performed better than models that only included the lake categorical factor (Table 2.1). Despite lower predictability, this method may be necessary for cases in which a single morphological predictor may be needed.

2.4 Discussion

In this study, we were able to detect general morphological and size-related patterns in how main prey categories are consumed by Arctic charr across Iceland. A novel method was presented in which the best morphological predictor was optimized while fitting a model that could account for complex relationships according to our hypotheses. This was possible only by the availability of a geographically broad dataset of Arctic charr diet and morphology collected during the Ecological Survey of Icelandic Lakes. We found some similarities that support past studies of smaller-scale systems, including ontogenetic constraints on piscivory and zooplanktivory, and differences in the mouth and body morphology between those that forage in the water column versus on the lake bottom. In addition, because analyses were performed on prey

categories that were formed based on natural associations within gut contents (Woods et al. 2011), comparisons of particular prey could be analyzed to understand which dietary items are related to the strongest morphological differences in Arctic charr.

2.4.1. Benefits of the methodology presented

The method presented yields three main benefits. First, although morphology and diet are inherently multivariate characteristics, the method presented is univariate, and therefore much more flexible in its ability to capture complex relationships. Most accessible multivariate analyses are based on the definition of a linear relationship among the multiple variables, and therefore are less useful at understanding complex relationships. Given that we expected to see bimodal relationships, multivariate analyses would not have been appropriate.

The second benefit of this methodology is that it addresses the issue of uncertainty in the importance of the predictor variable while maintaining a linear framework. An alternative could have been to include all three relative warp axes (m_1, m_2, and m_3) as predictors into the model directly. However, the greater dimensionality would have made the model prohibitively complex to be defined as a 4th degree polynomial. Morphology is a good example of a case in which uncertainty in the predictor may be extreme, since it is inherently multidimensional, may be measured with a variety of methods, and may differ among study systems. This study shows that this uncertainty is well-founded, given that different dietary categories, and even different models within a dietary category, yielded different optimal predictors. The transformation of morphological variables and subsequent optimization presented here would be useful for a variety of other possible cases in which the exact predictor is unknown. However, a prerequisite for this transformation is that the predictor variables are orthogonal, so that they can be represented as a Cartesian coordinate system.

Finally, the development of a correction function that reflected standard error and data point density was extremely useful for graphical interpretation of the resulting models. The corrections removed regions of the graphs in which either variability around the estimate was high or data densities were low, both of which lead to low confidence in predictions. Therefore regions of higher confidence could then be

analyzed and compared among resources. Although multiplication by the correction function yielded predictions that were not directly interpretable in their values, relative resource use among models was more easily comparable.

2.4.2. Trends in morphology and size with diet

Many morphological features have direct bearing on the efficiency with which an individual captures and consumes a given type of prey. At the same time, these features set functional constraints to foraging and feeding (Webb 1984, Webb 1986, Adams and Huntingford 2002b). Hence, one would expect a strong correlation between trophic morphology and diet. While this may be so in the case of a specialist, things tend to get blurred when dealing with more opportunistic predators. However, many fish fall into that category. Diet data from fish can be notoriously difficult to analyze, despite their usefulness in understanding a species' ecology and how species fit into a broader ecosystem context. A variety of noise and confounding processes may obscure underlying patterns, such as a lack of temporal integration or the presence of other unmeasured factors that can affect food acquisition. These can include factors such as predation risk, the cost of learning new search images, patchily distributed prey, or temporally stable behavioral specialization by individuals (Bolnick et al. 2003, Araújo et al. 2007, Ydenberg et al. 2007). For this reason, it is not surprising that the variation attributable to morphology and size is much smaller than that attributed to individual differences among lakes (Table 2.1). Despite these challenges, the method presented here was effective at capturing meaningful dietary trends in a polymorphic species.

Caudal peduncle length, and body depth have been repeatedly shown to affect swimming ability. More streamlined fish are more adept at sustained swimming in either pelagic environments or habitats with a constant flow (Andersson 2003), whereas deep-bodied fish can more easily produce bursts of swimming and are more maneuverable (Webb 1984, Webb 1986, Hawkins and Quinn 1996, Walker 1997). Our results partially agree with this trend: thinner bodies were associated with consumption of cladocerans / copepods and chrironomid pupae, and deeper bodies were associated consumption of the tadpole shrimp category. Tadpole shrimp are capable swimmers, so that deeper bodies

of their predators may aid in burst swimming necessary for their capture in addition to a benthic orientation of the mouth.

On the other hand, snail consumption, the most common form of benthivory, was not clearly associated with deeper bodies, even though benthivory has previously been correlated with deep bodies in Arctic charr (Fraser et al. 1998). Snail consumption in our study was instead associated with longer thinner bodies and caudal peduncles. Potentially this is due the lack of burst-swimming necessary for snail capture, or the relatively low quality of snails as a resource, potentially indicating that body shape is limited by starvation. However, snail consumers did exhibit a down-turned mouth, which corresponds closely with our expectations for benthivory (Sandlund et al 1992, Malmquist et al. 1992). In addition, there were two peaks of size in resource use, which closely corresponds with our expectations based on the presence of both large and small benthivorous morphs that exist in Iceland (Sandlund et al. 1992, Snorrason and Skúlason 2004, Kristjánsson 2008) and in Scotland (Adams et al. 1998, Adams and Huntingford 2002b, Adams et al. 2008).

The cladoceran category also showed two general peaks: a large one at smaller sizes, and a shallow one at larger sizes, both generally with a similar morphology. The first peak corresponds with the ontogenetic trends of zooplankton attack rate peaking in young Arctic charr around 15 cm (Byström and Andersson 2005). The second peak is much shallower, and likely represents more rare specialized forms in certain lakes, such as Thingvallavatn (Malmquist et al. 1992), that go through an ontogenetic niche shift to eat zooplankton as it remains energetically advantageous at larger sizes (Forseth et al. 1994). Furthermore, zooplanktivorous fish were found to have longer heads in this study, especially for those that consume the cladoceran category. This result corresponds well with past studies of zooplanktivorous Arctic charr that have longer jaws and more delicate features (Johnson 1980, Adams et al. 1998, Adams and Huntingford 2002a, Snorrason and Skúlason 2004), as well as zooplanktivorous stickleback (McPhail 1984, Schluter 1993).

Although pea clams and chironomid larvae were consumed in association with each other and were therefore placed into the same dietary category (Woods et al. 2010), the division of two distinct peaks in this study (Fig. 2.3) likely indicates differences in size-related

consumption between these resources. Because Arctic charr begin life as zoobenthivores, chironomid larvae are expected to be eaten by small benthic fish (Sandlund et al 1992, Malmquist et al. 1992). Some small Arctic charr are also heavily dependent on chironomid larvae over zooplankton due to habitat restrictions as a result of predator avoidance: chironomid larvae are relatively more abundant than zooplankton in the safer littoral areas (Byström et al. 2004). On the other hand, the consumption of pea clams, which are substantially larger, may be constrained by gape limitation. Histograms of sizes when consuming these two resources from our data (not shown) indicate a peak shifted toward smaller sizes for chironomid larvae and larger sizes for pea clams, supporting this conclusion.

High levels of piscivory were only found over 20 cm, which corresponds well with past descriptions of an ontogenetic shift toward piscivory at this size in both Icelandic Arctic charr (Malmquist et al. 2002) and other polymorphic species (Kahilainen and Lehtnonen 2003), most likely as a result of size constraints for this feeding strategy. Optimal morphology of piscivores also agreed with our expectations by having a more streamlined body shape (Snorrason and Skúlason 2004, Arbour and Hutchings 2011). However, this body shape, supposed to be adapted for more pelagic habitats, is not in contrast with other forms, since the peak for piscivore morphology was so broad (Fig. 2.3). In addition, the similarity in the optimal morphology for snail and fish consumption was not surprising, given that these two prey categories were commonly consumed together (Woods et al. 2011), likely due to a similarity in prey habitat (littoral stony areas) and a tendency for benthic prey to subsidize piscivores (Schindler and Scheurell et al. 2002, Vander Zanden and Fetzer 2007).

2.4.3. Dietary relationships in an evolutionary and ecological context

This study presented an effective method for analyzing dietary data that accounted for our expectations of complex Arctic charr foraging patterns. Some morphotypes described using this method corresponded with our hypotheses based on known morphs or ontogenetic trends. This included a generalized streamlined form for piscivores, a streamlined form with delicate and long head features for zooplanktivores, down-turned mouths for benthivores, and high benthivory at both small and

large sizes. However, this analysis also showed some unexpected morphological predictions, such as the slim bodies of fish consuming snails, the deeper bodies of fish consuming the tadpole shrimp category, and the similarity in body shape between Arctic charr consuming the cladoceran and chironomid pupae categories.

The small sizes and down-turned mouths observed in our study also correspond with predictions of paedomorphism, which is thought of as a possible mechanism for faster morphological evolution in Arctic charr (Snorrason and Skúlason 2004). Our results for snail consumption appear to support this, since clear peaks in resource use at two different sizes with a similar morphology are apparent across lakes (Fig. 2.3). The relatively high peaks for both large and small sizes indicate that these two forms are common across lakes in Iceland, possibly indicating rapid rates of evolution (see Sigursteinsdóttir and Kristjánsson 2005, Kristjánsson 2008 for more on this discussion).

The support for bimodality in size extends beyond snail consumption to other forms of benthivory, notably pea clam / chironomid larvae consumption; however, morphology differs greatly between these two forms of zoobenthos consumption. Instead, our study indicated that of all the dietary categories, the snail category appears to be the only one to have induced down-turning in the mouth. Instead, consumption of tadpole shrimp and pea clams induced a larger head and deep body, characteristics that correspond with other studies of Arctic charr benthivory (Arbour and Hutchings 2011). This contrast highlights the need to higher taxonomic resolution in prey items when referring to feeding modes such as "benthivory" so that study results and designation of "benthic" morphs may be comparable. This result can also be important in the design of experiments since different forms of "benthivory" apparently induce different types of morphological variation.

Dietary trends in general must be interpreted as resulting from a combination of food availability and other environmental conditions, as well as food preference and adaptive foraging behaviors. In this study, by including a categorical lake factor in all models, we were able to detect trends in morphology and size to predict diet as it generally occurs across lakes. All lake-specific variation was accounted for instead by the lake coefficients (e.g., density dependence, environmental characteristics, adaptive foraging behavioral responses to

environmental). Therefore, these relationships can be used to indicate how Arctic charr characteristics generally relate to prey consumption based on morphology and size. Broad geographical analyses of variation among populations, such as the one presented here, are necessary to both understand how these patterns have arisen and how populations affect the ecosystems in which they reside. To increase the predictive ability of models such as those presented, more detailed information on how Arctic charr behaviorally react to lake-specific characteristics (e.g., density-dependence, resource availability) are needed.

2.5 References cited

Adams, C.E., and Huntingford, F.A. 2002a. Inherited differences in head allometry in polymorphic Arctic charr from Loch Rannoch, Scotland. *J. Fish Biol. 60:* 515-520.

Adams, C.E., and Huntingford, F.A. 2002b. The functional significance of inherited differences in feeding morphology in a sympatric polymorphic population of Arctic charr. *Evol. Ecology 16:* 15-25.

Adams, C.E., Fraser, D., Huntingford, F.A., Greer, R.B., Askew, C.M., and Walker, A.F. 1998. Trophic polymorphism amongst Arctic charr from Loch Rannoch, Scotland. *J. Fish Biol. 52:* 1259-1271.

Adams, C.E., Wilson, A.J., and Ferguson, M.M. 2008. Parallel divergence of sympatric genetic and body size forms of Arctic charr, *Salvelinus alpinus*, from two Scottish lakes. *Biol. J. Linnean Soc. 95:* 748-757.

Andersson, J. 2003. Effects of diet-induced resource polymorphism on performance in Arctic charr (*Salvelinus alpinus*). Evol. Ecol. Res. 5: 213 – 228.

Andersson, J., and Persson, L. 2005. Behavioural and morphological responses to cannibalism in Arctic charr (*Salvelinus alpinus*). *Evol. Ecol. Res. 7:* 767-778.

Andersson, J., Byström, P., Claessen, D., Persson, L., and De Roos, A.M. 2007. Stabilization of population fluctuations due to cannibalism promotes resource polymorphism in fish. Am. Nat. 169: 820 – 829.

Andersson, J., Byström, P., Persson, L., and De Roos, A.M. 2005. Plastic resource polymorphism: effects of resource availability on Arctic charr (*Salvelinus alpinus*) morphology. *Biol. J. Linnean Soc. 85:* 341-351.

Araújo, M.S., Bolnick, D.I., Machado, G., Giaretta, A.A., and dos Reis, S.F. 2007. Using $\delta^{13}C$ stable isotopes to quantify individual-level variation. Oecologia 152: 643 – 654.

Arbour, J.H., Hardie, D.C., and Hutchings, J.A. 2011. Morphometric and genetic analyses of two sympatric morphs of Arctic charr(*Salvelinus alpinus*) in the Canadian High Arctic. Can. J. Zool. 89: 19 – 30.

Bolker, B.M. 2008. *Ecological Models and Data in R.* Princeton University Press, Princeton. 408. pp.

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., and Forister, M.L. 2003. The ecology of individuals: incidence and implications of individual specialization. Am. Nat. 161: 1 – 28.

Bookstein, F.L. 1991. *Morphometric Tools for Landmark Data: Geometry and Biology.* Cambridge University Press, New York. 435 pp.

Brönmark, C. 1994. Effects of Tench and Perch on interactions in a freshwater, benthic food chain. – Ecol. 75: 1818 – 1828.

Brynjarsdottir, J., and Stefánsson, G. 2004. Analysis of cod catch data from Icelandic groundfish surveys using generalized linear models. *Fish. Res. 70:* 195-208.

Byrd, R.H., Lu, P., Nocedal, J., and Zhu, C. 1995. A limited memory algorithm for bound constrained optimization. SIAM J. Scientific Computing 16: 1190–1208.

Byström, P. and Andersson, J. 2005. Size-dependent foraging capacities and intercohort competition in an ontogenetic omnivore (Arctic char). *Oikos 110:* 523-536.

Byström, P., Andersson, J., Persson, L., and De Roos, A.M. 2004. Size-dependent resource limitation and foraging-predation risk trade-offs: growth and habitat use in young Arctic char. *Oikos 104:* 109-121.

Calisi, R.M., and Bentley, G.E. 2009. Lab and field experiments: are they the same animal? Hormones and Behavior 56: 1 - 10.

Caut, S., Roemer, G.W., Donlan, C.J., & Courchamp, F. 2006. Coupling stable isotopes with bioenergetics to estimate interspecific interactions. Ecol. App. 16: 1893-1900.

Dieckmann, U., Metz, J.A.J., Doebeli, M., and Tautz, D. 2004. Introduction. In: Adaptive Speciation. Cambridge University Press, Cambridge. 460 pp.

Emmerson, M. and Raffaelli, D. 2004. Predator-prey body size, interaction strength and the stability of a real food web. J. Anim. Ecol. 73: 399 – 409.

Forseth, T., Ugedal, O., and Jónsson, B. 1994. The energy budget, niche shift, reproduction and growth in a population of Arctic charr, *Salvelinus alpinus*. *J. Animal Ecol. 63:* 116-126.

Fraser, D., Adams, C.E., and Huntingford, F.A. 1998. Trophic polymorphism among Arctic charr *Salvelinus alpinus* L., from Loch Ericht, Scotland. *Ecol. Freshwater Fish 7:* 184-191.

Griffiths, D. 1994. The size structure of lacustrine Arctic charr (Pisces: Salmonidae) populations. Biol. J. Linn. Soc. 51: 337 – 357.

Harmon, L.J., Matthews, B., Des Roches, S., Chase, J.M., Shurin, J.B., and Schluter D. 2009. Evolutionary diversification in stickleback affects ecosystem functioning. Nature 458: 1167 – 1170.

Hawkins, D.K. and Quinn, T.P. 1996. Critical swimming velocity and associated morphology of juvenile coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. Can. J. Fish. Aquat. Sci. 53: 1487 – 1496.

Hershey, A.E. et al. 1999. A geomorphic-trophic model for landscape control of Arctic lake food webs. – BioScience 49: 887 – 897.

Hjelm, M., and Persson, L. 2001. Size-dependent attack rate and handling capacity: inter-cohort competition in a zooplanktivorous fish. Oikos 95: 520 – 532.

Johnson, L. 1980. The Arctic charr, *Salvelinus alpinus*. *In* Charrs: salmonid fishes of the genus *Salvelinus*. Ed. Balon, E.K. Dr. W. Junk Publishers, The Hague, Netherlands, pp. 15 – 98.

Jonsson, B., and Jonsson N. 2001. Polymorphism and speciation in Arctic charr. J. Fish Biol. 58: 605 – 638.

Kahilainen, K., and Lehtonen, H. 2003. Piscivory and prey selection of four predator species in a whitefish dominated subarctic lake. *J. Fish Biol. 63:* 659-672.

Kapralova, K.H., Morrissey, M.B., Kristjánsson, B.K., Ólafsdóttir, G.A., Snorrason, S.S., and Ferguson, M.M. Evolution of adaptive diversity and genetic connectivity in Arctic charr (*Salvelinus alpinus*) in Iceland. Heredity 106: 472 – 487.

Karst-Riddoch, T.L., Malmquist H.J., and Smol, J.P. 2009. Relationships between freshwater sedimentary diatoms and environmental variables in Subarctic Icelandic lakes. Fund. and Appl. Limnol. 175: 1-28.

Kondoh, M., and Ninomiya, K. 2009. Food-chain length and adaptive foraging. Proc. R. Soc. B 276: 3113 – 3121.

Kristjánsson BK. 2008. Fine scale phenotypic diversity of Arctic charr (*Salvelinus alpinus*) in relation to ecological characters. Ph.D. Thesis, Zoology Department. University of Guelph.

Loeuille, N. 2010. Consequences of adaptive foraging in diverse communities. Functional Ecology 24: 18 – 27.

Malmquist, H.J., Antonsson, T., Guðbergsson, G., Skúlason, S., and Snorrason, S.S. 2000. Biodiversity of macroinvertebrates on rocky substrate in the surf zone of Icelandic lakes. Verh. Internat. Verein. Limnol. 27: 1-7.

Malmquist, H.J., Snorrason, S.S., Skúlason, S., Jónsson, B., Sandlund, O.T., Jónasson, P.M. 1992. Diet differentiation in polymorphic Arctic charr In Thingvallavatn, Iceland. *J. Anim. Ecol. 61:* 21-35.

McPhail, J.D. 1984. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): morphological and genetic evidence for a species pair in Enos Lake, British Columbia. Can. J. Zool. 62: 1402 – 1408.

Nelder, J. A. and Mead, R. (1965) A simplex algorithm for function minimization. *Computer Journal* **7**, 308–313.

Neubert, M.G., Blumenshine, SC., Duplisea, D.E., Jonsson, T. and Rashleigh, B. 2000. Body size and food web structure: testing the equiprobability assumption of the cascade model. Oecologia 123: 241 – 251.

Parsons, K.J., Sheets, H.D., Skúlason, S., and Ferguson, M.M. 2011. Phenotypic plasticity, heterochrony, and ontogenetic repatterning during juvenile development of divergent Arctic charr (*Salvelinus alpinus*). J. Evol. Biol. 24: 1640 – 1652.

Robinson, B.W., and Wilson, D.S. 1994. Character release and displacement in fishes: a neglected literature. Am. Nat. 144: 596 – 627.

Rohlf, F.J. 2004. Thin-plate-spline software freely available at http://life.bio.sunysb.edu/morph/

Sandlund, O.T., Gunnarson, K., Jónasson, P.M., Jónsson, B., Lindem, T., Magnusson, K.P., Malmquist, H.J., Sigurjónsdóttir, H., Skúlason, S., and Snorrason, S.S. 1992. The Arctic charr *Salvelinus alpinus* in Thingvallavatn. *Oikos 64:* 305-351.

Schindler, D.E., and Scheurell, M.D. 2002. Habitat coupling in lake ecosystems. Oikos 98: 177-189.

Schindler, D.E., S.R. Carpenter, J.J. Cole, J.F. Kitchell and M. Pace. 1997. Influence of food web structure on carbon exchange between lakes and the atmosphere. Science 277: 248-250.

Schindler, D.W., and Smol, J.P., 2006. Cumulative effects of climate warming and other human activities on freshwaters of Arctic and subarctic North America. Ambio 35: 160 – 168.

Schluter, D. 1993. Adaptive radiation in sticklebacks: size, shape and habitat use efficiency. Ecology 74: 699 – 709.

Schluter, D. 1996. Ecological speciation in postglacial fishes. Phil. Trans. R. Soc. Lond. B 351: 807-814.

Sigursteinsdóttir, R.J., and Kristjánsson, B.K. 2005. Parallel evolution, not always so parallel: comparison of small benthic charr, *Salvelinus alpinus*, from Grimsnes and Thingvallavatn, Iceland. *Environ. Biol. Fishes 74:* 239-244.

Skúlason, S., and Smith, T.B. 1995. Resource polymorphisms in vertebrates. *TREE 10:* 366-370.

Skúlason, S., Snorrason, S.S., and Jónsson, B. 1999. Sympatric morphs, populations and speciation in freshwater fish with emphasis on arctic charr. pp. 70-92 In Evolution of Biological Diversity, eds. A.E. Magurran & R.M. May.

Smith, T.B., and Skúlason, S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. Ann. Rev. Ecol. System. 27: 111 – 133.

Snorrason, S.S., and Skúlason, S., 2004. Adaptive Speciation in northern freshwataer fishes. In: Adaptive Speciation, eds. Dieckmann, U., Doebeli, M., Metz, J.A.J., & Tautz, D. pp. 210-228. Cambridge University Press.

Snorrason, S.S., Skúlason, S., Jónsson, B., Malmquist, H.J., Jónasson, P.M., Sandlund, O.T., and Lindem, T. 1994. Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces; Salmonidae): morphological divergence and ontogenetic niche shifts. Biol. J. Linn. Soc. 52: 1-18.

Stefánsson, G. 1996. Analysis of groundfish survey abundance data: Combining the GLM and delta approaches. *ICES J. Mar. Sci. 53:* 577-588.

Stefánsson, G., and Pálsson, Ó. 1997. Statistical evaluation and modelling of the stomach contents of Icelandic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 54: 169-181.

Vander Zanden, M.J., and Fetzer, W.W. 2007. Global patterns of aquatic food chain length. Oikos 116: 1378-1388.

Vanni, M.J. 2002. Nutrient cycling by animals in freshwater ecosystems. Ann. Rev. Ecol. Syst. 33:341-370.

Walker, J.A. 1997. Ecological morphology of lacustrine threespine stickleback *Gasterosteus aculeatus* L. (Gasterosteidae) body shape. *Biol. J. Linn. Soc.* 61: 3 – 50.

Webb, P.W. 1984. Body form, locomotion and foraging in aquatic vertebrates. Am. Zool. 24: 107 – 120.

Webb, P.W. 1986. Effect of body form and response threshold on the vulnerability of four species of teleost prey attacked by largemouth bass (*Micropterus salmoides*). Can. J. Fish. Aquat. Sci. 43: 763 – 771.

Ydenberg, R.C., Brown, J.S., and Stephens, D.W. 2007. Foraging: an overview. In: *Foraging Behavior and Ecology*. Stephens, D.W., Brown, J.S., and Ydenberg, R.C., eds. University of Chicago Press, Chicago. 608 pp.

3 Metrics for detecting phenotypic polymorphism and correlations with the lake environment in Arctic charr *Salvelinus alpinus* across Iceland

3.0 Abstract

Phenotypic polymorphism is the occurrence of multiple discrete forms that can be distinguished by one or more phenotypic attributes, but have no barrier to physically separate them. Past studies of phenotypic polymorphism have typically investigated particular case studies in detail; however, this study aims to compare patterns of phenotypic polymorphism among study systems. Cross-system comparisons are necessary for understanding the role of intraspecific diversity in an ecosystem context, as well as what environmental conditions have led to polymorphism. Comparative studies have been hampered by the variety of methods used to document polymorphism, and therefore, the dearth of standard metrics with which to compare systems. The first goal of this study was to apply two methods by which polymorphism may be identified, using Icelandic Arctic charr *Salvelinus alpinus* as the study system. Arctic charr are extremely diverse in morphology, ecology, growth, and reproductive characteristics both within and among lakes, and are especially diverse in Iceland. The two methods use mixture models to detect resource polymorphism by 1) testing for the presence of multiple Von Bertalanffy growth curves, and 2) testing for bimodality in multivariate morphology. The study's second goal was to identify conditions under which resource polymorphism is most likely to occur

using random forest and multiple regression models. Ecological correlations indicated that in Iceland, polymorphic populations tend to occur in deep lakes at higher elevations and with low nutrient concentrations, higher zooplankton consumption, and few brown trout, *Salmo trutta*. It appeared that greater nutrient input into lakes via leeching from surrounding terrestrial vegetation was necessary for more extreme cases differentiation to occur. These correlations supported the ideas that more isolated regions with greater limnetic habitat availability and high intraspecific competition promoted phenotypic polymorphism. This pattern is predicted from the theory that frequency-dependent selection is a main driving force behind differentiation. In addition, conditions beyond the lake (i.e., of the surrounding watershed) appear to affect evolutionary processes of lake fauna. Our methods for detecting polymorphism are broadly applicable and can be used whenever needing to define and measure low levels of phenotypic or ecological diversity.

3.1 Introduction

Conservation of biological diversity is commonly justified beyond its aesthetic value (Jepson & Canney 2003) as it can enhance ecosystem functioning (Cardinale et al. 2006). However, little emphasis is traditionally placed on the importance of intraspecific diversity, such as phenotypic polymorphism, even though it can have important consequences on functional attributes of ecosystems (Harmon et al. 2009). Phenotypic polymorphism is characterized by the occurrence of discrete forms within a population that differ by one or more phenotypic attributes, yet are not hindered by physical or geographic barriers. Because the strength of this phenotypic polymorphism may vary on a continuum from vague ecological differences to phenotypic differentiation strong enough to warrant species status, this concept has been extremely important in the development of ecological speciation theory (Schluter et al. 1996). However, polymorphism also appears constrained to certain taxa and situations (e.g., post-glacial temperate freshwater fishes, sensu Schluter 1996; Robinson & Wilson 1994; Skúlason & Smith 1995; Smith & Skúlason 1996). Regional comparisons are therefore urgent to gain a better understanding of 1) the evolutionary implications of how this diversity arises, and 2) the

ecological or conservation implications of how this form of diversity can affect ecosystems.

In any study, trade-offs exist between how much focus can be placed on 1) detailing the idiosyncrasies of a particular attribute versus 2) comparing a general aspect of that attribute across many systems. In studying phenotypic polymorphism, hereafter referred to as polymorphism, the former type of study has prevailed, yielding a series of case studies that are biased toward highly differentiated attributes and lack coherence across studies. Cross-system comparisons would yield a more balanced view, yet are rare (but see Griffiths 1994, Landry et al. 2007, Siwertsson et al. 2010), potentially due to the problem that common metrics first need to be defined.

The availability of biological and limnological data from a wide diversity of ~50 lakes found within the Ecological Survey of Icelandic Lakes (ESIL) database yielded a rare opportunity in which intraspecific diversity of the salmonid fish Arctic charr *Salvelinus alpinus* could be compared across geographically and environmentally broad conditions. Arctic charr exhibit resource polymorphism, defined as the presence of phenotypic polymorphism that is associated with differences in resource or habitat use (Skúlason & Smith 1995; Smith & Skúlason 1996). The term is used broadly across many taxa and study systems, indicating that the boundaries used to define resource polymorphism vary, even within the same species (Jonsson & Jonsson 2001). For example, differences between sympatric forms of Arctic charr may include differentiation in growth rates and maturity (Griffiths 1994; Klemetsen 2010), whereas others may only differ in morphology and diet (Jónsson & Skúlason 2000; Adams et al. 2007), or reproductive and early life history characteristics (Skúlason et al. 1989; Skúlason et al. 1996; Adams et al. 2006).

The first goal of this study was to develop standard methods by which populations can be defined as polymorphic, monomorphic, or some intermediate status. To assess our method, we compared our ability to detect polymorphism to published reports documenting phenotypic and genetic differences (Jónsson & Skúlason 2000; Jónsson 2002; Jónsson & Malmquist 2002; Wilson et al. 2004) and expert knowledge mostly based on observations of individuals maturing at both small and large sizes within a population. The second goal was to predict these metrics of polymorphism with ecological data to test

hypotheses regarding the establishment and maintenance of polymorphism.

3.1.1. Hypotheses regarding the origin of resource polymorphism

Resource polymorphism is most simply observed as bimodality in a trait. In general, frequency-dependent selection is thought to be the primary evolutionary factors leading to bimodality (van Valen 1965, Dieckmann et al. 2004). For example, resource polymorphism may arise when a single population increases in density, after which intraspecific competition for a preferable resource increases due to decreasing per capita availability of the resource. At some critical point, it becomes beneficial to be efficient at obtaining less preferable but more abundant resources, and selection becomes disruptive on phenotypic attributes associated with foraging (Skúlason & Smith 1995). The relative fitness of a morphological characteristic therefore depends on its frequency in relation to alternative morphological characteristics, resulting in stable frequency-mediated selection (Dieckmann et al. 2004).

However, frequency dependence is not the only explanation for observing bimodality in a population. For example, predation risk can promote differential habitat use, leading to divergent selection in small-bodied fish species (Abrams 2000; Rundle, Vamosi & Schluter 2003; Vamosi & Schluter 2002; Doucette, Skúlason and Snorrason 2004; Langerhans et al. 2004). Predation has also been suggested as a mechanism promoting size divergence of Arctic charr due to the abilities of small benthic forms to hide among substrate (Snorrason and Skúlason 2004) or the abilities of cannibalistic individuals to reach large sizes (Griffiths 1994). Although frequency dependence is difficult to measure, empirical studies have shown that high population densities lead to wider resource use (Svanbäck & Persson 2004), intraspecific competition can indeed lead to morphological divergence (Schluter 1994; Bolnick 2004; Svanbäck & Bolnick 2007), frequency-dependent selection can be detected in a polymorphic system (Schluter 2003), and population stability promotes divergent selection (Andersson et al. 2007). In addition, divergence is thought to occur under ecological conditions that promote frequency-dependent selection by yielding high niche availability (Knudsen et al. 2006). We therefore hypothesize that polymorphism should be more frequent under the following conditions:

1. Higher intraspecific competition is necessary to cause the frequency-dependent selection that leads to bimodality (Schluter 1994; Bolnick 2004; Svanbäck & Bolnick 2007, Dieckmann et al. 2004) and could be detected in three ways:
    a. Higher altitudes may yielding lower species diversity, because these regions are more isolated and more recently deglaciated. Areas of recent deglaciation tend to exhibit higher rates of diversification in fish, have more barriers to migration, and are thought to have promote species adaptability through high environmental variability (Bernatchez & Wilson 1998; Robinson & Schluter 2000, Griffiths 2006). Decreased interspecific competition in areas of low fish diversity may therefore allow for greater intraspecific competition
    b. Along the same lines, low abundance of known competitors (i.e., brown trout) would allow for greater availability of niches and a prevalence of intraspecific competition (Griffiths 1994; Robinson & Wilson 1994; Skúlason & Smith 1995, Schluter 1996; Griffiths 2006).
    c. High conspecific densities (Griffiths 1994) could directly indicate greater competition.
2. Greater availability of limnetic resources, relative to benthic resources, may be a prerequisite for the development of polymorphism through niche expansion (Jonsson & Jonsson 2001, Skúlason, Snorrason & Jónsson 1999). Four environmental correlates with polymorphism may indicate this trend:
    a. Low nutrient levels could indicate high limnetic productivity and a link with polymorphism (Siwertsson et al. 2010). Greater limnetic food consumption could be detected through correlations with environmental variables linked to zooplankton consumption in Icelandic Arctic charr (high silicon dioxide concentrations, low nutrient levels, high chironomid pupae densities: Woods et al. 2011).
    b. Low limnetic zooplankton abundance could indicate greater consumption of these resources (Landry, Vincent & Bernatchez 2007).
    c. Greater lake depth (Vonlanthen et al. 2009) or size (Griffiths 1994; Siwertsson et al. 2010) could indicate a greater availability of discrete habitats and total volume

of limnetic resource. Alternatively, intermediate lake sizes may promote polymorphism by providing a more even availability of littoral and benthic habitats, thereby preventing discrete phenotypes from dominating (Bolnick & Lau 2008).

3. High predator densities (i.e., brown trout) may be necessary if polymorphism is maintained by divergent selection based on increased vulnerability to predation at intermediate trait values or differential habitat use, rather than frequency dependence (Abrams 2000; Rundle, Vamosi & Schluter 2003; Vamosi & Schluter 2002; Doucette, Skúlason and Snorrason 2004; Langerhans et al. 2004).

3.2 Methods

3.2.1. Biological attributes of Arctic charr

Two types of phenotypic attributes of Arctic charr were analyzed for this study: length-at-age and morphology. Fish were sampled once per lake sometime during the months August – September during 1992 – 2004 as part of the Ecological Survey of Icelandic Lakes (ESIL). In each lake, 11 (22 for lakes >10 km^2) single-mesh, single-strand nylon gill nets (Lundgren series) were set in the littoral zone from ~2 m depth outwards perpendicular to shore and left overnight for 12 hours. Gill nets were 25 m x 1.5 m with the mesh sizes 10, 12.5, 15.5, 19.5, 21.5, 24.0, 29.0, 35.0, 43.0, 55.0, and 60.0 mm, knot to knot. For Arctic charr caught, photographs were taken, fork length was measured to the nearest 0.5 cm, and otoliths were removed from a subsample of up to 100 individuals for age determination. Otoliths were cleaned with a solution of methyl salicylate and annual growth rings were counted under a dissecting microscope. In total, 51 lakes were included in age and morphological analyses (Table 3.1).

Morphological variables were derived from scanned images using a geometric morphometric approach in TPS software (TPSDig V. 2.1, TPSUtil V. 1.40, TPSRel V. 2.4, Rohlf, 2004, life.bio.sunysb.edumorph). Eighteen landmarks and 6 sliding landmarks were placed at homologous locations on images of each fish (Chapter 2, Fig 2.1). Sliding landmarks are defined in one direction, but are allowed to slide in the other direction between the two adjacent landmarks. For

example, the sliding landmark placed on the anterior edge of the adipose fin may slide between the posterior dorsal fin landmark and posterior adipose fin landmark, but is fixed in the direction perpendicular to these adjacent landmarks (Chapter 2, Fig 2.1). Landmark configurations were unbent to remove the mean curve in fish bodies (although not its variability), aligned, rotated, and scaled to form a generalized orthogonal least-squares Procrustes average configuration. Partial warp scores for each individual were formed by comparing the relative departure in configuration of individuals from the average configuration, and analyzed with a relative warp analysis, which is analogous to a principal component analysis and results in scores on orthogonal relative warp axes for each individual (Bookstein 1991; Rohlf et al. 2004). The first three relative warps were used as morphological variables (m_1, m_2, m_3).

Table 3.1. Lakes included in analyses are shown with their geographic coordinates, year sampled, database number that corresponds with labels in Fig. A3.1, and the number of expected morphs according to expert knowledge (Exp. K). Values of 0 indicate monomorphism; 1 indicates polymorphism. The number of morphs detected in the model with minimum AICc included K = 1, 2, or 3 for Von Bertalanffy growth curve models (VB K) or K = 1 or 2 for bivariate morphology models (M K). The number of individuals placed in each morph is indicated by N1, N2, and N3, which are ordered according to corresponding coefficient estimates in Tables A3.1 and A3.2. Differentiation (D) was calculated for populations detected as K = 2. Effect Sizes (η^2) were calculated for morphological combinations that yielded K = 2: M12 (m_1 and m_2), M23 (m_2 and m_3), or M13 (m_1 and m_3). Lakes with asterisks were excluded from environmental analyses due insufficient data

Lake	Year	Lat. (N)	Long. (W)	Lake	Exp K	VB K	VB N1	VB N2	VB N3	D	M K	M N1	M N2	η^2 M12	η^2 M23	η^2 M13
Apavatn	1993	64º10´	20º38´	1	1	2	21	39	0	0.520	1	31	0	-	-	-
Elliðavatn	1993	64º05´	21º48´	2	1	1	51	0	0	-	1	35	0	-	-	-
Eyrarvatn	1992	64º25´	21º36´	3	1	1	59	0	0	-	1	35	0	-	-	-
Galtaból	1992	65º15´	19º43´	4	2	2	24	16	0	0.882	1	29	0	-	-	-
Glammastaðavatn	1992	64º26´	21º35´	6	1	2	36	21	0	0.676	2	7	27	0.454	-	-
Hraunhafnarvatn	1993	66º31´	16º02´	7	1	1	39	0	0	-	1	37	0	-	-	-
Hvítárvatn	1994	64º36´	19º52´	8	2	1	57	0	0	-	1	31	0	-	-	-
Kötluvatn	1993	66º30´	16º30´	9	1	2	51	9	0	0.643	1	38	0	-	-	-
Langavatn	1993	64º07´	18º49´	10	1	2	31	20	0	0.681	1	27	0	-	-	-
Mjóavatn	1992	65º15´	19º48´	11	1	2	25	35	0	0.592	1	17	0	-	-	-
Selvatn	1992	65º57´	20º03´	13	1	1	39	0	0	-	1	37	0	-	-	-
Sigurðarstaðavatn	1993	66º29´	16º18´	14	1	1	46	0	0	-	1	45	0	-	-	-
Stóra-Viðarvatn	1993	66º14´	15º50´	17	2	3	18	24	13	-	1	36	0	-	-	-

(Continued)

Table 3.1 (Continued). Lakes included in analyses are shown with their geographic coordinates, year sampled, database number that corresponds with labels in Fig. A3.1, and the number of expected morphs according to expert knowledge (Exp. K). Values of 0 indicate monomorphism; 1 indicates polymorphism. The number of morphs detected in the model with minimum AICc included K = 1, 2, or 3 for Von Bertalanffy growth curve models (VB K) or K = 1 or 2 for bivariate morphology models (M K). The number of individuals placed in each morph is indicated by N1, N2, and N3, which are ordered according to corresponding coefficient estimates in Tables A3.1 and A3.2. Differentiation (D) was calculated for populations detected as K = 2. Effect Sizes (η^2) were calculated for morphological combinations that yielded K = 2: M12 (m_1 and m_2), M23 (m_2 and m_3), or M13 (m_1 and m_3). Lakes with asterisks were excluded from environmental analyses due insufficient data.

Svínavatn	1993	65º32´	20º06´	19	2	3	20	24	21	-	1	60	0	-	-	-
Úlfljótsvatn	1993	64º06´	21º02´	20	2	2	63	16	0	0.510	1	51	0	-	-	-
Vatnshlíðarvatn	1992	65º31´	19º38´	21	2	1	28	0	0	-	1	27	0	-	-	-
V-Friðmundarvatn	1992	65º18´	14º41´	22	1	2	63	12	0	0.394	1	18	0	-	-	-
Y-Deildarvatn	1993	66º24´	15º58´	23	1	2	19	17	0	0.470	1	25	0	-	-	-
Ölvesvatn	1992	65º58´	20º05´	24	1	1	46	0	0	-	1	32	0	-	-	-
Haukadalsvatn	1994	65º35´	21º37´	28	2	2	45	14	0	0.862	2	18	28	0.148	-	0.325
Hítarvatn	1994	64º53´	21º55´	29	1	2	12	37	0	0.546	1	43	0	-	-	-
Oddastaðavatn	1994	64º54	22º13´	30	1	1	39	0	0	-	1	38	0	-	-	-
Vatnsholtsvatn	1994	64º49´	23º16´	31	1	1	44	0	0	-	1	34	0	-	-	-
Ánavatn	1994	65º13´	15º31´	32	1	2	19	38	0	0.731	1	34	0	-	-	-
Sænautavatn	1994	65º16´	15º31´	33	1	2	40	20	0	0.375	1	36	0	-	-	-
Eiðavatn	1994	65º24´	14º21´	34	1	1	25	0	0	-	1	24	0	-	-	-
Urriðavatn	1994	65º17´	19º51´	35	1	2	43	6	0	0.098	1	39	0	-	-	-
Thiðriksvallavatn	1995	65º41´	21º46´	36	1	1	7	0	0	-	1	40	0	-	-	-
Högnavatn	1995	65º48´	22º10´	37	2	3	28	10	41	-	1	75	0	-	-	-

(Continued)

Table 3.1 (Continued). Lakes included in analyses are shown with their geographic coordinates, year sampled, database number that corresponds with labels in Fig. A3.1, and the number of expected morphs according to expert knowledge (Exp. K). Values of 0 indicate monomorphism; 1 indicates polymorphism. The number of morphs detected in the model with minimum AICc included K = 1, 2, or 3 for Von Bertalanffy growth curve models (VB K) or K = 1 or 2 for bivariate morphology models (M K). The number of individuals placed in each morph is indicated by N1, N2, and N3, which are ordered according to corresponding coefficient estimates in Tables A3.1 and A3.2. Differentiation (D) was calculated for populations detected as K = 2. Effect Sizes (η^2) were calculated for morphological combinations that yielded K = 2: M12 (m_1 and m_2), M23 (m_2 and m_3), or M13 (m_1 and m_3). Lakes with asterisks were excluded from environmental analyses due insufficient data.

Ásbjarnarvatn-S	1996	65º03´	18º48´	39	1	2	38	47	0	0.382	2	13	37	0.306	-	0.321
Hópið	1996	65º31	20º30	41	1	2	22	36	0	0.366	-	-	-	-	-	-
Vesturhópsvatn	1996	65º28´	20º39´	42	1	1	59	0	0	-	1	37	0	-	-	-
Langavatn*	1996	65º49´	17º17´	43	2	2	48	12	0	0.565	1	40	0	-	-	-
Reyðarvatn*	1996	65º06´	18º32´	44	2	1	42	0	0	-	1	21	0	-	-	-
Fljótsbotn	1997	63º52´	18º54´	47	2	2	71	9	0	0.394	1	65	0	-	-	-
Frostastaðavatn*	1997	64º01´	19º03´	48	1	3	18	17	24	-	1	34	0	-	-	-
E. Gíslholtsvatn*	1997	63º57´	20º29´	49	1	1	14	45	0	-	1	58	0	-	-	-
Hestvatn*	1997	64º01´	20º42´	50	2	2	33	37	0	0.639	1	64	0	-	-	-
Hlíðarvatn*	1997	63º52´	21º43´	51	1	1	42	11	0	-	2	40	11	-	0.114	-
Hólmavatn*	1997	65º02	20º33	52	1	-	-	-	-	-	-	6	0	-	-	-
Arnarvatn Stóra*	1997	64º57´	20º19´	53	1	2	61	16	0	0.172	1	18	0	-	-	-
Úlfsvatn*	1997	64º53´	20º35´	54	1	3	25	19	23	-	2	19	6	-	0.491	-
Langisjór	1998	64º10´	18º17´	57	1	1	20	0	0	-	1	17	0	-	-	-
Skorradalsvatn	1998	64º27´	21º09´	58	2	2	61	37	0	0.626	1	71	0	-	-	-

(Continued)

Table 3.1 (Continued). Lakes included in analyses are shown with their geographic coordinates, year sampled, database number that corresponds with labels in Fig. A3.1, and the number of expected morphs according to expert knowledge (Exp. K). Values of 0 indicate monomorphism; 1 indicates polymorphism. The number of morphs detected in the model with minimum AICc included K = 1, 2, or 3 for Von Bertalanffy growth curve models (VB K) or K = 1 or 2 for bivariate morphology models (M K). The number of individuals placed in each morph is indicated by N1, N2, and N3, which are ordered according to corresponding coefficient estimates in Tables A3.1 and A3.2. Differentiation (D) was calculated for populations detected as K = 2. Effect Sizes (η^2) were calculated for morphological combinations that yielded K = 2: M12 (m_1 and m_2), M23 (m_2 and m_3), or M13 (m_1 and m_3). Lakes with asterisks were excluded from environmental analyses due insufficient data.

Lagarfljót	1998	65º10´	14º38´	59	2	2	51	67	0	0.457	1	29	0	-	-	-
Thuríðarvatn*	1998	65º36´	15º10´	60	1	2	7	60	0	0.347	2	30	7	-	-	0.563
Heiðarvatn	1998	65º14´	14º10´	61	1	2	40	20	0	0.705	1	40	0	-	-	-
Skriðuvatn	1998	64º57´	14º38´	62	1	2	69	10	0	0.315	2	54	7	-	-	0.505
Sandvatn	1998	65º18´	14º41´	64	2	2	15	32	0	0.458	1	40	0	-	-	-
Thríhyrningsvatn	1998	65º10´	15º46´	65	2	1	62	0	0	-	2	31	19	0.834	-	-
Hafravatn	1998	64º07´	21º44´	67	2	1	12	0	0	-	-	11	0	-	-	-
Total lakes K > 1	-	-	-	-	17	38					8					

3.2.2. Detecting polymorphism

In extreme cases, polymorphism may show clearly distinct growth curves or morphologies, but in other cases, it may be difficult to distinguish between different phenotypes. Therefore we sought objective criteria by which broad variability in biological attributes could be distinguished from the presence of overlapping groups. To do this, we first collected expert knowledge from published reports and ESIL survey data (Jónsson & Skúlason 2000; Jónsson & Malmquist 2002; Wilson et al. 2004) that indicate the presence of forms that appear morphologically different or grow to and mature at small sizes (~15 cm) in the presence of larger Arctic charr (Table 3.1). This knowledge was used as a baseline with which to compare results gained from the fitting of mixture models to Arctic charr biological attributes. Statistical evidence for the presence of polymorphism was then evaluated as the model with the lowest AICc among 1) a growth curve model containing either 1, 2 or 3 Von Bertalanffy growth functions, and 2) monomodal, bimodal, and trimodal multivariate normal distributions fit to bivariate morphology data.

To perform the first test among growth curve models, a model with only a single Von Bertalanffy (VB) growth function (Eq. 1) was first fit as:

$$\mu = L_{\infty}(1 - e^{-\kappa a}) \qquad \text{Eq. 1}$$

where length (μ) was predicted using a = age data, L_{∞} = asymptotic length parameter, and κ = curvature parameter. Normal errors were assumed (i.e., $\varepsilon \sim N(\mu, \sigma)$), so the sum of the negative log likelihoods from a normal probability density function was minimized to estimate the three parameters ($L_{\infty}, \kappa, \sigma$). Two separate VB functions were then fit to the data by minimizing the negative log of a likelihood function based on a mixture distribution of two normal density functions:

$$L = \prod (p \frac{1}{\sqrt{2\pi\sigma_1^2}} e^{-\frac{x-\mu_1}{2\sigma_1^2}} + (1-p) \frac{1}{\sqrt{2\pi\sigma_2^2}} e^{-\frac{x-\mu_2}{2\sigma_2^2}}) \qquad \text{Eq. 2}$$

where μ_1 and σ_1 are parameters defining first normal distribution in the mixture, μ_2 and σ_2 are parameters defining the second normal distribution, and p is the proportion that the first distribution contributes

to the mixture. In this case, μ_1 and μ_2 in Eq. 2 are defined by two separate VB functions, each with a set of parameters (L_∞, κ). The likelihood of a single data point is therefore a mixture of the likelihoods that it came from each distribution, and this model represents the situation in which multiple morphs coexist within a population. Assignment of individual data points to one or the other growth curve can then be made by calculating what proportion of that individual's likelihood was attributable to each growth curve and assigning the individual to the growth curve with the maximal proportion. This model was then extended to fit 3 growth curves:

$$L = \prod(p_1 \frac{1}{\sqrt{2\pi\sigma_1^2}} e^{-\frac{x-\mu_1}{2\sigma_1^2}} + p_2 \frac{1}{\sqrt{2\pi\sigma_2^2}} e^{-\frac{x-\mu_2}{2\sigma_2^2}} + (1 - p_2 - p_3) \frac{1}{\sqrt{2\pi\sigma_3^2}} e^{-\frac{x-\mu_3}{2\sigma_3^2}})$$

Eq. 3

where p_2 refers to the proportion that the second distribution contributed to the mixture, and μ_3 and σ_3 are parameters for the third normal distribution as defined by the fit of a third VB function.

Polymorphism in morphology was detected within each lake by assuming multivariate normal error for morphology (i.e., $\varepsilon \sim$ MVN(**μ**, **E**)) where **μ** is a vector of morphological variable means (e.g., **μ** = ($\overline{m_1}$, $\overline{m_2}$, $\overline{m_3}$)) and **E** is the covariance matrix, and their dimensions depend on the number of morphological variables included. Multivariate normal distributions were chosen because preliminary analyses indicated that univariate distributions of morphological variables were close to normal, with some possibly informative deviations in some lakes. A unimodal model of morphology was fit simply by estimating these parameters within MVN(**μ**, **E**), whereas a bimodal model was fit by estimating a mixture model of multiple multivariate normal distributions. For a bimodal mixture model, the parameters included were two separate vectors of means (**μ**), 2 covariance matrices (**E**), and a proportional contribution p of the first multivariate distribution (i.e., the same as Eq. 2 except univariate density functions are extended to be multivariate density functions). Trimodality in morphology was fitted using a mixture model of three multivariate normal distributions (i.e., 3 separate vectors of means (**μ**), 3 covariance matrices (**E**), and 2 proportional contributions p_1 and p_2 of the first and second multivariate distributions respectively, similar to Eq. 3).

Especially for morphological models with 2 or 3 components, model overfitting was a risk, particularly with relatively small available samples (Table 3.1). Therefore, the best-fit model was chosen among models with 1, 2 and 3 components (K) as the one with the lowest Akaike's Information Criterion corrected for small sample sizes (AICc). Preliminary analyses indicated that fitting morphological models with all three variables included (i.e., trivariate distributions) always resulted in unimodal distributions, so three possible bivariate combinations of morphological variables were used instead (i.e., m_1 and m_2, m_2 and m_3, m_1 and m_3). Although univariate tests are also possible, bivariate tests were preferred so that any within-component covariance of morphological traits could be estimated, as these may reflect biologically important distinctions between morphs. This allows for differences between component distributions to be more accurately visualized. These tests are not independent, however; results are only used from the tests with the greatest Differentiation (see below). The package mixtools v. 0.4.4 in R statistical software v. 2.13.0 was used to fit unimodal multivariate normal distributions and finite mixtures of multivariate normal distributions with an EM algorithm (Benaglia et al. 2009); all other analyses were performed using base packages (R Development Core Team 2011).

Fitted distributions with highly uneven numbers of members (i.e., one distribution with very few members) tended to yield higher likelihoods than more even distributions. Because we found this result less biologically informative than more evenly defined distributions, starting values of morphological models were randomly chosen 30 times and we retained the model that minimized the corrected Aikaike's Information Criterion (AICc) within the constraint of each group having more than five members. This five-member cut off was chosen because in results, most lakes categorized as polymorphic, but having a relatively small number of individuals assigned to one component (< 15), gained additional support from either expert knowledge or morphological tests, whereas none of the lakes with fewer than five individuals assigned to one component were likewise supported (see Results).

3.2.3. Calculating differentiation

Only the presence of polymorphism was detected in the previous analysis, whereas strength of polymorphism could be reflected by the degree of overlap between the two forms. For morphology, this can be reflected using Effect Size (η^2), which is calculated as 1 – Wilks' λ from a multivariate ANOVA using the component assignments as a categorical predictor. Because our growth curve analysis was based on a non-linear model, this ANOVA-related definition is inappropriate, however. We therefore describe below a metric of Differentiation (D) we define that is based on the same concept as Effect Size to use as an indicator distinction among growth curves.

For a categorical predictor of univariate data, Effect Size (η^2) is normally calculated as the sum of squared errors due to treatments or groups (between-treatment error) divided by the total sum of squares. If the two-curve fit is taken to be the presence of a treatment, and a one-curve fit is taken to be the absence of treatment, then a measure similar to the ANOVA-based between-treatment error can be calculated in our study as the sum of the squared differences between individual predictions from the two-curve model and from the one-curve model. The total sum of squares was then taken as the sum of the squared residuals of the single-curve model, and the sum of squared between-curve differences was divided by this to yield D. However, unlike a true Effect Size, this value may exceed 1. Because predictions are necessary for calculating D, individuals were first assigned to the most likely growth curve using the proportions of likelihood attributable to each growth curve as described in the previous section. In analyses of morphology, assignments are based on "posterior" probabilities, an output from mixtools that uses the same method.

The relative sensitivity of D values was then examined by comparing lakes that 1) were expected to be polymorphic according to expert knowledge *and* gained support from at least one of the two polymorphism tests, and 2) were *not* expected to be polymorphic *and* gained support from exactly one polymorphism test. We then chose a cut-off value for D to represent an appreciable degree of differentiation (D*) by simultaneously minimizing the number of lakes in first category with $D < D^*$ and maximizing the number of lakes in the second category with $D < D^*$. However, because the calculation of D relies on

assignments made by the first tests, D* is simply used for descriptive purposes, and original categorizations were used for further analysis.

3.2.4. Predicting polymorphism with ecological variables

To test for support of hypotheses 1 – 3 listed in the Introduction, we predicted both our categorical and continuous measures of polymorphism using environmental variables taken or calculated from the ESIL database (see for details Malmquist et al. 2000; Karst-Riddoch, Malmquist & Smol 2009; Woods et al. 2011). To predict the detection of either polymorphism or monomorphism, we first used random forest categorization models described below. However, preliminary analyses using random forest regression trees to predict Differentiation and Effect Size indicated little predictive ability, so multiple regressions were instead used with backward AICc selection on an initial model including all ecological predictor variables.

Physical and chemical variables included mean depth (MD, m), pH (PH), altitude (ALT, m), surface temperature (ST, °C), conductivity (COND, µS / cm), alkalinity (ALK, meq / l), total phosphorus (TP, µg / l), total nitrogen (TN, µg / l), total organic carbon (TOC, mg / l), sulfate (SO4, mg / l), and silicon dioxide (SiO2, mg / l). To correct for skew, these variables were all log-transformed, except for SiO2 and SO4 which were square-root transformed.

A variety of biotic predictors were also calculated from the ESIL database and previous studies (Woods et al. 2011). Arctic charr catch per unit effort (ACA, # per gillnet per hour) and brown trout catch per unit effort (BTA, # per gillnet per hour) were calculated from the gill net collection procedure described above. Atlantic salmon *Salmo salar* were rarely caught in lakes so were excluded from analyses. The presence of threespine stickleback *Gasterosteus aculeatus* was detected using minnow traps and was included as a binary factor (SP). A Shannon index of diversity for invertebrates collected from stones (SH) was calculated from littoral habitat invertebrate surveys from the ESIL project (Malmquist et al. 2000). Fish abundances (BTA and ACA) were transformed by log(x + 1), but SH was normal and not transformed. Prey abundances from ESIL invertebrate surveys were calculated within prey categories defined by Woods et al. (2011). In that study, six categories of prey were defined and named by their most prominent

taxon: limnetic cladocerans and copepods composed the *Bosmina* category (B), chironomid pupae and terrestrial insects composed the chironomid pupae category (C), snails and caddisfly larvae composed the snail category (S), tadpole shrimp and both limnetic and benthic copepods and cladocerans composed the tadpole shrimp category (T) and pea clams and chironomid larvae alongside worms and small crustaceans were major components of the pea clam category (P) (Woods et al. 2011). In ESIL surveys, invertebrates were collected and counted from the shallow (0.2 – 0.5 m), rocky, littoral habitat, the off-shore sediment habitat, and the pelagic habitat (see for details Malmquist et al. 2000; Karst-Riddoch, Malmquist & Smol 2009; Woods et al. 2011). Counts within each category were converted to biomass (mg) by multiplying a weight representative of the order of magnitude for each species and then summing within categories (see Woods et al. 2011 for details). Volumetric zooplankton densities were multiplied by mean depth to yield m^{-2} areal measures comparable to those of benthic invertebrates, and all were transformed by $\log(x + 1)$. Environmental data were not available for all lakes, so analyses were restricted to the 41 of the 51 lakes with complete data.

Associations between the presence of polymorphism and environmental characteristics were investigated using a random forest model, which is a machine learning method that compares favorably to other methods for modeling classification data (Breiman 2001; Prasad, Iverson & Liaw 2006). In this method, a random forest is "grown" by collecting a number of classification trees formed by fitting a classification tree to a different bootstrap sample of the data. For each classification tree, a set of explanatory variables are tested to determine which one best splits the data into possible classes (i.e., lakes with monomorphic versus polymorphic charr populations) with the least number of misclassified data points. Each split leads to two nodes, with data points predicted to occur as a certain class within that node. Final classifications for each data point are then aggregated across individual trees to yield a collection of votes (1 per tree) for an overall prediction based on the proportion of votes from the forest. We chose to use bootstrapping without replacement to reduce bias in importance measures of explanatory variables (Strobl 2007). The overall error rate of the model was calculated by forming predictions for the data that were not collected in the bootstrap sample (i.e., "out-of-bag" data), and calculating a misclassification rate over all data points (OOB error rate).

Preliminary analyses of single classification trees indicated that the maximum number of explanatory variables within single trees is likely not to be high. Therefore, the maximum number of nodes was set to 8, and the number of trees grown was set to 100,000. The package randomForest v. 4.6-2 (Liaw & Wiener 2002) was used within the statistical software R v. 2.13.0 (R Development Core Team 2011).

Random forest models can detect effects even if they are non-linear or have complex interactions with other explanatory variables, but the flexibility of this framework may also lead to the incorporation of improper variables in over-parameterized models (Eustace, Pringle and Denham 2011). In a step-wise model reduction method (Diaz-Uriarte & Alvarez de Anderes 2006; Genuer, Poggi & Tuleau-Malot 2010; Sethi 2010), an initial model fit first included all explanatory variables, which were ordered according to importance using two measures: 1) Mean Decrease in Accuracy, measured by the decrease in OOB that occurs when that explanatory variable is replaced by a permutation of itself, and 2) a decrease in node impurity as measured by the Gini Index, which characterizes the explanatory variable's ability to distinguish classes at a given split. The first directly relates to the following model selection criterion, whereas the second is more stable for small sample sizes (Breiman 2002; Liaw and Wiener 2002; Strobl et al. 2007). Explanatory variables were first ranked using both indices and listed by the greater of the two ranks. The least important explanatory variables were then successively deleted if their removal from the model did not reduce the OOB error rate.

Because model results may change depending on 1) the number of explanatory variables subsampled, and 2) the threshold proportion of votes for prediction (e.g., default majority vote, 0.5), these were also varied. Thresholds were tested at 0.4, 0.5, and 0.6 of votes necessary for classification, whereas the subset size of explanatory variables was tested at each value 1 – 9. Our sample of 41 lakes is rather small for evaluating the model based on cross-validation methods beyond those provided by OOB, so we instead used a receiver operating characteristic (ROC) curve (Zou et al. 2007) of the fitted values to evaluate model performance with ROCR package v. 1.0-4 (Sing et al. 2005) in R statistical software. The area underneath ROC curves (AUC) reflects the trade-off in model performance between true positive and false positive classification: 0.5 reflects a model no better than chance whereas 1.0 reflects perfect correspondence between predictions and data. Partial

dependence plots were used to show the marginal effect on classification probability of each explanatory variable retained in the reduced model.

3.3 Results

3.3.1. Biological attributes of Arctic charr

In total, 2803 fish from 50 lakes with length-at-age data, 7 – 118 per lake, were included in growth curve analyses. For morphological analyses, 1879 were included from 50 lakes, 6 – 71 per lake. The first relative warp axis (m_1) accounted for 24.2% the total variation and reflected bending around the abdominal section, as well as head depth and caudal peduncle length. Negative m_1 scores also indicated expansion of the lower head, yielding a more upturned mouth, whereas positive m_1 scores yielded an expansion of the upper head yielding a more downturned mouth. The second relative warp axis (m_2) accounted for 15.6% of the total variation; individuals with positive scores had relatively larger heads and shorter bodies, especially in the caudal peduncle region. Negative scores indicated individuals with relatively smaller heads and longer bodies and caudal peduncles. The third relative warp (m_3) accounted for 11.8% of the total variation. Individuals with negative scores had relatively smaller heads, shorter and deeper caudal peduncles, and deep bodies. Individuals with positive scores had longer heads, longer and narrow bodies, and narrower caudal peduncles (Chapter 2, Fig 2.1).

3.3.2. Detecting polymorphism and calculating differentiation

Only 17 populations were thought to be polymorphic according to expert knowledge, whereas this study led to 34 of 51 populations being classified as polymorphic. Twenty-six of those were supported with only length-at-age data, 1 was supported with only morphological data, and 7 were supported with both. Of the 33 lakes supported with length-at-age data, a model with three growth curves had the best fit in 5 lakes, whereas 2 growth curves were best for the other 28 lakes. Eight lakes were supported with 2-component mixtures of morphological variables. Parameter values of final models can be found in Appendix 3 (Tables

A3.1 – A3.2). Analyses of the relative sensitivity of D and Effect Size (η^2) indicated that values greater than approximately D* = 0.4 showed appreciable differentiation (Table 3.1, Fig 3.1 – 3.2). Only one lake below D* had both expert knowledge of polymorphism *and* support from polymorphism tests, whereas 5 lakes below D* had no expert knowledge of polymorphism, yet were categorized by polymorphism by a single test (see Methods). Increasing D* beyond 0.45 led to greater numbers in the first case.

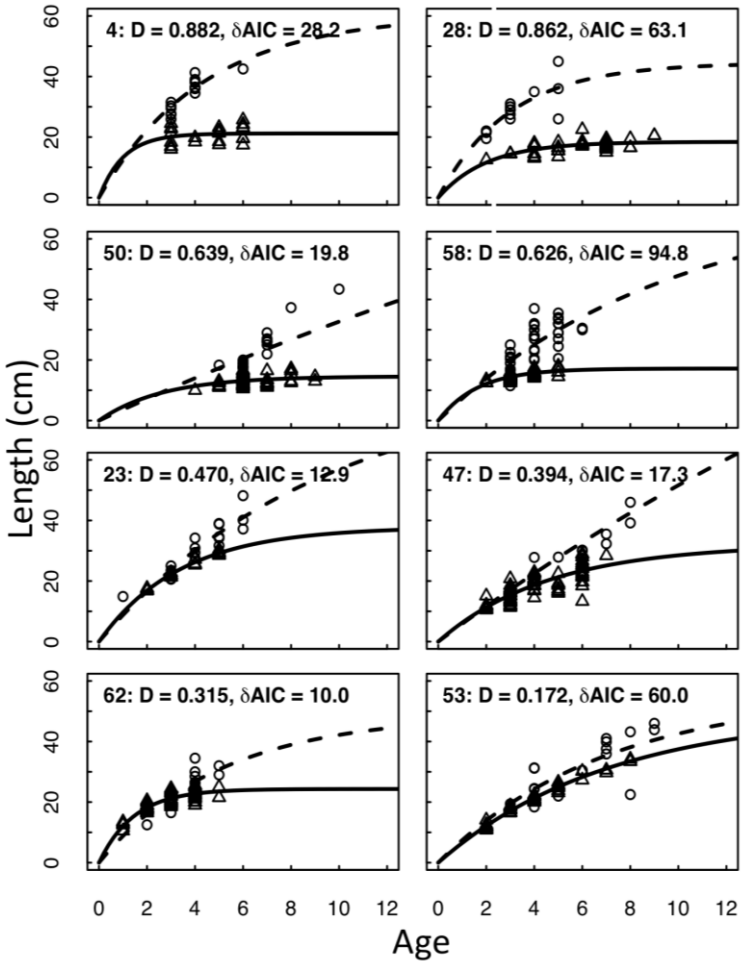


Figure 3.1. Examples showing two-growth curve Von Bertalanffy model fits (K = 2). Differentiation (D) and change in AICc (δAIC) are shown with lake database numbers (Table 3.1, Fig. A3.1). Circles are individuals assigned to the dashed growth curve; triangles are individuals assigned to the solid growth curve. Panels are generally ordered as examples of low to high differentiation moving upward.

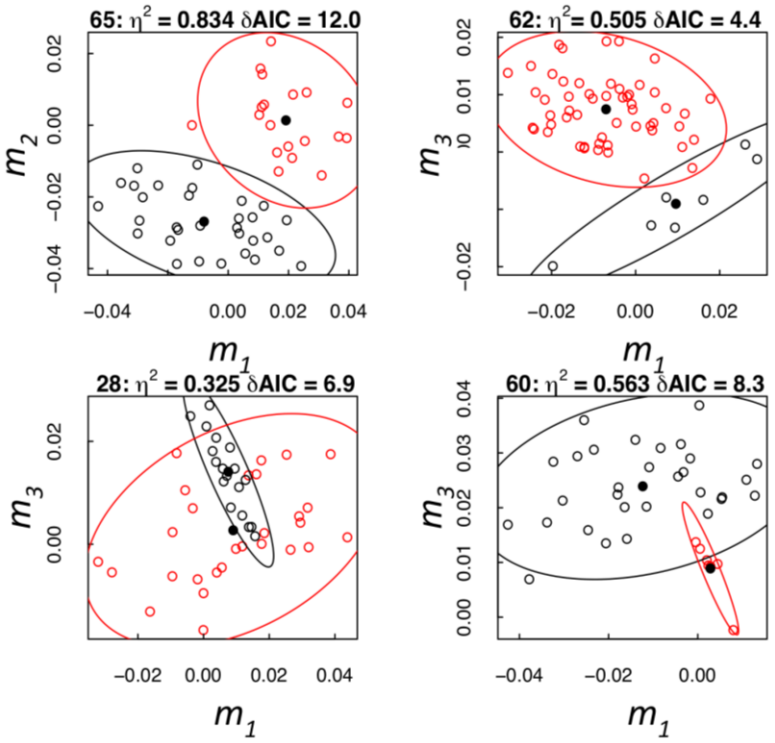


Figure 3.2. Examples showing bivariate morphology bimodal model fits (K = 2). Effect Size (η^2), and change in AICc (δAIC), and lake database numbers are indicated (Table 3.1, Fig. A3.1). Open circles in black indicate individuals belonging to one morph, open circles in grey indicate individuals belonging to the other morph, filled circles indicate mean values of each morph, and ellipses delineate the 95% confidence intervals for each bivariate normal density function. Axes labels (m_1, m_2, m_3) refer to the first, second and third relative warps, respectively. Panels are generally ordered as examples of low to high differentiation moving upward.

3.3.3. Predicting polymorphism with ecological variables

To analyze correspondence between ecology and the presence of polymorphism, we combined results from growth curve and morphology methods because there was a high correspondence between the two methods and only one lake was classified based on morphology alone. The random forest model performed best when the number of subset explanatory variables was set to 3. Seven explanatory variables were included in the best model (OOB error rate = 29.3%): BTA, ALT, SiO2, MD, SH, TP, and ACA (in order of Gini index). In this model, 5 / 15 monomorphic and 24 / 26 polymorphic lakes were correctly

classified. Although some variables could be excluded without changing OOB or misclassification rates, all were included according to the stepwise model selection procedure (Diaz-Uriarte & Alvarez de Anderes 2006; Genuer, Poggi & Tuleau-Malot 2010; Sethi 2010). The best threshold proportion of votes for prediction was found to be 0.6 and needed to remain within [0.58, 0.62] to maintain a low error rate. This model had generally low AUC of 0.628, indicating only moderate predictive ability.

BTA and ALT showed clear and opposing trends in partial dependence plots: polymorphic charr tended to occur in lakes with fewer brown trout and a higher altitude, indicating support for higher polymorphism in areas of low salmonid diversity (Hypothesis 1a). Many of the other variables showed non-linear trends or apparent thresholds (Fig 3.3): polymorphism was related to 1) higher SiO2 values, apparently as a threshold around mid-values, 2) all but very high SH values, 3) high or low (but not medium) TP values, and 4) medium – high MD values. The higher SiO2 values and medium TP values indicated a possible correspondence with low nutrient concentrations. Because high SiO2 and low nutrient concentrations were conditions under which Icelandic Arctic charr were found to consume more zooplankton (Woods et al. 2011), this supports Hypotheses 2a. Hypothesis 2c was directly supported in our study by medium – high MD values associated with polymorphism. A partial dependence plot from the second model showed that all but very low ACA values yielded high polymorphism probability, indicating support for Hypothesis 1c.

To analyze correlations between degree of differentiation and ecological variables, the greater of Effect Size and D for each lake was used as an indicator. These were then log(x + 1) transformed and standardized to yield standard coefficients in the multiple regression, whose values can be directly compared as relative effect strengths. Only 21 lakes classified as containing 2 morphs (K = 2) and having sufficient environmental data were included. Multiple regressions by AICc backward selection yielded a model with positive correlations of differentiation with BTA, ALT, MD, ACA, C, TOC, COND, and ALK, and negative correlations with B, TN, and PH. Residual deviance was 1.676 on 10 df and null deviance was 21.000 on 21 df, yielding a model that explained 92% of variation in the data.

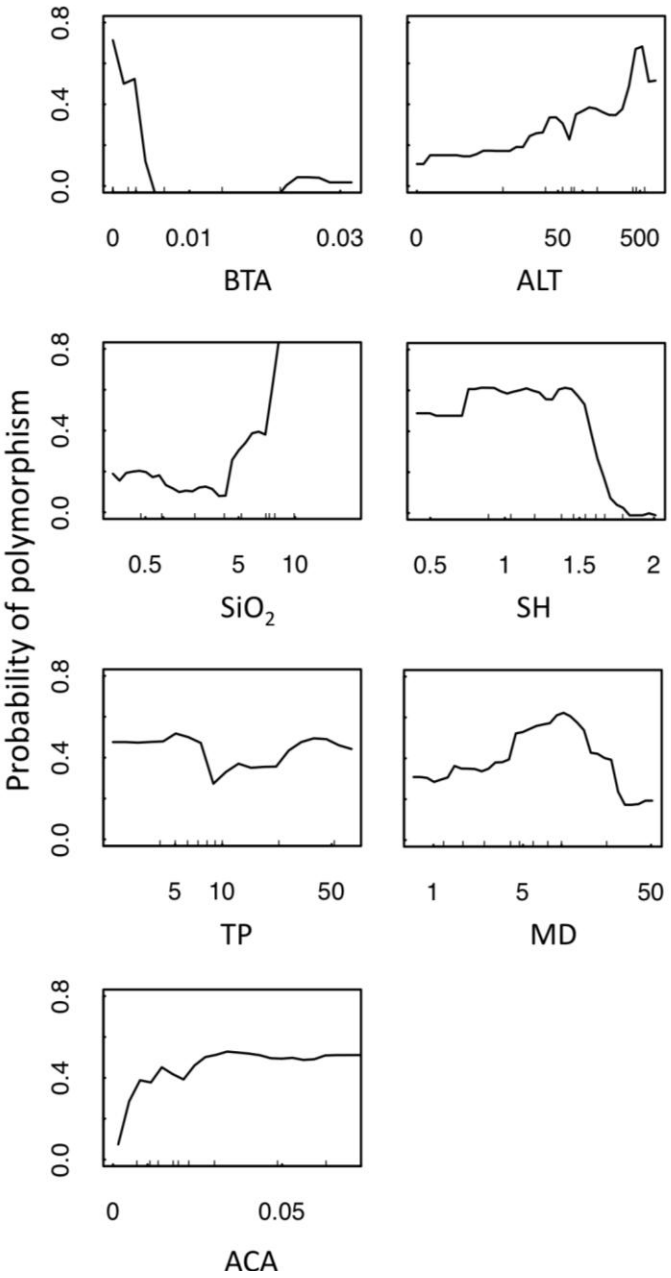


Figure 3.3. Partial dependence plots showing marginal effects of ecological variables on probability of a polymorphic classification in the best random forest model (BTA, ALT, SiO2, SH, TP, MD, and ACA).

Table 3.2. For lakes designated K = 2, the greater value of either Differentiation or Effect Size was predicted using multiple regression of ecological variables. Coefficient estimates (Est.), standard errors for these (SE), T statistics (T), and P-values are indicated for each model term selected during backward- model selection.

	Est.	SE	T	P
Intercept	-0.728	0.155	-4.687	0.001
Total organic carbon (TOC)	1.688	0.410	4.120	0.002
Chironomid pupae category density (C)	1.117	0.230	4.858	0.001
Conductivity (COND)	1.037	0.165	6.269	0.000
Arctic charr abundance (ACA)	0.892	0.173	5.164	0.000
Mean depth (MD)	0.606	0.267	2.266	0.047
Altitude (ALT)	0.558	0.224	2.493	0.032
Brown trout abundance (BTA)	0.514	0.189	2.716	0.022
Alkalinity (ALK)	0.506	0.170	2.971	0.014
Total nitrogen (TN)	-2.173	0.311	-6.982	0.000
Bosmina category density (B)	-2.074	0.250	-8.292	0.000
pH (PH)	-0.909	0.152	-5.962	0.000

3.4 Discussion

This study presented novel and useful methods for detecting phenotypic polymorphism at low levels, and then demonstrated their usefulness in comparing populations spanning a wide geographical range. This type of comparative study is rarely done (but see Griffiths 1994, Landry et al. 2007, Siwertsson et al. 2010), although it is imperative for gaining an understand the origins of biodiversity within an ecological context. Without pinpointing the early stages of speciation, it is impossible to study both how biodiversity proliferates and how it functions within surrounding ecosystems.

3.4.1. Correspondence with hypotheses regarding the origin of intraspecific diversity

Hypotheses 1a and 1b are linked in a manner that would be difficult to disentangle under any natural circumstances: high altitude, recently deglaciated regions naturally have fewer species due to the more difficult circumstances for colonization: high variability (on geological

time scales) and greater migration barriers (Bernatchez & Wilson 1998; Robinson & Schluter 2000, Griffiths 2006). In addition, monomorphic populations in lower elevations may be constrained as such due to higher gene flow. Therefore, support for these two hypotheses generally refer to the same circumstance. Hypothesis 1c further supports these, because higher conspecific Arctic charr densities would be expected under low competitor density (i.e., less brown trout) (Langeland et al. 1991, Hesthagen et al. 1997, Jansen et al. 2002, Helland et al., 2011). However, Hypothesis 1c also provides a crucial link to the potential underlying mechanisms causing polymorphism: an increase in density with polymorphism would be expected under frequency-dependent selection, but not necessarily under divergence due to lower fitness at intermediate trait values, for example due to greater predation rates. This rules out the potential that polymorphism is most often related to predation pressure (Hypothesis 3). However, although Arctic charr exhibit very little cannibalism in Icelandic lakes during the summer (Chapter 1), there is still the possibility that predation pressure may increase during winter, and would not be detected by our test.

We also detected a dependence of polymorphism on limnetic food availability (Hypothesis 2, Skúlason, Snorrason & Jónsson 1999), which occurs at low nutrient concentrations (Woods et al. 2011), most likely as a result of high limnetic productivity (Siwertsson et al. 2010). The same pattern has been found in the differentiation of whitefish into zooplanktivorous forms (Siwertsson et al. 2010). Medium – large, although not the largest, lakes tended to have polymorphic populations, thereby corresponding directly with patterns found in stickleback (Bolnick & Lau 2008) and with the generally positive relationship with depth by Griffiths (1994). Again, similar results have been found for lake whitefish differentiation (Vonlanthen et al. 2009, Siwertsson et al. 2010).

Our study of the ecological correlations with Differentiation (i.e., polymorphic life histories) yielded results that correspond well with those listed above: the strongest effects included positive correlations with Arctic charr abundance (ACA, Hypothesis 1c), density of chironomid pupae prey category (C, Hypothesis 2a), total organic carbon (TOC), and conductivity (COND), as well as negative correlations with limnetic cladoceran / copepod abundance (B, Hypothesis 2b), total nitrogen (TN, Hypothesis 2a), and pH. As discussed above, low nutrient levels have indicated high limnetic

productivity under similar circumstances (Siwertsson et al. 2010). Likewise, consumption of copepods and cladocerans was correlated with low nutrient and high chironomid pupae availability by Woods et al. (2011, Hypothesis 2a), and the presence of zooplanktivorous whitefish forms has been associated with decreased zooplankton abundances (Hypothesis 2b, Landry et al. 2007).

Although none of our hypotheses directly address total organic carbon, conductivity, and pH, these are well-known to change with terrestrial vegetation: leaching from surrounding poorly drained heath or bogs causes increases in total organic carbon, higher conductivity and lower pH (Pienitz et al. 1997, Karst-Riddoch et al. 2009). Therefore, this secondary analysis, which reflects the degree of polymorphism rather than its presence, indicates that the more extreme expression of polymorphism may depend on increased absolute levels of nutrient loading via increased terrestrial vegetation. This runs counter to the trend found for the greater incidence of polymorphism at higher altitudes, since these are also characterized by lower terrestrial vegetation (LaPerriere et al. 2003). Therefore, to initiate polymorphism, some balance apparently needs to be struck between the prerequisites of 1) high enough zooplankton production (greater depth, high limnetic productivity, increased zooplankton consumption) and 2) low enough competition (higher altitudes, low competitor density). Following this step, differentiation appears to be enhanced by the attributes of higher nutrient loading from surrounding watersheds and high chironomid production, perhaps via the availability of appropriate fine-grained sediment habitat in deep lakes with greater sedimentation rates. This pattern may indicate chironomid pupae as an important, stable resource in areas or during periods of low limnetic resources (Schindler & Scheuerell 2002). Therefore evolutionary potential of Arctic charr may be influenced not only be the lake environment, but by characteristics of the surrounding watershed.

3.4.2. Detecting polymorphism

The method presented here is effective at detecting bimodality and trimodality in growth rate and morphology. Thirteen of the 17 lakes expected to be polymorphic based on expert knowledge secured support as such from this analysis; those that did not gain support included Hvítárvatn, Vatnshlíðarvatn, Reyðarvatn, and Hafravatn (Table 3.1).

Hafravatn likely had too small of a sample (N = 11) and was excluded from morphological analyses for this reason. The others may have had inadequate or not fully representative samples. For example, having too slight of an age range can easily reduce the fit of multiple growth curves. Alternatively, for lakes that show morphological differentiation in the absence of growth rate differentiation (e.g., Vatnshlíðarvatn), the informative morphological traits may not have been captured by morphological variables used in this study. This may explain why so fewer lakes were found to be divergent in morphology rather than growth rate: only one lake secured support entirely from morphological analyses (Thríhyrningsvatn). Twenty-one lakes detected as polymorphic in growth rate were not expected based on expert knowledge, possibly indicating that this method is detecting more than just polymorphism, such as intercohort growth variation. Therefore, the 14 of these that were not corroborated with morphological evidence, and especially the 5 of these that do not show appreciable differentiation ($D < D^*$), should be investigated further to ensure correct classification.

As with any statistical analysis, the detectability of the mixture model method is sensitive to sample sizes, and especially differences in sample size between potential forms. However, unlike standard ANOVA methods frequently used to distinguish between groups designated a priori, this method assigns individuals to groups after defining the best mixture model. Therefore, it can be sensitive to outliers for the same reason that outliers are designated as such in an ANOVA: they do not fit the assumed normal distribution. Therefore, in an ANOVA, outliers would be removed, but in this analysis they may be designated as their own group. In particularly variable natural populations, oddities are perhaps more common than would be expected from a theoretical distribution, although this may not biologically reflect the presence of an entire additional form, as expected from polymorphism. Unfortunately, it may be impossible to distinguish between the presence of oddities versus insufficient sampling of a second morph. For example, uneven sampling may result when catch rates differ among morphs due to differences in habitat or body size (Finstad, Jansen & Langeland 2000). Considering the effort needed to gain enough data to do broad-scale comparative analyses, uneven sampling is likely to occur, so overclassification as polymorphic may be a persistent problem when using these methods. In this study, the

minimum designation of 5 individuals per component and the use of AICc were helpful in reducing sensitivity.

In addition, there are other problems inherent in interpreting statistical results in a biological context, although these would likely remain given any statistical method. First, emphasis was placed on the presence of a bimodal distribution over a single distribution with a wide variance. However, both may be biologically meaningful in understanding how populations transition from monomorphic to polymorphic states. Second, Differentiation was used in this study only to characterize bimodal populations due to the problem of defining a measure that would be meaningful in both bimodal and trimodal populations. Finally, although polymorphic populations are interpreted here as being temporally stable, it is possible that some populations with weaker differentiation actually reflect environmental variation or groups of cohorts with different growth rates or morphologies. Population dynamical mechanisms may cause bimodality to develop within a population due to a combination of seasonal effects of different-sized prey and size-specific foraging (Griffiths 1994; Borcherding et al. 2010).

3.4.3. Conclusions

This study exemplifies how diversity below the species level may be quantified for further cross-system comparisons to study the origin or function of phenotypic polymorphism. However, the methods presented are broadly applicable beyond this purpose. For example, the standard methods for calculating Differentiation could be used as a temporal indicator in conservation to monitor the effects of losses in biodiversity on ecosystems (Olden et al. 2004). In addition, these or similar mixture models may be used in resource management to identify or account for mixtures of stocks or cohorts (e.g., Thorson, Stewart, & Punt 2011; Podlaski 2010). Standard methods for quantifying bimodal populations can therefore serve to define a wide variety of biological units and place them within a functional context.

3.5 References cited

Abrams, P.A. (2000) Character shifts of prey species that share predators. *American Naturalist,* 156 (Suppl.), S45–S61.

Adams, C.E., Fraser, D., Wilson, A.J., Alexander, G., Ferguson, M.M. & Skúlason, S. (2007) Patterns of phenotypic and genetic variability show hidden diversity in Scottish Arctic charr. *Ecology of Freshwater Fish*, 16, 78–86.

Adams, C.E., Hamilton, D.J., Mccarthy, I., Wilson, A.J., Grant, A., Alexander, G., Waldron, S., Snorrason, S.S., Ferguson, M.M. & Skúlason, S. (2006) Does breeding site fidelity drive phenotypic and genetic sub-structuring of a population of Arctic charr? *Evolutionary Ecology*, 20, 11–26.

Andersson, J., Byström, P., Claessen, D., Persson, L. & De Roos, A.M. (2007) Stabilization of population fluctuations due to cannibalism promotes resource polymorphism in fish. *American Naturalist*, 169, 820–829.

Benaglia, T., Chauveau, D., Hunter, D.R. & Young, D. (2009) mixtools: An R Package for Analyzing Finite Mixture Models. *Journal of Statistical Software*, 32, 1–29. URL http://www.jstatsoft.org/v32/i06/.

Bernatchez, L. & Wilson, C.C. (1998) Comparative phylogeography of Nearctic and Palearctic fishes. *Molecular Ecology*, 7, 431–452.

Bolnick, D.I. (2004) Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution* 58, 608–618.

Bolnick, D.I. & Lau, O.L. (2008) Predictable patterns of disruptive selection in sticklebacks of postglacial lakes. *American Naturalist*, 172, 1–11.

Bookstein, F.L. (1991) *Morphometric Tools for Landmark Data: Geometry and Biology*. Cambridge University Press, New York, New York, USA.

Borcherding, J., Beeck, P., DeAngelis, D.L. & Scharf, W.R. (2010) Match or mismatch: the influence of phenology on size-dependent life history and divergence in population structure. *Journal of Animal Ecology*, 79, 1101–1112.

Breiman, L. (2001) Random forests. *Machine Learning*, 45, 5–32.

Breiman, L. (2002) Manual on setting up, using, and understanding random forests v3.1. URL: http://oz.berkeley.edu/users/breiman/Using_random_forests_V3.1.pdf, last accessed 13 July 2011.

Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M. & Jouseau, C. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. **Nature,** *443*, 989–992.

Diaz-Uriarte, R. & Alvarez de Andres, S. (2006) Gene selection and classification of microarray data using random forest. *BMC Bioinformatics* 7, 3–15.

Dieckmann, U., Metz, J.A.J., Doebeli, M. & Tautz, D. (2004) *Adaptive Speciation*. Cambridge University Press, Cambridge.

Doucette, L.I., Skúlason, S. & Snorrason, S.S. (2004) Risk of predation as a promoting factor of species divergence in threespine sticklebacks (*Gasterosteus aculeatus* L.). *Biological Journal of the Linnean Society*, 82, 189–203.

Eustace, A.H., Pringle, M.J. & Denham, R.J. (2011) A risk map for gully locations in central Queensland, Australia. *Eurasian Journal of Soil Science*, 62, 431–441.

Finstad, A.G., Jansen, P.A. & Langeland, A. (2000) Gillnet selectivity and size and age structure of an alpine Arctic char (*Salvelinus alpinus*) population. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 1718–1727.

Genuer, R., Poggi, J.M. & Tuleau-Malot, C. (2010) Variable selection using random forests. *Pattern Recognition Letters*, 31, 2225–2236.

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

Griffiths, D. (2006) Pattern and process in the ecological biogeography of European freshwater fish. *Journal of Animal Ecology*, 75, 734–751.

Harmon, L.J., Matthews, B., Des Roches, S., Chase, J.M., Shurin, J.B. & Schluter D. (2009) Evolutionary diversification in stickleback affects ecosystem functioning. *Nature*, 458, 1167–1170.

Helland, I.P., Finstad, A.G., Forseth, T., Hesthagen, T. & Ugedal, O. (2011) Ice-cover effects on competitive interactions between two fish species. *Journal of Animal Ecology*, 80, 539–547.

Hesthagen, T., Jonsson, B., Ugedal, O. & Forseth, T. (1997) Habitat use and life history of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) in some low acidity lakes in central Norway. *Hydrobiologia*, 348, 113–126.

Hudson, A.G., Vonlanthen, P. Müller, R. & Seehausen, O. (2007) The geography of speciation and adaptive radiation in coregonines. *Advances in Limnology*, 60, 111–146.

Jansen, P.A., Slettvold, H., Finstad, A.G. & Langeland, A. (2002) Niche segregation between Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*): an experimental study of mechanisms. *Canadian Journal of Fisheries and Aquatic Science*, 59, 6–11.

Jepson, P. & Canney, S. (2003) Values-led conservation. *Global Ecology and Biogeography*, 12, 271–274.

Jónsson, B. & Skúlason, S. (2000) Polymorphic segregation in Arctic charr *Salvelinus alpinus* (L.) from Vatnshlídarvatn, a shallow Icelandic lake. *Biological Journal of the Linnean Society*, 69, 55–74.

Jónsson, B. 2002. Parallel sympatric segregation in Arctic charr and threespined stickleback in Lake Galtaból, Iceland. *Fisheries Science*, 68 (Supp. 1), 459–460.

Jonsson, B., and Jonsson, N. (2001) Polymorphism and speciation in Arctic charr. *Journal of Fish Biology*, 65, 605–638.

Jónsson, I.R. & Malmquist, H.J. (2002) *Research on Thríhyrningsvatn 1998*. Veidimálastofnun, Institute of Freshwater Fisheries: VMST-R/0202. [In Icelandic]

Karst-Riddoch, T.L., Malmquist H.J. & Smol, J.P. (2009) Relationships between freshwater sedimentary diatoms and environmental variables in Subarctic Icelandic lakes. *Fundamental and Applied Limnology* 175, 1–28.

Klemetsen, A. (2010) The charr problem revisited: exceptional phenotypic plasticity promotes ecological speciation in postglacial lakes. *Freshwater Reviews*, 3, 49–74.

Landry, L., Vincent, W.F. & Bernatchez, L. (2007) Parallel evolution of lake whitefish dwarf ecotypes in association with limnological features of their adaptive landscape. **Journal Evolutionary Biology,** *20*, 971–984.

Langeland, A., L'Abée-Lund, J.H., Jonsson, B. & Jonsson, N. (1991) Resource partitioning and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. *Journal of Animal Ecology*, 60, 895–912.

Langerhans, R.B., Layman, C.A., Shokrollahi, A.M. & DeWitt, T.J. (2004) Predator-driven phenotypic diversification in *Gambusia affinis*. *Evolution*, 58, 2305–2318.

LaPerriere, J.D., Jones, J.R. & Swanson, D.K. (2003) Limnology of lakes in Gates of the Arctic National Park and Preserve, Alaska. *Lake and Reservoir Management*, 19, 108–121.

Liaw, A. & Wiener, M. (2002) Classification and regression by randomForest. *R News*, 2, 18– 22. URL: http://www.r-project.org/doc/Rnews/Rnews_2002-3.pdf, last accessed 13 July 2011.

Malmquist, H.J., Antonsson, T., Guðbergsson, G., Skúlason, S. & Snorrason, S.S. (2000) Biodiversity of macroinvertebrates on

rocky substrate in the surf zone of Icelandic lakes. *Verhandlungen des Internationalen Verein Limnologie,* 27, 1–7.

Olden, J., Poff, N.L., Douglas, M.R., Douglas, M.E. & Fausch, K.D. (2004) Ecological and evolutionary conséquences of biotic homogenization. *Trends in Ecology and Evolution*, 19, 18–24.

Pienitz, R., Smol, J.P. & Lean, D.R.S. (1997) Physical and chemical limnology of 59 lakes located between the southern Yukon and the Tuktoyaktuk Peninsua, Northwest Territories (Canada). *Canadian Journal of Fisheries and Aquatic Sciencs,* 54, 330–346.

Podlaski, R. (2010) Two-component mixture models for diameter distributions in mixed-species, two-age cohort stands. *Forest Science*, 56, 379–390.

Prasad, A.M., Iverson, L.R. & Liaw, A. (2006) Newer classification and regression tree techniques: bagging and random forests for ecological prediction. *Ecosystems*, 9, 181–199.

R Development Core Team (2011) *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. URL http://www.R-project.org, last accessed 13 July 2011.

Robinson, B.W. & Schluter, D. (2000) Natural selection and the evolution of adaptive genetic radiation in northern freshwater fishes. *Adaptive Genetic Variation* (eds Mousseau, T.A., Sinervo, B. & Endler, J.), pp. 65–94. Oxford University Press, Oxford.

Robinson, B.W. & Wilson, D.S. (1994) Character release and displacement in fishes: a neglected literature. *American Naturalist*, 144, 596–627.

Rohlf, F.J. (2004) Thin-plate spline software. URL: http://life.bio.sunysb.edu/morph/, last accessed 13 July 2011.

Rundle, H.D., Vamosi, S.M. & Schluter, D. (2003) Experimental test of predation's effect on divergent selection during character displacement in sticklebacks. *Proceedings of National Acadamy of Science USA*, 100, 14943–14948.

Schindler, D.E. & Scheuerell, M.D. (2002) Habitat coupling in lake ecosystems. *Oikos*, 98, 177–189.

Schluter, D. (1994) Experimental evidence that competition promotes divergence in adaptive radiation. *Science*, 266, 798–801.

Schluter, D. (1996) Ecological speciation in postglacial fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 351, 807–814.

Schluter, D. (2003) Frequency dependent natural selection during character displacement in sticklebacks. *Evolution*, 57, 1142–1150.

Sethi, S.A. (2010) *Fisheries management with people in mind: assessing and managing risk*. PhD thesis, University of Washington, Seattle, Washington, USA.

Sing, T., Sander, O., Beerenwinkel, N. & Lengauer, T. 2005. ROCR: visualizing classifier performance in R. *Bioinformatics*, 21, 3940–3941.

Siwertsson, A., Knudsen, R., Kahilainen, K.K., Praebel, K., Primicerio, R. & Amundsen, P.A. (2010) Sympatric diversification as influenced by ecological opportunity and historical contingency in a young species lineage of whitefish. *Evolutionary Ecology Research*, 12, 929–947.

Skúlason, S. & Smith, T.B. (1995) Resource polymorphisms in vertebrates. *Trends in Ecology and Evolution*, 10, 366–370.

Skúlason, S., Snorrason, S.S. & Jónsson, B. (1999) Sympatric morphs, populations and speciation in freshwater fish with emphasis on arctic charr. *Evolution of Biological Diversity* (eds Magurran, A.E. & May, R.M), pp. 70–92. Oxford University Press, Oxford.

Skúlason, S., Snorrason, S.S., Noakes, D.L.G. & Ferguson, M.M. (1996) Genetic basis of life history variations among sympatric morphs of Arctic char, *Salvelinus alpinus*. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 1807–1813.

Skúlason, S., Snorrason, S.S., Noakes, D.L.G., Ferguson, M.M. & Malmquist, H.J. (1989) Segregation in spawning and early life-history among polymorphic Arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. *Journal of Fish Biology*, 35, 225–232.

Smith, T.B. & Skúlason, S. (1996) Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics*, 27, 111–133.

Snorrason, S.S. & Skúlason, S. (2004) Adaptive Speciation in northern freshwater fishes. *Adaptive Speciation* (eds, Dieckmann, U., Doebeli, M., Metz, J.A.J. & Tautz, D.), pp. 210–228. Cambridge University Press, Cambridge.

Strobl, C., Boulesteix, A.L., Zeileis, A. & Hothorn, T. (2007) Bias in random forest variable importance measures: Illustrations, sources and a solution. *BMC Bioinformatics* 8, 25–45.

Svanbäck, R. & Bolnick, D.I. (2007) Intraspecific competition drives increased resource use diversity within a natural population.

Proceedings of the Royal Society B: Biological Sciences, 274, 839–844.

Svanbäck, R. & Persson, L. (2004) Individual diet specialization, niche width, and population dynamics; implications for trophic polymorphisms. *Journal of Animal Ecology*, 73, 973–982.

Thorson, J.T., Stewart, I.J. & Punt, A. (2011). Accounting for fish shoals in single- and multi-species survey data using mixture distribution models. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 1681-1693.

Vamosi, S.M. & Schluter, D. (2002) Impacts of trout predation on fitness of sympatric sticklebacks and their hybrids. *Proceedings of the Royal Society B: Biological Sciences*, 269, 923–930.

Van Valen, L. (1965) Morphological variation and width of ecological niche. *American Naturalist*, 99, 277–290.

Vonlanthen, P., Roy, D., Hudson, A.G., Larglader, C.R., Bittner, D. & Seehausen, O. (2009) Divergence along a steep ecological gradient in lake whitefish (*Coregonus* sp.). *Journal of Evolutionary Biology*, 22, 498–514.

Wilson, A.J., Gíslason, D., Skúlason, S., Snorrason, S.S., Adams, C.E., Alexander, G., Danzmann, R.G. & Ferguson, M.M. (2004) Population genetic structure of Arctic charr, *Salvelinus alpinus* from northwest Europe on large and small spatial scales. *Molecular Ecology*, 13, 1129–1142.

Zou, K.H., O'Malley, A.J. & Mauri, L. (2007) Receiver-operating characteristic analysis for evaluating diagnostic tests and predictive models. *Circulation*, 115, 654–657.

4 Resource polymorphism and diversity of Arctic charr *Salvelinus alpinus* in a series of isolated lakes in southwestern Alaska

4.0 Abstract

Arctic charr *Salvelinus alpinus* tend to exhibit extremely variable phenotypes both within and among lakes in Iceland, Europe, Russia, and Canada, but little is known about Arctic charr in Alaska. In this study, we characterized morphological, dietary, and life history variation in Arctic charr from four geographically proximate but isolated lakes in southwestern Alaska: Iliamna Lake, Summit Lakes, Lower Tazimina Lake, and Caribou Lakes. We expected that polymorphism would be detected in Lower Tazimina and Summit lakes based past studies indicating that Arctic charr tend to become polymorphic in deep, isolated lakes that have few co-occurring species. We also expected to find a relationship between Arctic charr morphology and diet in monomorphic populations. Such pattern would indicate individual diet specialization, which is thought to promote the development of stable polymorphism. Arctic charr sampled from each lake were tested for the presence of polymorphism using mixture models of Von Bertalanffy growth curves and morphometric variables. Only one morph was evident in three of the lakes but two morphs were found in Lower Tazimina Lake. Thus, individuals assigned to each form were compared to detect further differences in diet, morphology, and gonadosomatic index. Arctic charr in the other three lakes were further characterized by analyzing how the relationship between body shape, as represented by geometric morphometric analyses, and diet differed among lakes.

Variability in life history of Arctic charr in Alaskan lakes appears to be as broad as those found elsewhere: growth rates differed among populations and forms within populations, yielding maximal estimated body sizes that ranged 18 – 63 cm. Mature individuals were found in large and small forms, and dietary specialization was extreme for the most distinct forms. Allometric and ontogenetic trends differed by lake. This variability is therefore important for understanding lake ecosystems of remote regions where this species is commonly dominant.

4.1 Introduction

The Arctic charr *Salvelnus alpinus* is one of a few vertebrates that exhibits high rates of resource polymorphism, in which phenotypic differences of discrete, sympatric groups are linked to resource use (Smith and Skúlason 1996). The Arctic charr is considered to be a single taxonomic species (Brunner et al. 2001), despite genetic evidence indicating substantial population divergence in some cases (Wilson et al. 2004, Kapralova et al. 2011). In some bodies of water this morphological variation reflects genetic differences (Skúlason et al. 1989, 1996, Adams and Huntingford 2002), but in others, morphology is highly plastic (Andersson 2003, Andersson et al. 2005, Klemetsen 2010). When heritable and functionally important, these differences are thought to reflect adaptive changes within a population (Adams and Huntingford 2002b). Many studies have therefore focused on the function and heritability of behavioral and morphological differences among morphs (Snorrason et al. 1994, Skúlason and Smith 1996, Andersson and Persson 2005, Byström and Andersson 2005, Sigursteinsdóttir and Kristjánsson 2005, Parsons et al. 2011). Because resource polymorphism can be associated with increased reproductive isolation of morphs, polymorphic model systems are relevant to the study of ecological speciation (Schluter 1996, Klemetson 2010).

The most extreme case of Arctic charr resource polymorphism is the divergence of four distinct forms in Thingvallavatn, Iceland: two specialize on benthic prey but differ greatly in size, the third is a zooplanktivore occupying pelagic zones, and the fourth, a piscivore that likely undergoes an ontogenetic niche shift from zooplanktivory to consume threespine stickleback *Gasterosteus aculeatus* (Skúlason et al. 1989, Snorrason et al. 1994, Jónasson et al. 1998, Snorrason and Skúlason 2004). Because colonization of lakes most likely occurred by

anadromous Arctic char, it is thought that the ancestral phenotype resembled the anadromous form. Thus, pelagic forms in lakes are thought to be the next most morphologically similar to the ancestral form, whereas benthic forms are more derived and specialized. Specialization in small benthic forms is supported both by having a narrow range in diet (Malmquist et al. 1992) and by the relatively low degree of phenotypic plasticity (Parsons et al. 2011).

Although most other lakes have fewer co-occurring forms, the extreme nature of divergence is not necessarily unique. Thus, lakes in Norway, Switzerland, and Russia host extremely different profundal forms and larger littoral forms that generally consume different prey available in each habitat (Klemetsen et al. 2010). Pelagic forms exhibiting zooplanktivory, piscivory, or both, co-occur with benthic forms in Scotland and Canada (Adams et al. 1998, Fraser et al. 1998, Guiguer et al. 2002, Power et al. 2005, Arbour et al. 2011). Piscivory is also exhibited by cannibalistic forms, which may lead to bimodal size distributions in populations (Griffiths 1994, Andersson et al. 2007, Arbour et al. 2011), as well as by large benthic forms in some locations (Adams et al. 1998, Fraser et al. 1998). However, in the presence of other species, Arctic charr tend to exist as a single, zooplanktivorous form (Langeland et al. 1991, Hesthagen et al. 1997, Jansen et al. 2002, Power et al. 2002, Forseth et al. 2003, Knudsen et al. 2010).

Although polymorphism in Arctic charr occurs across a wide geographical range in the subarctic, still little is known about variation in Arctic charr from some vast regions, such as Alaska. This is partially due to the focus of many studies on a few locations with extreme variation, and partially due to the inaccessibility of many subarctic regions. Past freshwater research in Alaska has been conducted primarily in accessible regions with high fish species richness and anadromous Pacific salmon species *Oncorhynchus* spp. present. In these systems, Arctic char tend to be large-bodied and piscivorous (Russell 1980, Scanlon 2000, Kreiner 2006, Denton 2007). However, even within the limited studies of more remote regions, Arctic charr and Dolly Varden life histories can vary substantially (Russell 1980, Scanlon 2000, Kreiner 2006, Scanlon 2000, Denton et al. 2010, Jaecks 2011). Remote, more recently deglaciated areas may contain fewer fish species due to harsher growing conditions at higher altitudes, greater barriers to migration, such as barrier waterfalls or rapids (Griffiths 2006), or greater environmental variability (Robinson and Schluter

2000). In addition, genetic analyses indicate that although fish in these regions show reduced genetic diversity, they also exhibit higher rates of speciation (Bernatchez and Wilson 1998). Since reduced interspecific competition and high resource availability are considered main contributors toward the development of resource polymorphism (Skúlason et al. 1999, Smith and Skúlason 1996), the potential for resource polymorphism in remote regions of Alaska is high.

The goal of this study was to analyze morphological and body size variation from four lakes in southwestern Alaska to give a broader understanding of ecological variability in Arctic charr from this region. We expected that polymorphism would be detected in some lakes based past studies indicating that Arctic charr tend to become polymorphic in deep, isolated lakes that have few co-occurring species (Griffiths 1994, Chapter 3). We therefore chose to examine Arctic charr from four lakes that varied widely in size, depth, elevation, and diversity. High variability in size at maturity and length-at-age has been mentioned in previous reports regarding Arctic charr in Alaska, but no attempt has been made to differentiate forms (Russell 1980, Kreiner 2006). To do this, we tested whether two Von Bertalanffy growth curves fit the data better than one using mixture models (Chapter 3). As indicated from elsewhere in Europe, we expected to find differences between forms in diet, morphology, spawn timing or habitat, relative gonad size, or growth patterns. In addition, because individual specialization is thought to be an important mechanism for the development of resource polymorphism (Bolnick et al. 2003, Knudsen et al. 2010, Knudsen et al. 2011), we also expected to find a relationship between Arctic charr morphology and diet, even in groups where no polymorphism was detected.

4.2 Methods

4.2.1. Study sites

The study lakes are all located in the Kvichak River system in Bristol Bay, southwestern Alaska (Fig. 4.1). Iliamna Lake is the largest lake in Alaska and the Kvichak River catchment, to which it belongs, contains up to 25 resident fish species (Kline et al. 1993). The Kvichak River connects Iliamna Lake to Bristol Bay, and its watershed supplies spawning and rearing habitat for the world's largest sockeye salmon

(*Oncorhynchus nerka*) population (Burgner 1991). For this reason, Iliamna Lake's ambient $\delta^{15}N$ values are elevated from the enormous influx of marine derived nutrients during annual salmon runs (Kline et al. 1993). Iliamna Lake was sampled at its eastern end on beaches near Porcupine Island, but this sample cannot be used to represent the full diversity of Arctic charr in the lake due to the lake's large size. Summit Lakes are a pair of small, deep headwater lakes situated ~15 km from Iliamna Lake and ~4 km from the Gulf of Alaska on a dividing mountain pass. Summit Lakes feed Chinkelyes Creek, which joins the Iliamna River to enter Iliamna Lake in the eastern end. However, a barrier waterfall on Chinkelyes Creek prevents upriver migration, so the slimy sculpin *Cottus cognatus* and Arctic charr are apparently the only resident fishes. Summit Lakes was also the only sample site surrounded by shrubbery rather than forest. Lower and Upper Tazimina Lakes are larger lakes (approx. 12.5 and 12.5 km long, 1.2 and 2.9 km maximum width respectively) in an approx. 900 km^2 forested glacial catchment basin for Tazimina River (Russell 1980). The fish fauna of Tazimina Lakes, which consist of Arctic charr, Arctic grayling *Thymallus arcticus*, slimy sculpin, and threespine stickleback, are separated from downstream Sixmile Lake by a large barrier waterfall in Tazimina River (~30 m height). This river flows into the Newhalen River, and therefrom into Iliamna Lake. Lower Tazimina Lake was sampled at the narrows of the southwestern end. Caribou Lakes are a series of high-elevation, small, shallow lakes located at the headwaters of the Koksetna River and surrounded by a combination of forest and tundra in the mountains north of Lake Clark. Little is known about these lakes, but they are fed by a combination of snowmelt and springs and drain into Lake Clark. The resident fishes, including Arctic charr, Arctic grayling, the pygmy whitefish *Prosopium coulterii*, and slimy sculpin, are likely separated from more diverse downstream fishes by several sets of rapids along the Koksetna River (Russell et al. 1980).

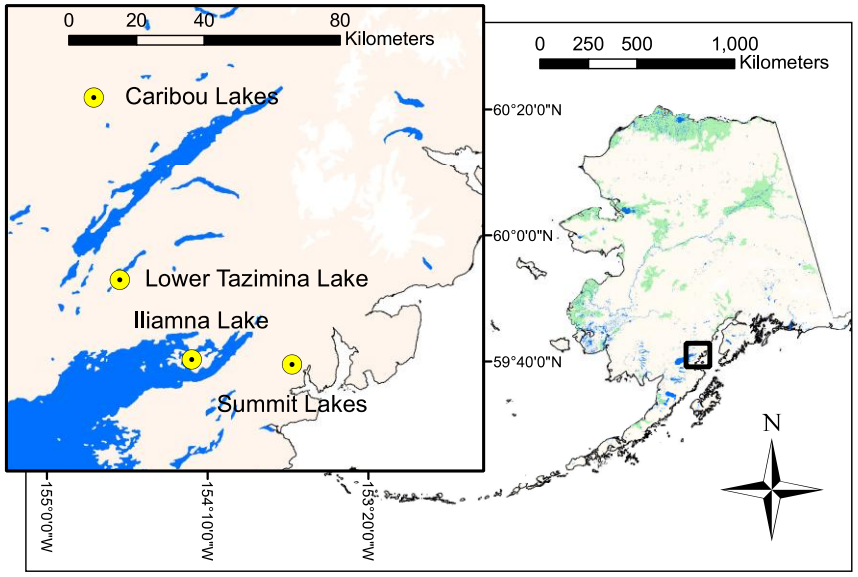


Figure 4.1. Sampling locations of the four lakes under study (see Table 4.1).

Thus, the four lakes we sampled are all in the same large drainage basin. One lake (Iliamna) receives a great supply of marine-derived nutrients due to Pacific salmon migrations. Each of the upper lakes is isolated from the others and from upstream migration by Iliamna Lake fish, and therefore has likely limited gene flow downstream. Physical data for Iliamna Lake were based on data from Kline et al. (1993), and altitude and surface area of Summit, L. Tazimina, and Caribou lakes were estimated using satellite imagery by including all lakes that were connected by less than 1 km (Table 4.1). Maximum depth was measured using a depth sounder in Summit Lake and was taken from a survey of Lake Clark National Park for L. Tazimina and Caribou Lakes (Russell, 1980).

4.2.2. Fish sampling

Most Arctic charr were sampled August – September 2010 (Table 4.1). Ten additional Arctic charr were sampled from Summit Lake on 24 August 2009, and length-at-age and gut content data from 16 additional fish from Iliamna Lake were included from another study conducted in June to September 2007-2008 (Denton et al. 2010). Arctic charr were caught in Iliamna Lake using a combination of angling and beach seining after chumming with Pacific salmon eggs at Fuel Dump Island.

Arctic charr from the other Alaskan lakes were collected using 2 – 3 sinking paneled gill nets: the first multifilament net contained sizes of 10, 13, 17, 20, 22, and 24 mm mesh sizes (57 m long x 1.6 m deep), the second monofilament net had mesh sizes 13, 19, 25, 38 and 50 mm mesh sizes (38.1 m long x 1.8 m deep), and the third monofilament net contained 13, 25, 51, and 102 mm mesh sizes (30.5 m long x 1.8 deep). Gill nets were set perpendicular to shore, were additionally set in deeper (~10 m) regions of Summit Lake, and were left overnight. For Arctic charr captured in 2010, gut contents were analyzed by sorting and categorizing prey contents as fish (various stickleback species for Iliamna Lake, slimy sculpin for all others), snails, pea clams, cinereus shrew, aquatic insect pupae, terrestrial insects and culicid larvae, caddisfly larvae, chironomid larvae, or zooplankton.

Digital images were taken of the charr from which fork lengths were measured using ImageJ v. 1.44o. Using TPS software 22 landmarks were placed on the images according to a previous study (Chapter 2). TPS software software (TPSDig V. 2.1, TPSUtil V. 1.40, TPSRel V. 2.4, Rohlf, 2004, life.bio.sunysb.edumorph) was then used to align, rotate, and scale landmarks, after which a relative warp analysis was used to summarize body shape variation.

Sex and maturity status were recorded, the latter categorized either as juvenile (no development in gonads: ovaries < 1/3 body length and eggs < 1 mm diameter; no development in testes), mature (any evidence of current or past gonadal development: lengthening of ovaries or increase in egg size; thickening of testes), or mature and ripening (close to spawning: ovaries span entire body length and eggs > 3mm; testes fully developed and possibly running). Total gill raker counts from the first arch and pyloric caecae counts were also recorded to ensure that fish fell within the ranges of Arctic charr and were not Dolly Varden *Salvelinus malma* (Russell 1980, Taylor et al. 2008). Otoliths were removed, ground and polished with fine sand paper, mounted on slides with crystal bond, and aged under a dissecting microscope.

Dorsal muscle plugs were taken for stable isotope analyses. Littoral stone and mud habitats (>1 m deep) were scoured for benthic invertebrate samples to be used as baseline values for stable isotope analyses, and zooplankton samples were taken using a 153 μ tow net in Alaska. Tows were vertical unless limitations due to shallow depths required horizontal towing. Zooplankton were left in lake water for at

least 3 hours and benthic invertebrates were left overnight to clear guts before being frozen. Samples were dried at 50° C, crushed, and sent to University of California (UC) Davis Stable Isotope Facility for analysis of natural levels of $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios using a Europa Hydra 20/20 continuous flow isotope ratio mass spectrometer. Ratios are expressed as parts per thousand difference relative to the international standard: $\delta = 1000 * (R_{sample} - R_{standard}) / R_{standard}$, where R is the ratio of the heavier, more rare isotope (^{13}C or ^{15}N) over the common isotope (^{12}C or ^{14}N). The international standard ratios based on V-PDB (Vienna Pee-Dee belemnite) carbon and atmospheric nitrogen were used for $R_{standard}$. Nylon, peach leaf, glutamic acid, and enriched glutamic acid standards were used to calibrate the spectrophotometer against NIST Reference Materials and indicated machine standard deviation as < 0.20 for $\delta^{13}C$ and < 0.50 for $\delta^{15}N$. For each species whose guts were examined, frequency of occurrence was calculated for each prey category and consolidated for comparison with stable isotope analyses (Table 4.2).

4.2.3. Stable isotope analysis

Before statistical analyses, stable isotope values were normalized for lipid content according to Kiljuenen et al. (2006), but as they found no relationship in invertebrates, no adjustment was made. Correcting for variation among lakes in $\delta^{13}C$ and $\delta^{15}N$ values at the base of the food chain is imperative for meaningful comparisons at higher trophic positions among study sites (Vander Zanden and Rasmussen 1999, Vander Zanden and Rasmussen 2001, Post et al. 2002). To calculate trophic position (TP) while taking into account baseline values, we used the following common mixture model: $TP_{sc} = \lambda_{base1} * b + \lambda_{base2} * (1 - b) + (\delta^{15}N_{sc} - [\delta^{15}N_{base1} * b + (\delta^{15}N_{base2} * (1 - b)])$. In this case, λ_{base1} and λ_{base2} are the trophic positions of the samples $\delta^{15}N_{base1}$ and $\delta^{15}N_{base2}$ used to calculate the bases of the first and second food chains (e.g., limnetic and benthic), $\delta^{15}N_{sc}$ is the sample from the secondary consumer whose TP is being calculated, and *a* represents the proportion of food chain 1 that contributes to the diet. Values for $\delta^{13}C$ can then be used to estimate *b* as $(\delta^{13}C_{sc} - \delta^{13}C_{base2}) / (\delta^{13}C_{base1} - \delta^{13}C_{base2})$, leaving 4 parameters necessary for the calculation of TP for secondary consumers: $\delta^{15}N_{base1}$, $\delta^{15}N_{base2}$, $\delta^{13}C_{base1}$, and $\delta^{13}C_{base2}$. To estimate these parameters, we used

snails as the benthic baseline and zooplankton as the limnetic baseline. Although freshwater mussels have been suggested as a more time-integrated value of the limnetic baseline (Post et al. 2002), these were not readily available in most lakes, or of such small size that benthic carbon sources likely influence $\delta^{13}C$ values. In addition, for Iliamna, Summit, and Caribou Lakes, the maximum $\delta^{13}C$ values from snails were not as extreme as values found for Arctic charr, so we assumed that our invertebrate sampling was insufficient and instead used the extreme values found for Arctic charr. Using these baselines with food chain 1 as benthic and food chain 2 as limnetic, we calculated TP and *b*, which reflects the proportion of carbon from the benthic food chain consumed (BFC). TP and BFC were then used to compare fish diets across lakes. All statistical analyses were performed using R v. 2.13.0 (R Development Core Team, 2011).

Table 4.1. Location, sampling date, sample sizes (N), environmental variables, and baseline values of $\delta^{15}N$ and $\delta^{13}C$ used for the limnetic and benthic food chains in stable isotope studies. The environmental variables include altitude (ALT), surface area (SA), and max depth (MAX). Ten additional Arctic charr from Summit Lake were caught 24 August 2009, and 16 additional Arctic charr length-at-age and gut content data were included from a 2007 study (Denton et al. 2010).

								Limnetic Base		Benthic Base	
	Lat.	Long.	Date	N	ALT	SA	MAX	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$
Summit Lake	59.7043	-153.68639	20-21 Aug 2010	16	152	0.60	20.00	2.20	-31.69	1.99	-16.87
Caribou Lake	60.4502	-154.62968	8 Dec 2010	45	550	1.20	5.00	3.82	-32.63	4.49	-16.29
L. Tazimina Lake	59.9626	-154.55540	6 Dec 2010	24	194	520.00	20.00	1.74	-33.34	0.38	-13.65
Iliamna Lake	59.7370	154.20806	23-30 Aug 2010	23	14	2622.00	393.00	5.51	-29.73	3.49	-10.27

Table 4.2. Frequency of occurrence of the prey items fish (Fis), snails (Sna), pea clams (Mus), zooplankton (Zoo), caddisfly larvae (Cad), terrestrial adult insects (Ter), aquatic insect pupae (Pup), and cinereus shrew (Shr) in each lake. Values > 0.2 are in bold. Data from Iliamna Lake are taken from Denton et al. (2010). Data for L. Tazimina Lake Cla., Ter. and Fis, were taken from Kreiner (2006).

Lake	Fis.	Sna.	Cla.	Zoo.	Cad.	Ter.	Pup.	Shr.
Iliamna Lake	**0.50**	**0.38**	0.00	0.00	0.00	0.00	0.00	0.00
Summit Lake	0.02	**0.29**	**0.22**	0.04	0.07	**0.42**	**0.78**	0.05
Caribou Lake	0.08	**0.71**	**0.58**	0.04	0.13	0.00	0.00	0.00
L. Tazimina Lake	0.08	**0.26**	0.17	**0.35**	0.00	**0.34**	0.09	0.00

4.2.4. Testing for polymorphism

Following the methods of Chapter 3, the fit of a mixture model containing two Von Bertalanffy growth curves (two-component model, K = 2) was compared to the fit of a single-component model (K=1). Error was assumed to be normal, so we calculated the likelihood of a given data point as the sum of 1) the likelihood of the data point given the parameters of the first growth curve, multiplied by an additional parameter *p* reflecting the proportional contribution of the first normal error distribution relative to the second, and 2) the likelihood of the data point given the parameters of the second growth curve, multiplied by (1 - *p*). The likelihood of a two-component mixture model is given by:

$$L = \prod (p \frac{1}{\sqrt{2\pi\sigma_1^2}} e^{-\frac{x-\mu_1}{2\sigma_1^2}} + (1-p) \frac{1}{\sqrt{2\pi\sigma_2^2}} e^{-\frac{x-\mu_2}{2\sigma_2^2}}) \qquad \text{Eq. 1}$$

where μ represents length prediction of a Von Bertalanffy curve:

$$\mu = L_\infty (1 - e^{-\kappa a}). \qquad \text{Eq. 2}$$

The Von Bertalanffy growth curve is defined by the parameters L_∞ (asymptotic length) and κ (curvature), and yields length predictions given age data *a*. The subscripts for μ and σ indicate separate predictions associated with the two curves fitted in the mixture model.

The model with the minimum Aikaike information criteria corrected for small sample size (AICc) was chosen as the best model. When the two-component model was chosen, the difference in AICc from the one-component model (δAICc) was shown to indicate its relative support; if δAICc > 2, then the two-component model showed

greater, rather than similar (δAICc < 2), support. When polymorphism was detected, individuals were assigned to the component whose proportion of that individual's summed likelihood was > 0.5.

4.2.5. Characterizing polymorphism

For populations found to be polymorphic, Student's T test was used to test for differences between assigned forms in TP, BFC, morphometric variables for fish in a similar size range (RW1, RW2, RW3), gill raker counts, pyloric caeca counts, and gonadosomatic index of ripening individuals (i.e., gonad mass divided by total body mass x 100).

4.2.6. Monomorphic variation

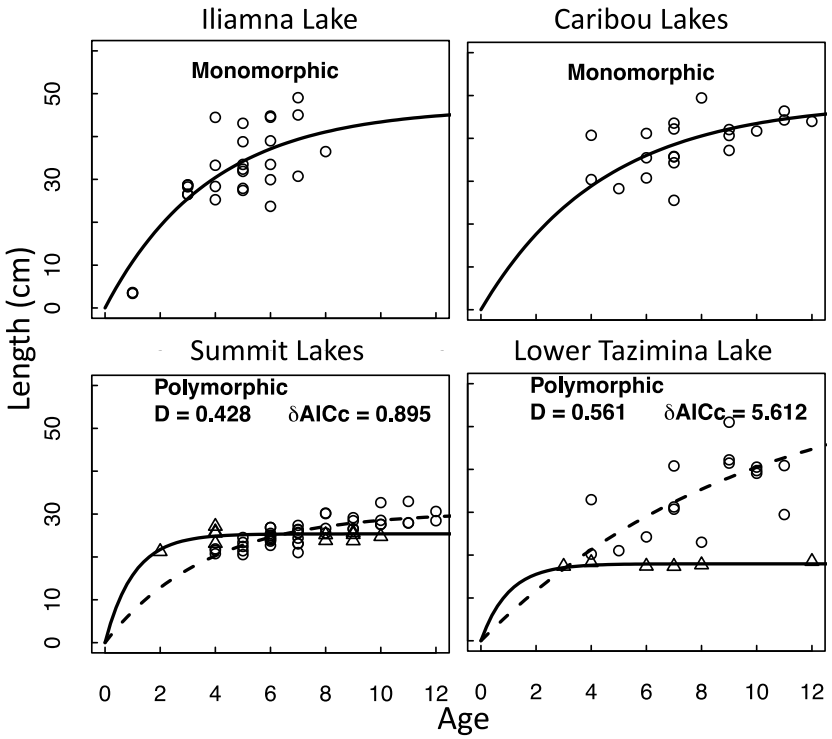
Following these analyses, within-population variation in morphology as it relates to diet was examined with the L. Tazimina Lake small form excluded. First, each morphometric variable (RW1, RW2, RW3) was predicted using Lake, Sex, and their interactions in linear models to determine whether morphology was affected by gender, and whether this effect differed among lakes. Second, the morphometric variables were each predicted using Lake, fork length, and their interactions to determine whether any morphometric variable represented allometric trends that differed by lake. If interactions were not significant, both interactions and Lake main effects were removed from the model. Third, morphometric variables were used as continuous predictors of TP and BFC in linear models. Lake was also included as a categorical variable, and the interactions between lake and each of the three predictors were used to test for differences in slope among lakes. Iliamna Lake was always used as the baseline to which the other lakes were compared.

4.3 Results

4.3.1. Testing for polymorphism

Only L. Tazimina Lake showed growth curve differentiation based the comparison of fits between a mixture model containing two Von Bertalanffy growth curves and a model with only a single growth curve using AICc (Fig. 4.2). For L. Tazimina Lake, six individuals were assigned to a separate form (referred to as the "small" form) with an

estimated maximum length of L_∞ = 17.967 ± 0.251 SE, curvature κ = 1.000 ± 0.206 SE, and standard deviation σ = 0.482 ± 0.170 SE, whereas 17 individuals were assigned to a large form with an estimated maximum length of L_∞ = 63.085 ± 21.227 SE, curvature κ = 0.103 ± 0.057 SE, and standard deviation σ = 6.956 ± 1.200 SE, P = 0.231. For Summit Lake, 32 individuals were assigned to one form with an estimated maximum length of L_∞ = 25.371 ± 0.785 SE, curvature κ = 0.969 ± 0.213 SE, and standard devation σ = 1.442 ± 0.566 SE, whereas 17 individuals were assigned to a second form with an estimated maximum length of L_∞ = 30.545 ± 1.383 SE, curvature κ = 0.272 ± 0.036 SE, and standard deviation σ = 1.998 ± 0.312 SE, P = 0.344. Differentiation was 0.561 for L. Tazimina Lake and 0.428 for Summit Lake, calculated as the sum of the squared residuals of the double growth curve model divided by the sum of the squared residuals from a single growth curve model. Single curves fit best in the other lakes (Iliamna Lake: L_∞ = 46.799 ± 7.151SE, κ = 0.263 ± 0.0837 SE, σ = 6.446 ± 0.846 SE; Summit Lakes: L_∞ = 27.569 ± 0.716 SE, κ = 0.424 ± 0.0573 SE, σ = 2.384 ± 0.227 SE; Caribou Lakes: L_∞ = 48.565 ± 3.394 SE, κ = 0.226 ± 0.046 SE, σ = 5.117 ± 0.739 SE).



Figu4.2. Mixture models of two growth curves were only more informative than single Von Bertalanffy growth curves in one of the four Alaskan Lakes tested. The associated change in AICc and value of Differentiation (D) are indicated.

4.3.2. Characterizing polymorphism

In the geometric morphometric analysis, first relative warp axis (RW1) accounted for 19.4% of the total variation and reflected bending around the abdominal section, as well as variation in head depth and caudal peduncle length. Negative m_1 scores indicated expansion of the lower head, yielding a more upturned mouth, whereas positive m_1 scores yielded an expansion of the upper head yielding a more downturned mouth. The second relative warp axis (RW2) accounted for 14.6% of the total variation; individuals with positive scores had larger heads and shorter bodies, especially in the caudal peduncle region whereas negative scores indicated opposite trait patterns. The third relative warp (RW3) accounted for 13.6% of the total variation and reflected variation in head length, caudal peduncle length, and body depth. Individuals with negative scores had relatively smaller heads, shorter and deeper caudal

peduncles, and deep bodies whereas individuals with positive scores had opposite trait values (Chapter 2, Fig. 2.1).

No significant differences were found between the assigned forms Summit Lake (Fig. 4.3; TP: $T_{53} = 0.119$, $P = 0.906$; BFC: $T_{53} = -0.007$, $P = 0.899$; RW1: $T_{53} = 0.001$, $P = 0.781$; RW2: $T_{53} = 0.723$, $P = 0.473$; RW3: $T_{53} = 1.525$, $P = 0.003$; GR: $T_{43} = -0.556$, $P = 0.265$; PC: $T_{45} = -4.27$, $P = 0.855$; GSI: $T_{12} = -0.838$, $P = 0.564$). Significant differences between the two forms within L. Tazimina Lake were found in all the variables tested except TP and RW2 (Fig. 4.3; TP: $T_{21} = 0.314$, $P = 0.756$; BFC: $T_{21} = -6.139$, $P < 0.001$; RW1: $T_9 = 3.556$, $P = 0.006$; RW2: $T_9 = -0.747$, $P = 0.474$; RW3: $T_9 = -5.246$, $P < 0.001$; GR: $T_{21} = 8.235$, $P < 0.001$; PC: $T_{18} = -4.21$, $P < 0.001$; GSI: $T_{12} = 15.47$, $P = 0.002$). All individuals of the small form contained only zooplankton in their guts, so that frequency of occurrence in the small form rose to 1.0 and in the larger form for zooplankton dropped to 0.08. Frequency of occurrence (F_o) in all other diet categories dropped to 0 for the small form and rose for the large form to $F_o' = (F_o*23 - 6)/23$, as the total sample size was 23 and the number of individuals assigned to the small form was 6 (Table 4.2). The small form in L. Tazimina Lake therefore consumed more limnetic resources, as confirmed by low BFC scores, and had deeper bodies with more down-turned heads (Fig. 4.3), higher gill raker counts, lower pyloric caecae counts, and larger gonads relative to body size for fish whose gonads were approaching spawning stages (GSI) (Fig. 4.4). Mean GSI for females and males of the small L. Tazimina form were (mean ± SE) 17.6% ± 1.6% and 5.5% ± 0.0% respectively, whereas mean GSI for females and males of the large L. Tazimina form were 10.0% (from one sample, no SE) and 3.2% ± 0.4% respectively.

4.3.3. Monomorphic variation

In the models to predict RW1, RW2, and RW3 using sex and its interaction with Lake in mature individuals, interactions were never significant, indicating that any differences between sexes were similar among lakes. Sex only had a significant effect on RW2 (RW1: $T_{64} = 1.009$, $P = 0.317$; RW2: $T_{64} = -2.904$, $P = 0.005$; RW3: $T_{64} = -1.696$, $P = 0.095$), indicating that males generally had smaller heads and longer bodies (lower RW2 scores). In the models to predict RW1, RW2, and RW3 using fork length and its interaction with Lake, interactions were

never significant, indicating that any allometric relationships were common across the lakes. Length was positively correlated with RW1 (T_{110} = 8.849, P = 0.004), uncorrelated with RW2 (T_{110} = 0.095, P = 0.759), and strongly negatively correlated with RW3 (T_{110} = -6.479, P < 0.001). Therefore, as fish grew in length they overall experienced a slight expansion of the upper head region and down-turning of the mouth (RW1), as well as a strong enlargement of the body around the head and deepening of the body and caudal peduncle (RW3).

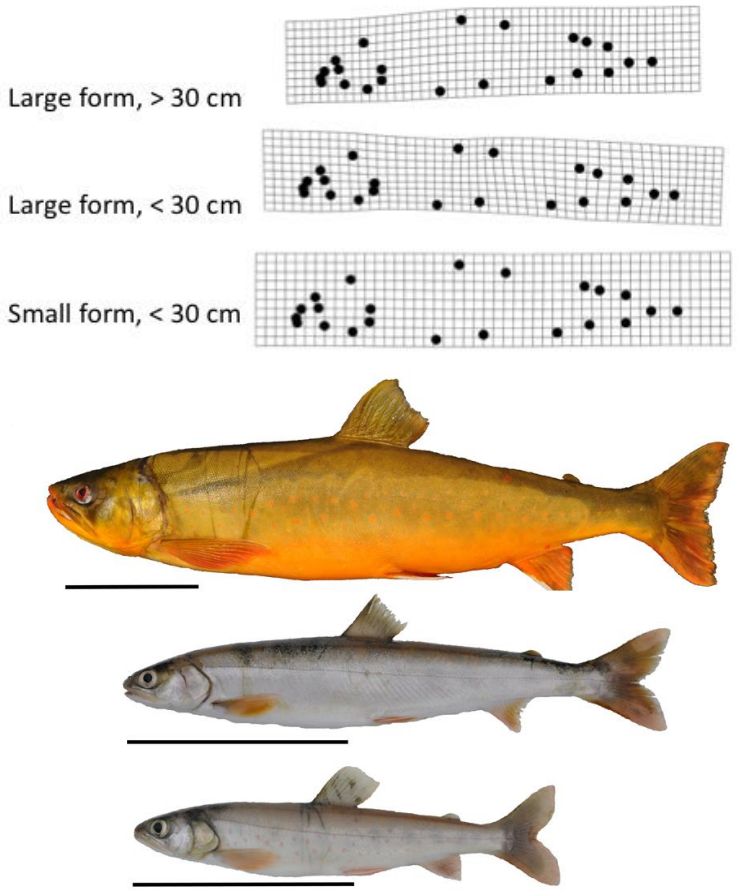


Figure 4.3. Morphometric differences in RW1 and RW3 between the small form, small individuals of the large form, and large individuals in Lower Tazimina Lake. Grid deformations from geometric morphometric analyses represent the 2x centroid configuration of each category (top). Images of each form depicted by grid deformations are shown on the bottom with 10 cm bars.

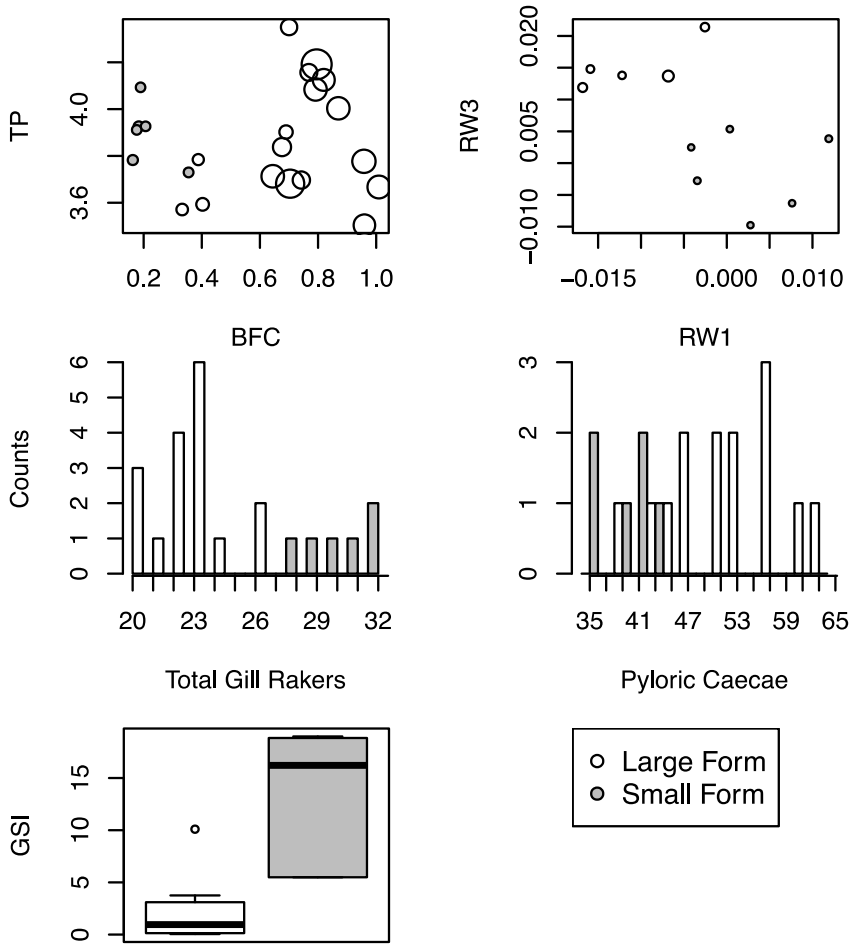


Figure 4.4. Further analyses of differences between the large and small forms in Lower Tazimina Lake indicated a greater consumption of limnetic resources (low BFC) but similar trophic positions (TP) (top left), different morphometric values (RW1, RW3) with fish of a similar size (top right), higher total gill raker counts (middle left), lower pyloric caeca counts (middle right), and higher gonadosomatic index (GSI) values (bottom).

The model predicting TP based on morphology, Lake, and their interactions was significant ($F_{15,96}$ = 6.424, P < 0.001), but the only significant main effect was RW3 (RW1: T_{96} = -1.185, P = 0.239; RW2: T_{96} = 0.783, P = 0.436; RW3: T_{96} = -2.033, P = 0.045; Summit Lake: T_{96} = -0.251, P = 0.802; Caribou Lake: T_{96} = 0.779, P = 0.282; Tazimina Lake: T_{96} = 1.364, P = 0.176). RW1 had a significant interaction only with Caribou Lake (with Summit: T_{96} = 0.433, P = 0.666; Caribou: T_{96} = 2.077, P = 0.041; Tazimina: T_{96} = -0.346, P = 0.730); RW2 had no

significant interactions (Summit: T_{96}: -0.963, P = 0.338; Caribou: T_{96} = -0.970, P = 0.334; Tazimina: T_{96} = -1.686, P = 0.095); and RW3 had a significant correlation with Summit and a marginal correlation with Caribou (Summit: T_{96} = 2.527, P = 0.013; Caribou: T_{96} = 1.867, P = 0.065; Tazimina: T_{96} = 1.396, P = 0.166). Therefore, Arctic charr in Summit and Caribou lakes became longer and had a more downturned mouth as their trophic position rose, whereas Arctic charr from L. Tazimina large form and Iliamna Lakes became deeper and gained more horizontally oriented mouths.

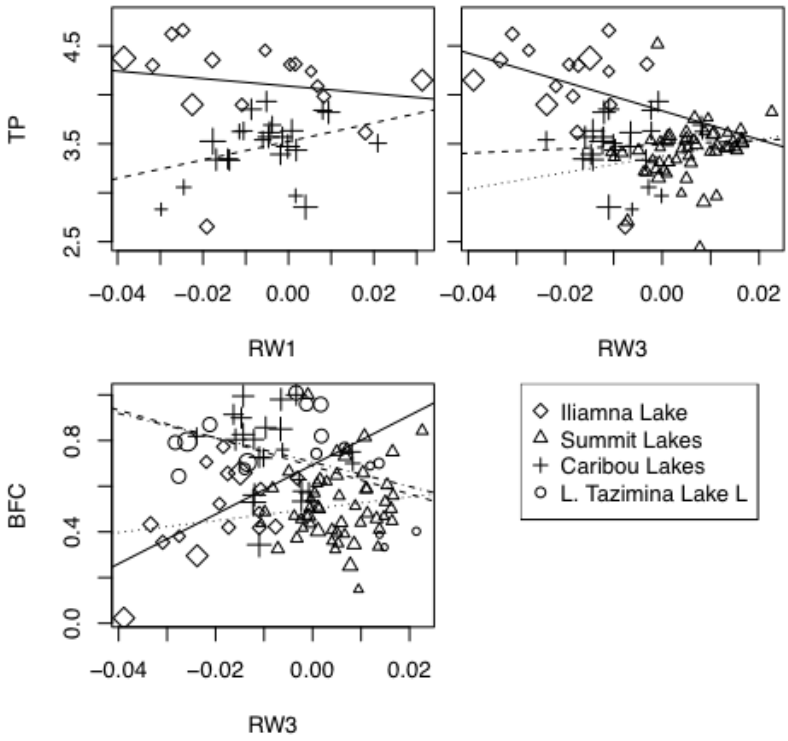


Figure 4.5. Morphometric variables (RW1, RW3) were correlated with trophic position (TP) and proportion carbon consumed from the benthic food chain (BFC: 1 = benthic, 0 = limnetic), but relationships varied by lake.

The model predicting proportion benthic food chain consumed (BFC) based on morphology, Lake, and their interactions was significant ($F_{15,96}$ = 4.503, P < 0.001), but the only significant main effect was RW3 and Summit Lake (RW1: T_{96} = 0.277, P = 0.782; RW2: T_{96} =1.190, P = 0.237; RW3: T_{96} = 2.703, P = 0.008; Summit Lake: T_{96} = -2.006, P = 0.048; Caribou Lake: T_{96} = -1.388, P = 0.168; Tazimina

Lake: T_{96} = -0.928, P = 0.356). RW1 had no significant interactions (with Summit: T_{96} = -0.761, P = 0.448; Caribou: T_{96} = -1.243, P = 0.217; Tazimina: T_{96} = 0.350, P = 0.727); RW2 had no significant interactions (Summit: T_{96}: 0.885, P = 0.398; Caribou: T96 = 1.622, P = 0.108; Tazimina: T_{96} = 0.960, P = 0.340); and RW3 had significant correlations with all three lakes (Summit: T_{96} = -1.958, P = 0.053; Caribou: T_{96} = -3.070, P = 0.003; Tazimina: T_{96} = -3.220, P = 0.002) (Fig. 4.5). Therefore, fish in Caribou Lake and the large form in Tazimina Lake showed a similar shift toward deepening bodies with greater benthic resource use at large sizes. Summit Lake and Iliamna Lake were instead more similar in their slopes of increasing benthic resource use with narrower bodies.

4.4 Discussion

We detected polymorphism in Arctic charr from two of the four Alaskan lakes under study by differentiation in growth curves, though only one of these showed any further ecological differences. Differences were found in feeding habits, body shape (when only fish of a similar size range were considered), counts of gill rakers and pyloric caeca, and proportional size of the gonads. Both stable isotope and gut content data indicated that the small form consumed almost entirely zooplankton, whereas the larger form went through an ontogenetic shift from consumption of zooplankton at small sizes to consumption of mostly snails, clams, terrestrial insects, and some fish at large sizes. Therefore, Arctic charr diversity in Alaskan lakes is likely greater than currently appreciated, and requires further investigation in remote regions. In Summit Lakes, growth curve differences may instead reflect differences among cohorts or combination of seasonal effects of different-sized prey and size-specific foraging (Griffiths 1994; Borchering et al. 2010), although further exploration is also warranted.

Our results correspond well with previously known limnetic-benthic species differentiation between Arctic charr forms (Malmquist et al. 1992, Snorrason et al. 1994, Snorrason and Skúlason 2004, Adams et al. 1998, Fraser et al. 1998, Arbour and Hutchings 2011). However the extremely small size range of the limnetic form, < 20 cm and qualifying as “dwarf” in other studies, is not common, and has only been found with relatively higher frequency in Russia (Alekseyev et al. 2002). Although small Arctic charr forms in Iceland are relatively

common, they are mostly benthic specialists (Kristjánsson 2008). Small limnetic forms have only been observed from ~2 / 50 lakes surveyed Iceland (Ecological Survey of Icelandic Lakes, unpublished data). A small limnetic form was reported in a single Canadian lake (Power et al. 2005b), but the diet of this form was composed of chironomid larvae and insects rather than zooplankton (although this may be a seasonal artefact). Small limnetic forms have not been reported from lakes in continental Europe, although other species in Europe such as lake whitefish *Coregonus lavaretus* may form small limnetic forms (Siwertsson et al. 2010). Instead, the more well-known small forms of Arctic charr in Europe are profundal (Jonsson and Jonsson 2001, Klemetsen 2010).

The high gill raker counts of the small L. Tazimina Lake form correspond well with past studies that indicate greater consumption of zooplankton by Arctic charr (Snorrason et al. 1994) and whitefish (Siwertsson et al. 2011, Lindsey 1981). In addition, body shape variables differed between the small limnetic form and small individuals (< 30 cm) of the larger form, even though they consumed similar resources within this size range. Despite the clearly limnetic diet and high gill raker counts, the small form appeared to have a more "benthic" morphometry in comparison with small individuals of the large form. The small form had higher RW1, indicating a more down-turned body with longer posterior and dorsal tail regions and a more down-turned mouth, and lower RW3 values, indicating a relatively deeper body (Fig. 4.2). The deeper bodies resemble those found for benthic forms by Arbour et al. (2011) and down-turned mouths are similar to Icelandic small benthic Arctic charr (Snorrason and Skúlason 2004). However, the differences we observed may also reflect allometric changes or behavioral differences in habitat use. As all fish were caught close to spawning time in shallow water (< 5 m), virtually nothing is known about non-spawning habitat use or behavioral acquisition of their separate resources. Small benthic forms in Iceland, which are common in shallow littoral habitats (Kristjánsson 2008), are also paedomorphic, retaining a juvenile morphology at maturity (Snorrason and Skúlason 2004). The small limnetic form in L. Tazimina Lake has retained some faint par marks, but differs in body shape and meristic characteristics from the co-occurring large benthic form. Therefore, paedomorphism may only be occurring in size and coloration.

Further correlations of morphology with dietary habits were found in the lakes containing monomorphic populations and in the large Lower Tazimina Lake form. Sex appeared to be rather unimportant in these interpretations, since morphological differences between sexes were only observed in the morphological variable that was not affected by length and was not correlated with stable isotope ratios (RW2). Trends found between body shape and stable isotope ratios were also not consistent across lakes, indicating that the ecology of Alaskan Arctic charr shifts greatly with circumstance. For example, Arctic charr in Caribou and Summit lakes became longer and had a more downturned mouth as their trophic position rose, whereas the Iliamna Lake fish showed an opposite shift, toward deeper bodies with more horizontal mouths (RW1 & RW3, Fig. 4.5). Because these morphometric variables were also correlated with size, these likely reflect ontogenetic shifts with size toward greater piscivory. However, piscivory in Iliamna Lake was dominated by predation on threespine stickleback (Denton et al. 2008), whereas only sculpin were consumed in Caribou Lake (Table 4.2) and L. Tazimina Lake (Kreiner 2006). Therefore, this correlation between morphology and a shift toward piscivory corresponds well with past studies indicating that piscivory may occur either in more limnetic habitats by more streamlined deeper-bodied fish with terminal mouths (Arbour et al. 2011, Snorrason and Skúlason 2004) or in more benthic habitats (Fraser et al. 1998, Adams et al. 1998).

Similarities among lakes showed a different trend when analyzing the proportion of the carbon incorporated from the benthic food chain (BFC). Caribou Lake and the large form in Tazimina Lake showed a similar shift toward deepening bodies with greater benthic resource use at large sizes. Summit Lake and Iliamna Lake were instead more similar in their slopes of increasing benthic resource use with narrower bodies. This appears to indicate a shift toward greater limnetic resource use with piscivory in Iliamna Lake, but the same explanation cannot be used for non-piscivorous Summit Lake Arctic charr. Instead, perhaps Arctic charr from Summit Lake also appear to be stunted (i.e., restricted to relatively smaller sizes), possibly indicating some level of energetic constraints or starvation that causes body narrowing.

Although resource polymorphism focuses on differences in morphology related to diet (Skúlason and Smith 1995, Smith and Skúlason 1996), niche divergence may occur for other resources as well, such as spawn timing or habitat. This divergence may promote

coexistence through temporal, spatial or size-related differentiation in resource use (Kotler and Brown 2007). Therefore, other ecological differences may occur between the forms described in L. Tazimina Lake. The great variability in Arctic charr ecology found among lakes in this study indicates that Arctic charr are extremely flexible in their life histories among populations, as has been found in other regions (Alekseyev et al. 2002, Snorrason and Skúlason 2004, Power et al. 2009, Klemetsen 2010, Chavarie et al. 2010). Therefore, regional genetic differences in colonization pool (Wilson et al. 2004) appear to make little difference in the species' ability to express high ecological and morphological variability, even if differences among regions in mean morphology exist. In addition, the strong differentiation found within Tazimina Lake indicates that there are likely other locations in western North America that exhibit polymorphism, especially as this has been found in eastern North American lakes (Guiguer et al. 2002, O'Connell and Dempson 2002, Power et al. 2005b, Power et al. 2009, Gallagher et al. 2010, Arbour et al. 2011). Many large regions within the distribution of Arctic charr are poorly studied, in part because of their isolation and remoteness. Studies of these regions are urgently needed, especially due to the potentially severe impacts of anthropogenic disturbance at high latitudes (Rouse et al. 1997, Schindler and Smol 2006).

4.5 References cited

Adams, C.E., and Huntingford, F.A. 2002. Inherited differences in head allometry in polymorphic Arctic charr from Loch Rannoch, Scotland. J. Fish Biol. 60: 515-520.

Adams, C.E., Hamilton, D.J., McCarthy, I., Wilson, A.J., Grant, A., Alexander, G., Waldron, S., Snorrason, S.S., Ferguson, M.M., and Skúlason, S. 2006. Does breeding site fidelity drive phenotypic and genetic sub-structuring of a population of Arctic charr? Evol. Ecol. 20: 11 – 26.

Adams, C.E., Wilson, A.J., and Ferguson, M.M. 2008. Parallel divergence of sympatric genetic and body size forms of Arctic charr, *Salvelinus alpinus*, from two Scottish lakes. Biol. J. Linnean Soc. 95: 748 -757.

Alekseyev, S.S., Samusenok, V.P., Matveev, A.N., and Pichugin, M.Y. 2002. Diversification, sympatric speciation, and trophic

polymorphism of Arctic charr, *Salvelinus alpinus* complex, in Transbaikalia. Environ. Biol. Fishes 64: 97 – 114.

Andersson, J. 2003. Effects of diet-induced resource polymorphism on performance in Arctic charr (*Salvelinus alpinus*). Evol. Ecol. Res. 5: 213 – 228.

Andersson, J., and Persson, L. 2005. Behavioural and morphological responses to cannibalism in Arctic charr (*Salvelinus alpinus*). Evol. Ecol. Res. 7: 767-778.

Andersson, J., Byström, P., Claessen, D., Persson, L., and De Roos, A.M. 2007. Stabilization of population fluctuations due to cannibalism promotes resource polymorphism in fish. Am. Nat. 169: 820 – 829.

Andersson, J., Bystrom, P., Persson, L., and De Roos, A.M. 2005. Plastic resource polymorphism: effects of resource availability on Arctic char (*Salvelinus alpinus*) morphology. Biol. J. Linnean Soc. 85: 341-351.

Bernatchez, L., and Wilson, C.C. 1998. Comparative phylogeography of Nearctic and Palearctic fishes. Molecular Ecology 7: 431 – 452.

Bolnick, D.I. et al. 2003. The ecology of individuals: incidence and implications of individual specialization. – Am. Nat. 161: 1 – 28.

Borchering, J., Beeck, P., DeAngelis, D.L., and Scharf, W.R. 2010. Match or mismatch: the influence of phenology on size-dependent life history and divergence in population structure. J. Anim. Ecol. 79: 1101 – 1112.

Brunner, P.C., Douglas, M.R., Osinov, A., Wilson, C.C., and Bernatchez, L. 2001. Holarctic phylogeography of Arctic charr (*Salvelinus alpinus* L.) inferred from mitochondrial DNA sequences. **Evolution 55:** 573-586.

Burgner, R.L. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). pp. 1-117. *In:* C. Groot & L. Margolis (ed.) Pacific salmon life histories, University of British Columbia Press, Vancouver.

Byström, P. and Andersson, J. 2005. Size-dependent foraging capacities and intercohort competition in an ontogenetic omnivore (Arctic char). Oikos *110:* 523-536.

Chavarie, L., Dempson, J.B., Schwarz, C.J., Reist, J.D., Power, G., and Power, M. 2010. Latitudinal variation in growth among Arctic charr in eastern North America: evidence for countergradient variation? Hydrobiologia 650: 161 – 177.

Crespi, B.J., and Teo, R. 2002. Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. Evolution 56: 1008 – 1020.

Denton, K.P., Rich, H.B., Jr., Moore, J.W., and Quinn, T.P. 2010. The utilization of a Pacific salmon *Oncorhynchus nerka* subsidy by three populations of charr *Salvelinus* spp. J. Fish Biol. 77: 1006 - 1023.

Fleming, I. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. Can. J. Fish. And Aquat. Sci. 55 (Suppl. 1): 59 – 76.

Forseth, T., Ugedal., O., Jonsson, B., and Fleming, I. 2003. Selection on Arctic charr generated by competition from brown trout. Oikos 101: 467 – 478.

Gallagher, C.P., and Dick, T.A. 2010. Trophic structure of a landlocked Arctic char *Salvelinus alpinus* population from southern Baffin Island, Canada. Ecol. Freshwater Fish 19: 39 - 50

Griffiths, D. 1994. The size structure of lacustrine Arctic charr (Pisces: Salmonidae) populations. Biol. J. Linn. Soc. 51: 337 – 357.

Guiguer, K.R.R.A., Reist, J.D., Power, M., and Babaluk, J.A. 2002. Using stable isotopes to confirm the trophic ecology of Arctic charr morphotypes from Lake Hazen, Nunavut, Canada. J. Fish. Biol. 60: 348 - 362.

Hesthagen, T., Forseth, T., Hegge, O., Saksgård, and Skurdal, J. 2004. Annual variability in the life-history characteristics of brown trout (*Salmo trutta*) Arctic charr (*Salvelinus alpinus*) in a subalpine Norwegian lake. Hydrobiologia 521: 177 – 186.

Hesthagen, T., Jonsson, B., Ugedal, O., and Forseth, T. 1997. Habitat use and life history of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) in some low acidity lakes in central Norway. Hydrobiologia 348: 113 – 126.

Jaecks, T.A., 2010. Population dynamics and trophic ecology of Dolly Varden in the Iliamna River, Alaska: life history of freshwater fish relying on marine food subsidies. Master's thesis, University of Washington, Seattle.

Jansen, P.A., Slettvold, H., Finstad, A.G., and Langeland, A. 2002. Niche segregation between Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*): an experimental study of mechanisms. Can. J. Fish. Aquat. Sci. 59: 6 – 11.

Jónasson P.M., Jónsson, B., and Sandlund, O.T. 1998. Continental rifting and habitat formation: Arena for resource polymorphism in Arctic charr. Ambio 27: 162-169.

Jonsson, B., and Jonsson, N. 2001. Polymorphism and speciation in Arctic charr. J. Fish Bio. 58: 605 - 639.

Jonsson, B., Skúlason, S., Snorrason, S.S., Sandlund, O.T., Malmquist, H.J., Jónasson, P.M., Gydemo, R., and Lindem, T. 1988. Life history variation of polymorphis Arctic charr (*Salvelinus alpinus*) in Thingvallavatn, Iceland. Can. J. Fish. Aquat. Sci. 45: 1537 – 1547.

Kapralova, K.H., Morissey, M.B., Kristjánsson, B.K., Ólafsdóttir, G.Á., Snorrason, S.S., and Ferguson. M.M. 2011. Evolution of adaptive diversity and genetic connectivity in Arctic charr (*Salvelinus alpinus*) in Iceland. Heredity 106: 472 – 487.

Kelly, J.F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology Can. J. Of Zool. 78: 1 – 27.

Kiljunen, M., Grey, J. Sinisalo, T., Harrod, C., Immonen, H., and Jones, R.I. 2006. A revised model for lipid-normalizing $\delta^{13}C$ values from aquatic organisms with implications for isotope mixing models. J. Applied Ecol. 43: 1213 – 1222.

Klemetsen, A. 2010. The charr problem revisited: exceptional phenotypic plasticity promotes ecological speciation in postglacial lakes. Freshwater Rev. 3: 49 – 74.

Klemetsen, A., Amundsen, P.-A., Knudsen, R., and Hermansen, B. 1997. A profundal, winter-spawning morph of Arctic charr *Salvelinus alpinus* (L.) in Lake Fjellfrosvatn, northern Norway. Nord. J. Freshwater Res. 73: 13 – 23.

Knudsen, R., Primicerio, R., Amundsen, P.A., and Klemetsen, A. 2010. Temporal stability of individual feeding specialization may promote speciation. J. Anim. Ecol. 79: 161 – 168.

Knudsen, R., Siwertsson, A., Adams, C.E., Garguño-Paz, M., Newton, J., and Amundsen, P.-A. 2011. Temporal stability of niche use exposes sympatric Arctic charr to alternatie selection pressures. Evol. Ecol. 25: 589 – 604.

Kotler, B.P., and Brown, J.S. 2007. Community Ecology pp. 397-436 in *Foraging Behavior and Ecology*. Eds. D.W. Stephens, J.S. Brown, and R.C. Ydenberg.

Kreiner, R. 2006. An investigation of Arctic char (*Salvelinus alpinus*) and lake trout (*Salvelinus namaycush*) in Lake Clark National Park. M.S. Thesis, University of Idaho. 76 pp.

Kristjánsson BK. 2008. Fine scale phenotypic diversity of Arctic charr (*Salvelinus alpinus*) in relation to ecological characters. Ph.D. Thesis, Zoology Department. University of Guelph.

Langeland, A., L'Abée-Lund, J.H., Jonsson, B., and Jonsson, N. 1991. Resource partitioning and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta.* J. Anim. Ecol. 60: 895 – 912.

Lindsey, C.C., 1981. Stocks are chameleons: plasticity in gill rakers of coregonid fishes. Can. J. Fish. Aquat. Sci. 38: 1497 – 1507.

Malmquist, H.J., Snorrason, S.S, Skúlason, S., Jonsson, B., Sandlund, O.T., and Jonasson, P.M. 1992. Diet differentiation in polymorphic Arctic charr in Thingvallavatn, Iceland. Journal of Anim. Ecol. 61: 21 – 35.

O'Connell, M.F., and Dempson, J.B. 2002. The biology of the Arctic charr, *Salvelinus alpinus*, of Gander Lake, a large, deep, oligotrphic lake in Newfoundland, Canada. Environ. Biol. Fish. 64: 115 – 126.

Parsons, K.J., Sheets, H.D., Skúlason, S., and Ferguson, M.M. 2011. Phenotypic plasticity, heterochrony, and ontogenetic repatterning during juvenile development of divergent Arctic charr (*Salvelinus alpinus*). J. Evol. Biol. 24: 1640 – 1652.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: Models, methods and assumptions. Ecol. 823: 703 – 718.

Power, M., Dempson, J.B., Reist, J.D., Schwarz, C.J., and Power, G. 2005a. Latitudinal variation in fecundity among Arctic charr populations in eastern North America. J. Fish Biol. 67: 255 – 273.

Power, M., O'Connell, M.F., and Dempson, J.B. 2005b. Ecological segregation within and among Arctic char morphotypes in Gander Lake, Newfoundland. Environ. Biol. Fish. 73: 263 – 274.

Power, M., Power, G., Reist, J.D., and Bajno, R. 2009. Ecological and genetic differentiation among the Arctic charr of Lake Aigneau, Northern Québec. Ecol. Freshwater fish 18: 445 – 460.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Robinson, B.W., and Schluter, D. 2000. Natural selection and the evolution of adaptive genetic radiation in northern freshwater fishes. *Adaptive Genetic Variation* (eds Mousseau, T.A., Sinervo, B. & Endler, J.), pp. 65–94. Oxford University Press, Oxford.

Rouse, W.R., Douglas, M.S.V., Heckey, R.E., Hershey, A.E., Kling, G.W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B.J.,

Roulet, N.T., and Smol, J.P. 1997. Effects of climate change on the waters of arctic and subarctic North America. Hydrol. Proc. 11: 873-902.

Russell, R. 1980. A Fisheries Inventory of Waters in the Lake Clark National Monument Area. Alaska Dept. of Fish and Game, Sportfish Division. 197 pp.

Scanlon, B.P. 2000. the ecology of the Arctic char and the Dolly Varden in Becharof Lake Drainage, Alaska. M.S. Thesis, University of Alaska. 103 pp.

Schindler, D.W., and Smol, J.P., 2006. Cumulative effects of climate warming and other human activities on freshwaters of Arctic and subarctic North America. Ambio 35: 160 – 168.

Schluter, D. 1996. Ecological speciation in postglacial fishes. Phil. Trans. R. Soc. Lond. B 351: 807-814.

Sigursteinsdóttir, R.J., and Kristjánsson, B.K. 2005. Parallel evolution, not always so parallel: comparison of small benthic charr, *Salvelinus alpinus*, from Grimsnes and Thingvallavatn, Iceland. Environ. Biol. Fishes 74: 239-244.

Skúlason, S., Snorrason, S.S., Noakes, D.L.G., and Ferguson, M.M. 1996. Genetic basis of life history variations among sympatric morphs of Arctic char, *Salvelinus alpinus*. **Can. J. Fish. Aquat. Sci.** 53: 1807-1813.

Skúlason, S., Snorrason, S.S., Noakes, D.L.G., Ferguson, M.M., and Malmquist, H.J. 1989. Segregation in spawning and early life-history among polymorphic Arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. J. Fish Biol 35: 225-232.

Smith, T.B., and Skúlason, S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. Ann. Rev. Ecol. System. 27: 111 - 133.

Snorrason, S.S., Skúlason, S.S., Jonsson, B., Malmquist, H.J., Jónasson, P.M., Sandlund, O.T., and Lindem, T. 1994. Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces; Salmonidae): morphological divergence and ontogenetic niche shifts. Biol. J. Linn. Soc. 52: 1 – 18.

Taylor, E.B., Lowery, E., Lilliestrale, A., Elz, A., and Quinn, T.P. 2008. Genetic analysis of sympatric charr populations in western Alaska: Arctic charr (*Salvelinus alpinus*) and Dolly Varden (*Salvelinus malma*) are not two sides of the same coin. J. Evol. Biol. 21: 1609 – 1625.

Vander Zanden, M.J., and Rasmussen, J.B. 1999. Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecol. 80: 1395 – 1404.

Vander Zanden, M.J., and Rasmussen, J.B. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. Limnol. Oceanogr. 46: 2061 – 2066.

Vander Zanden, M.J., Chandra, S., Allen, B.C., Reuter, J.E., and Goldman, C.R. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) Basin. Ecosystems 6: 274 – 288.

Wilson, A.J., Gíslason, D., Skúlason, S., Snorrason, S., Adams, C.E., Alexander, G., Danzmann, R.G., and Ferguson, M.M. 2004. Population genetic structure of Arctic charr *Salvelinus alpinus* from northwest Europe on large and small spatial scales. Mol. Ecol. 13: 1129 – 1142.

5 Food web structure in subarctic lakes with low interspecific but high intraspecific fish diversity: a comparison between Iceland and Alaska

5.0 Abstract

The study of subarctic lake food webs is important to both ecologists and evolutionary biologists because such lakes contain few fish species to occupy upper trophic levels. Their dietary habits may therefore strongly affect food web structure. In addition, species that exhibit resource polymorphism, such as Arctic charr *Salvelinus alpinus* and threespine stickleback *Gasterosteus aculeatus*, may also affect food webs through high intraspecific dietary variation. Therefore, the objective of this study was to compare food webs containing polymorphic fish species with various numbers of fish species present. This study compared food web structure in 7 Icelandic lakes and 4 Alaskan lakes using natural variation in stable isotope ratios $\delta^{13}C$ and $\delta^{15}N$ to estimate trophic position and relative use of benthic and limnetic carbon sources. The first goal was to compare fish resource use among lakes to determine whether differences could be explained by resource partitioning both within and among species. Analyses indicated that interlake variability was high in some species, even when intralake variability was not. Differences in resource use between Icelandic and the Alaskan lakes appear related to species interactions. The second goal was to analyze whether resource polymorphism in Arctic charr, the presence of prey fish, or diet of the prey fish affect variability in Arctic charr resource use. Results indicated that polymorphism increased the

range in benthic versus limnetic resource use in Arctic charr when morphological differentiation was involved. The presence of threespine stickleback as prey increased breadth in trophic position and attainable body sizes in Arctic charr. Greater use of limnetic resources by stickleback was also transmitted to higher trophic levels. The third goal was to test whether dietary breadth was correlated with environmental trends. Greater breadth in limnetic over benthic resource use by Arctic charr was positively related to 1) depth, yielding evidence for the hypothesis that greater limnetic habitat availability increases limnetic resource use, and 2) surface temperature, indicating that stratification or run-off may be important. Greater breadth in trophic position was related to surface area, indicating that greater colonization potential of higher trophic-level may be important.

5.1 Introduction

Arctic and subarctic lakes are extreme freshwater environments, and food web structure gains complexity through the inclusion of vertebrates, i.e., fish. Only fish with a tolerance for cold, less productive environments with short growing seasons can inhabit these regions, leading to low fish diversity at more extreme latitudes (Pienitz et al. 1997, Edmundson and Mazumder 2002). Recent deglaciation, high environmental variability, and barriers related to colonization also tend to keep fish diversity low in these regions (Bernatchez & Wilson 1998, Robinson & Schluter 2000, Griffiths 2006), as well as affect limnological attributes. For example, lakes surrounded by barren land may have little nitrogen loading from terrestrial vegetation (Pienitz et al. 1997, LaPerriere et al. 2003). Limited terrestrial vegetation may also result in low phosphorous and dissolved organic carbon levels, due to reduced leaching (Pienitz et al. 1997). On the other hand, high phosphorous levels may result from greater erosion and run-off in less vegetated areas (LaPerriere et al. 2003). Nitrogen limitation is therefore not uncommon (Levine and Whalen 2001, LaPerriere et al. 2003), possibly resulting in reduced limnetic productivity that affects whole-lake metabolic patterns and nutrient cycles (Åberg et al. 2007, Ask et al. 2009). In unproductive lakes, the limnetic food chain may have substantial quantities of carbon from benthic (Cole et al. 2006, Rautio and Vincent 2007, Cole et al. 2011) or allochthonous sources (Karlsson et al. 2003, Carpenter et al. 2005, Rautio and Vincent 2007), linking fish

production with benthic resources (Sierszen et al. 2003, Vadeboncouer et al. 2005).

Given these conditions in subarctic and arctic lakes, the relative contributions of limnetic and benthic carbon to fish diets likely varies with 1) physical and chemical attributes of the environment that control food availability, 2) behavioral tendencies of the inhabiting species to use certain resources over others, and 3) species interactions that may reduce the effective range of food available. In the first case, the input of terrestrial insects as an allochthonous food source, which can be substantial, likely does the same, as it changes with terrestrial habitat (Kawaguchi and Nakano 2001, Cole et al. 2006) and limnetic production (Carpenter et al. 2005). In the second case, species may consume a narrow range of dietary items due to constraints in efficiency related to size or morphology, or they may exhibit a high degree of morphological and dietary variability, for example when the species exhibits resource polymorphism (Skúlason and Smith 1995). In the third case, dietary behavior may also depend on interspecific interactions, such as competition (Langeland et al. 1991, Hesthagen et al. 1997, Forseth et al. 2003) or predation (L'Abée-Lund et al. 1992, L'Abée-Lund et al. 1993, Tonn et al. 2004, Amundsen et al. 2009). Therefore, an understanding of environmental factors, variation within the species, and species interactions are necessary components for studying variation in subarctic food webs.

This study analyzed food webs of subarctic lakes, focusing on fish food habits. We used the naturally varying stable isotopes ratios $\delta^{13}C$ and $\delta^{15}N$, supported by diet data, to compare how food webs vary with the species present and environmental characteristics. In freshwater studies, the ratio ^{13}C to its lighter isotope ^{12}C has been commonly used to distinguish benthic carbon sources, which tend to have an enriched isotope ratio (i.e., higher $\delta^{13}C$ value) relative to limnetic, terrestrial, or profundal carbon sources due to a boundary layer effect (Vander Zanden and Rasmussen 1999, Jeppesen et al. 2002, Hershey et al. 2006). The ratio of ^{15}N to its lighter isotope ^{14}N is a convenient measure of trophic position due to its tendency to fractionate as it is metabolized, thereby becoming enriched by approximately 3.4‰ with each increase in trophic position (Cabana and Rasmussen 1996, Post et al. 2002). Stable isotope ratios are integrated over the time span of the organism's tissue turnover rate (Gannes et al. 1998, Kelly et al. 2000), yielding a powerful

tool to augment gut content studies, which only reveal recent consumption (Gannes et al. 1998, Kelly et al. 2000). However, diet studies yield higher taxonomic resolution and are helpful in distinguishing potentially confounding dietary sources; therefore, the comparison of stable isotope data with diet data is an important step for grounding interpretations (Matthews and Mazumder 2004).

The first goal of this study was to detect whether species varied among lakes in allometric trends of resource use and whether these differences could be explained by resource partitioning both within and among species. By using stable isotope signatures of $\delta^{13}C$ and $\delta^{15}N$, we analyzed relative use of the benthic versus limnetic food chains and trophic positions of fish communities in 11 subarctic lakes in Iceland and Alaska. Our study focused on these sites because both are of similar latitude, have similar postglacial histories, and contain resident Arctic charr *Salvelinus alpinus* and threespine stickleback *Gasterosteus aculeatus*; yet, they differ greatly in species diversity and geological activity. Iceland has relatively depauperate flora and fauna due to the great colonization distance from continental sources (Jónasson et al. 1998). Therefore, we expected that increased interspecific interactions due to greater diversity of the region would reduce intraspecific diversity in Arctic charr, but that generally similar dietary strategies would be conserved between regions.

Second, we analyzed whether resource polymorphism in Arctic charr, the presence of prey fish, or diet of the prey fish affect variability between benthic versus limnetic resource use in Arctic charr resource use. We focus on lakes with Arctic charr and threespine stickleback, because both consume a wide range of resources and may exhibit resource polymorphism, in which morphological differences are associated with differential resource consumption (Robinson and Wilson 1994, Skúlason and Smith 1995). Threespine stickleback are main prey for Arctic charr when present (L'Abée-Lund et al. 1992, Amundssen 1994, Guðbersson 2004), but can also compete for resources with juvenile Arctic charr (Klemetsen et al. 2002). If stickleback are a main food source for Arctic charr, their variability in benthic versus limnetic food chains should be transmitted up the food chain.

Finally, we tested whether dietary breadth, as indicated by ranges in benthic versus limnetic food chain use and trophic position, was

correlated with environmental trends. We expected dietary breadth to increase under conditions of greater limnetic food availability, which could be achieved in 1) deeper lakes that have larger ratios of limnetic : benthic habitats (Wetzel 1990), 2) lakes with a larger surface area, which may yield more diverse prey due to colonization effects and habitat diversity (Post et al. 2000), or 3) lower altitude lakes, since lower terrestrial vegetation at higher latitudes and altitudes reduces limnetic nutrient availability (Pienitz et al. 1997, Edmundson and Mazumder 2002, LaPierre et al. 2003). However, low altitudes are also associated with higher benthic invertebrate abundance and diversity (Malmquist et al. 2000), possibly counteracting any trend of greater availability of limnetic food on a relative scale to benthic availability.

5.2 Methods

5.2.1. Study sites

The study lakes were chosen for access and because they contained resource polymorphism and low species diversity. Thingvallavatn, a large, deep lake, in a geologically young region of Iceland, is mostly spring-fed, and contains four coexisting Arctic charr morphs as well as a productive Arctic charr fishery (Snorrason and Skúlason et al. 2004). Spring-fed lakes tend to be high in nutrient and ion concentrations due to their situation on geologically young, easily erodible postglacial bedrock (Karst-Riddoch et al. 2009). Threespine stickleback have differentiated into two forms in this lake, and travel little between the two protected habitats of macrophyte *Nitella opaca* beds and littoral rocky zones due to predation risk (Kristjánsson et al. 2002). Galtaból, Vestur Friðmundarvatn, Vatnhlíðarvatn, Högnavatn, and Thríhyrningsvatn are all located at high elevations, although their surrounding vegetation and water sources vary. Karst-Riddoch et al. (2009) classified Galtaból and Thríhyrningsvatn as valley lakes, characterized by greater depths, fewer nutrients and dissolved organic carbon (DOC) from less vegetated catchments, and dilute ionic concentrations. Galtaból is also thought to contain two forms of stickleback likewise occupying deeper mud and shallow littoral areas, although little information on dietary differences is available (Jónsson 2002). Vestur Friðmundarvatn was classified as a plateau lake, characterized by a shallow depth and higher nitrogen, ion, and DOC

concentrations due to leaching from poorly drained vegetated (heath) catchments and greater wind-induced resuspension. Judging from the chemical characteristics and heath surroundings of Vatnshlíðarvatn, Sigurðurstaðavatn, and the lakes containing only stickleback (Hólmavatn, Hólsvatn, and Sauravatn), these lakes would likely be included in this category. In addition, although Sigurðurstaðavatn does not appear to be influenced by marine water, as indicated by low conductivity, it is separated from the ocean only by a few meters of a shallow waterfall over a rocky beach that acts as a fish barrier. However, the lake may still be influenced by the marine environment in other manners, such as the transfer of marine nutrients by insects or seabirds and the presence of a normally marine *Gammarus* sp. as a common food for Arctic charr (Chapter 1). Högnavatn was categorized as a direct-runoff lake, which is similar to valley lakes in having low vegetative cover but is warmer and shallower with greater DOC, nitrogen, and ion concentrations.

The Alaskan lakes are all located in southwestern Alaska. Iliamna Lake is the largest lake in Alaska and the Kvichak River catchment, to which it belongs, contains up to 25 resident (non-anadromous) fish species (Kline et al. 1993). The Kvichak River connects Iliamna Lake to Bristol Bay, and its watershed supplies spawning and rearing habitat for one of the most productive Bristol Bay sockeye salmon (*Oncorhynchus nerka*) fisheries. For this reason, Iliamna Lake's ambient $\delta^{15}N$ values are elevated by the influx of marine derived nutrients during annual salmon runs (Kline et al. 1993). Iliamna Lake was sampled at its eastern end at sites near the University of Washington (UW) field camp. Summit Lakes are a set of two small, deep headwater lakes situated ~15 km from Iliamna Lake and ~4 km from the Gulf of Alaska on a dividing mountain pass. Summit Lakes are isolated from Iliamna Lake by a barrier waterfall, so that only the slimy sculpin *Cottus cognatus* and Arctic charr are resident fishes. Summit Lake was also the only Alaskan lake that was surrounded by shrubbery rather than forest. Lower and Upper Tazimina lakes also drain into Iliamna Lake via the Newhalen River. They are relatively large lakes (approx. 12.5 and 12.5 km long, 1.2 and 2.9 km maximum width respectively) in an approx. 900 km^2 forested glacial catchment basin (Russell 1980). The fishes of the Tazimina lakes (Arctic charr, Arctic grayling *Thymallus arcticus*, slimy sculpin, and threespine stickleback), are separated from downstream Sixmile Lake by a large barrier waterfall in the Tazimina River (~30 m

height). Lower Tazimina Lake was sampled at the narrows of the southwestern end. Caribou Lakes are a series of high-elevation small, shallow lakes located at the headwaters of the Koksetna River and surrounded by a combination of forest and tundra in the mountains north of Lake Clark National Park. Little is known about these lakes, but they are fed by a combination of snowmelt and springs. The resident fishes, including Arctic charr, Arctic grayling, the pygmy whitefish *Prosopium coulterii*, and slimy sculpin, are likely separated from more diverse downstream fishes by several sets of rapids along the Koksetna River in the Lake Clark drainage system (Russell et al. 1980). Thus the four Alaskan lakes we sampled are all in the same large drainage basin. It should be emphasized that Iliamna Lake is very large and our sampling cannot be taken to represent the diversity of charr in the entire lake.

5.2.2. Fish sampling and environmental data

Arctic charr were sampled in Icelandic lakes during one sampling event July – September 2009 (Table 5.1) by setting a wide range in mesh sizes from a Lundgren series of 5 – 7 single-strand nylon sinking gill nets in the littoral zone perpendicular to shore, from ca. 2 m depth out- and downwards, and then left either for ~ 2 hr (Vatnhlíðarvatn) or overnight. The gill nets were 25 m long and 1.5 m high with mesh sizes 12.5, 15.5, 19.5, 21.5, 24.0, 29.0, 35.0, 43.0, and 55.0 mm knot to knot. Threespine stickleback were caught with minnow traps in 1 – 2 m water of littoral zones. In Thingvallavatn, stickleback were also caught offshore in minnow traps at ~14 m depth. Environmental data for Icelandic lakes were derived from the Ecological Survey of Icelandic Lakes (ESIL) database (see Malmquist et al. 2000, Karst-Riddoch et al. 2009, and Chapter 1 for details). Environmental data included volume as a hyperbolic sinusoid (HVOL), calculated as 0.43 x maximum depth x surface area (Post et al. 2000); surface area (SA), mean depth (D), surface temperature (ST), altitude (ALT), total nitrogen to total phosphorous ratio (TNTP), and two diversity indices taken from invertebrate surveys of the littoral stone habitat: the Shannon index (SH) and Margalef's D (MD). In the ESIL project, stone habitat invertebrates were sampled from the shallow (0.2 – 0.5 m) rocky littoral habitat at 4 – 6 stations spread around the lakeshore, from which 5 10 – 15 cm stones from 20 – 50 cm depth were taken and

sampled for invertebrates (Malmquist et al. 2000). Details of prey group formation are given in Chapter 1, but abundance of possible prey groups were consolidated as fish (threespine stickleback), snails (*Radix peregra*), unionid pea clams (*Pisidium* spp.), adult aquatic insects, benthic cladocerans, zooplankton, caddisfly larvae (*Limnephilus* and *Apatania* spp.), terrestrial insects, chironomid larvae, aquatic insect pupae, amphipods (*Gammarus* sp.), and tadpole shrimp (*Lepidurus arcticus*).

The Alaskan lakes were sampled August – September 2010 (Table 5.1) but 10 additional Arctic charr were sampled from Summit Lake on 24 August 2009, and data from 16 Arctic charr, 3 Arctic charr fingerling (< 4 cm), 3 sockeye fingerling (< 4 cm), 6 sculpin, and 6 threespine stickleback from Iliamna Lake were included from sampling in June to September 2007-2008 (Denton et al. 2010). Arctic charr and the rainbow trout *Oncorhynchus mykiss* were caught in Iliamna Lake using a combination of angling and beach seining at Fuel Dump Island. As the northern pike *Esox lucius* is difficult to target in Iliamna Lake, it was captured from a small neighboring lake (Stonehouse Lake, positioned only ~10 m from Iliamna Lake shore) that contains no other fish species and included only for descriptive purposes. Arctic charr, Arctic grayling, and pygmy whitefish were collected using 2 – 3 sinking paneled gill nets: the first multifilament net contained sizes of 10, 13, 17, 20, 22, and 24 mm mesh sizes (57 m long x 1.6 m deep), the second monofilament net had mesh sizes 13, 19, 25, 38 and 50 mm mesh sizes (38.1 m long x 1.8 m deep), and the third monofilament net contained 13, 25, 51, and 102 mm mesh sizes (30.5 m long x 1.8 deep). Gill nets were set perpendicular to shore, were additionally set in deeper (~10 m) regions of Summit Lake, and were left overnight. For all lakes, threespine stickleback and slimy sculpin were captured using minnow traps. Physical data for Iliamna Lake were based on data from Kline et al. (1993), and ALT and SA of Summit, Lower Tazimina, and Caribou lakes were estimated using satellite imagery by including all lakes that were connected by less than 1 km. Maximum depth was measured using a depth sounder in Summit Lake and was taken from a survey of Lake Clark National Park for Lower Tazimina and Caribou lakes (Russell, 1980). For Arctic charr, Arctic grayling, and pygmy whitefish captured in 2010, gut contents were analyzed by sorting and categorizing prey contents as fish (various stickleback species for Iliamna Lake, slimy sculpin for all others), snails, pea clams, cinereus shrew, aquatic insect

pupae, terrestrial insects (including culicid larvae), caddisfly larvae, chironomid larvae, or zooplankton.

For all Arctic charr, Arctic grayling, pygmy whitefish, and threespine stickleback, pictures were taken from which standard lengths (threespine stickleback) and fork lengths (all others) were measured using ImageJ v. 1.44o. For Arctic charr, sex and maturity status, categorized either as categorized either as juvenile (no development in gonads: ovaries < 1/3 body length and eggs < 1 mm diameter; no development in testes) or mature (any evidence of current or past gonadal development: lengthening of ovaries or increase in egg size; thickening of testes), were checked to aid in the assignment of individuals to different forms in polymorphic lakes.

Past studies have established the presence of polymorphism in lakes under study in Iceland (Jónsson and Skúlason 2000, Jónsson 2002, Chapter 3) and Alaska (Chapter 4). For Icelandic lakes known to be polymorphic, morphs were assigned visually according to a combination of pictures and maturity status at small sizes. In all cases, the first form was either more limnetic or piscivorous, and the second form reflected a benthic specialist, typically smaller and with a more subterminal mouth and deeper maxilla. Morph assignment in Icelandic lakes was based on Chapter 4.

Table 5.1. Location, sampling date, environmental variables, and baseline values of δ15N and δ13C used for the limnetic and benthic food chains in stable isotope studies. Lake numbers correspond with those in the ESIL database. The environmental variables include altitude (ALT), surface temperature (ST), surface area (SA), max depth (MAX), mean depth (D), ratio total nitrogen to total phosphorous (TNTP), and stone habitat benthic invertebrate diversity as measured by the indices Margalef's D (MD) and Shannon index (SH). When a base group is listed alone, it was used for both δ15N and δ13C; otherwise, A (& B) indicates that A only was used for δ15N and the average of A and B was used for δ13C, and A / B indicates that A only was used for δ15N and B only was used for C δ13C. Groups included copepods (Cop), cladocerans (Clad), pea clams (Mus), snails (Snail), chironomid larvae (Chir), stickleback (ST), and Arctic charr (AC).

													Limnetic base			Benthic base		
Lake	No.	Latitude	Longitude	Date	ALT	ST	SA	MAX	D	TNTP	MD	SH	$\delta^{15}N$	$\delta^{13}C$	Group	$\delta^{15}N$	$\delta^{13}C$	Group
Hólmavatn	25	65.15	20.93333	26-Jul-10	490	6.8	0.6	3	1.5	23.57	-	-	7.3	-25.81	Cop	0.54	-11.02	Snail / ST
Hólsvatn	55	64.51667	22.13333	30-Jul-10	14	10	1.4	1.5	0.8	20.26	-	-	5.57	-23.4	Cop / ST	2.85	-22.22	Snail / ST
Sauravatn	56	64.66667	22.11667	30-Jul-10	35	10.2	0.8	0.6	0.3	19.76	-	-	3.44	-27.46	Mus / ST	0.45	-24.47	Snail (& Chir)
Vatnhlíðarvatn	21	65.51667	19.63333	17-Jul-10	280	9.5	0.7	4	2	16.18	1.65	1.64	3.39	-25.94	Clad (& Cop)	3.43	-20.52	Snail (& Chir)
Högnavatn	37	65.8	22.16667	13-Aug-10	410	7.4	0.3	3	2	12	1.33	0.86	-0.14	-23.96	Clad (& Cop)	1.56	-14.92	Snail (& Chir)
Thríhyrningsvatn	65	65.16667	15.76667	7-Sep-10	570	11.4	3.6	33	10	9	1.23	1.39	1.51	-30.47	Clad (& Cop)	0.22	-15.98	Snail / AC
Galtaból	4	65.25	19.71667	27-28 Aug 2010	450	9.9	1.2	10	4.1	20.14	1.11	1.43	6.53	-23.63	Cop	2.4	-10.81	Snail / AC
Sigurðurstaðavatn	14	66.48333	16.3	21-22 July 2010	0	8	2	3	1.3	23	1.93	1.57	-0.89	-19.97	Clad	0.95	-14.12	Snail / AC
V. Friðmundarvatn	22	65.3	14.68333	15-Sep-10	441	9	6	2.3	1.2	12.41	1.7	1.38	2.38	-26.25	Mus	-0.44	-16.69	Snail / AC
Thingvallavatn	-	64.16667	21.1333	1-5 Sept 2010	100	10	84	114	34	1.75	-	-	4.61	-33.56	Cop / AC	-0.01	-8.23	Snail / AC
Summit Lake	-	59.70413	-153.68639	20-21 Aug 2010	152	-	0.6	20	-	-	-	-	2.2	-31.69	Clad	1.99	-16.87	Snail / AC
Caribou Lake	-	60.45012	-154.62968	8-Dec-10	550	-	1.2	5	-	-	-	-	3.82	-32.63	Clad	4.49	-16.29	Snail / AC
L. Tazimina Lake	-	59.96206	-154.5554	6-Dec-10	194	-	520	20	-	-	-	-	1.74	-33.34	Clad	0.38	-13.65	Snail
Iliamna Lake	-	59.7375	154.20806	23-30 Aug 2010	14	-	2622	393	-	-	-	-	5.51	-29.73	Clad	3.49	-10.27	Snail / AC

Dorsal muscle plugs were taken for stable isotope analyses of all species except rainbow trout, from which caudal fin clips were taken, and northern pike, from which caudal muscle plugs were taken. For both Alaskan and Icelandic lakes, littoral stone and mud habitats (>1 m deep) were scoured for benthic invertebrate samples to be used as baseline values for stable isotope analyses, and zooplankton samples were taken using 125 μ plankton tow net in Iceland and a 153 μ tow net in Alaska. Tows were vertical unless limitations due to shallow depths required horizontal towing. Zooplankton were left in lake water for at least 3 hours and benthic invertebrates were left overnight to clear guts before being sampled. All samples from Iceland were preserved in 95% EtOH for a few weeks, whereas all samples from Alaska were frozen. Both were dried at 50° C, crushed, and sent to University of California (UC) Davis Stable Isotope Facility for analysis of natural levels of $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios using a Europa Hydra 20/20 continuous flow isotope ratio mass spectrometer. Ratios are expressed as parts per thousand difference relative to the international standard: $\delta = 1000 * (R_{sample} - R_{standard}) / R_{standard}$, where R is the ratio of the heavier, more rare isotope (^{13}C or ^{15}N) over the common isotope (^{12}C or ^{14}N). The international standard ratios based on V-PDB (Vienna Pee-Dee belemnite) carbon and atmospheric nitrogen were used for $R_{standard}$. Nylon, peach leaf, glutamic acid, and enriched glutamic acid standards were used to calibrate the spectrophotometer against NIST Reference Materials and indicated machine standard deviation as < 0.20 for ^{13}C and < 0.50 for ^{15}N. For each species whose guts were examined, frequency of occurrence was calculated for each prey category and consolidated for comparison with stable isotope analyses (Table 5.2).

5.2.3. Stable isotope analysis

Before statistical analyses, stable isotope values were 1) corrected for ethanol preservation (Icelandic samples only), 2) corrected for the reduced ability of small fish muscle tissue to reflect whole-body values, and 3) normalized for lipid content. For the first step, Icelandic stickleback samples were corrected for ethanol preservation according to the mean difference between samples preserved in ethanol or not ($\delta^{13}C$: -0.45, $\delta^{15}N$: -0.07; Vander Zanden et al. 2003). Icelandic Arctic charr samples were corrected by using a linear relationship with length found for Arctic charr by Kelly et al. (2006), but predicted values for the

maximum and minimum lengths of their Arctic charr were used to correct individuals above (-0.27 and -0.49) and below (-1.07 and -0.23) the length range of their data, respectively. The $\delta^{13}C$ and $\delta^{15}N$ for Icelandic aquatic invertebrate samples were adjusted for ethanol preservation using mean parameters calculated for aquatic invertebrates by Ventura and Jeppesen et al. (2009). For the second step, all stickleback, sculpin, and sockeye $\delta^{15}N$ values < 9 cm length were reduced by 0.32 according to Schielke and Post (2010). For the third step, all fish were normalized for lipid content according to Kiljuenen et al. (2006), but as they found no relationship in invertebrates, no adjustment was made.

Methods for correcting $\delta^{13}C$ and $\delta^{15}N$ values for variability at the base of the food chain is imperative for meaningful comparisons at higher trophic positions among study sites (Vander Zanden and Rasmussen 1999, Vander Zanden and Rasmussen 2001, Post et al. 2002). To calculate trophic position (TP) while taking into account baseline values, we used the following common mixture model: $TP_{sc} = \lambda_{base1} \times a + \lambda_{base2} \times (1 - a) + (\delta^{15}N_{sc} - [\delta^{15}N_{base1} \times a + (\delta^{15}N_{base2} \times (1 - a)])$. In this case, λ_{base1} and λ_{base2} are the trophic positions of the samples $\delta^{15}N_{base1}$ and $\delta^{15}N_{base2}$ used to calculate the bases of the first and second food chains (e.g., limnetic and benthic), $\delta^{15}N_{sc}$ is the sample from the secondary consumer whose TP is being calculated, and *a* represents the proportion of food chain 1 that contributes to the diet. Values for $\delta^{13}C$ can then be used to estimate *a* as $(\delta^{13}C_{sc} - \delta^{13}C_{base2}) / (\delta^{13}C_{base1} - \delta^{13}C_{base2})$, leaving 4 parameters necessary for the calculation of TP for secondary consumers: $\delta^{15}N_{base1}$, $\delta^{15}N_{base2}$, $\delta^{13}C_{base1}$, and $\delta^{13}C_{base2}$. To estimate these parameters, we sampled as many invertebrate groups as could be found, and then chose bases as the groups that gave the most consistently low $\delta^{15}N$ value or extreme $\delta^{13}C$ values. Snails and chironomid larvae from the subfamily Orthocladiinae or the tribe Tanytarsini had the most consistently high values of $\delta^{13}C$, so these values were averaged when available as the base for benthic food chain (Table 5.1, Fig 5.1). These chironomids consistently had higher $\delta^{15}N$ than snails, so only snails were used for the $\delta^{15}N$ base value. Likewise, when both copepods and cladocerans were available in large enough quantities, they consistently showed similar low $\delta^{13}C$ values, but copepods always had a substantially higher $\delta^{15}N$ value.

Table 5.2. Frequency of occurrence for Arctic charr (AC), Arctic grayling (AG), and pygmy whitefish (PW) of the prey items fish (Fis), snails (Sna), pea clams (Mus), aquatic adult insects (Aqu), benthic cladocerans (Ben), zooplankton (Zoo), caddisfly larvae (Cad), terrestrial adult insects (Ter), chironomid larvae (Chi), aquatic insect pupae (Pup), amphipod (Amp), tadpole shrimp (Tad), and cinereus shrew (Shr) in each lake. Values > 0.2 are in bold. Data from Iliamna Lake are taken from Denton et al. (2010).

	Lake	Fis.	Sna.	Cla.	Aqu.	Ben.	Zoo.	Cad.	Ter.	Chi.	Pup.	Gam.	Lep.	Shr.
	V. Friðmundarvatn	**0.59**	0.00	**0.22**	0.00	0.01	0.01	0.00	0.05	0.16	**0.28**	0.00	0.00	0.00
	Högnavatn	0.01	0.18	**0.35**	0.00	0.09	0.03	**0.25**	0.02	**0.65**	0.03	0.00	**0.77**	0.00
	Thríhyrningsvatn	0.00	**0.37**	**0.24**	0.01	0.00	0.13	0.00	0.08	0.17	**0.28**	0.00	0.09	0.00
	Galtaból	**0.64**	**0.64**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Sigurðurstaðavatn	**0.72**	0.19	0.00	0.01	0.13	0.06	0.00	0.03	0.19	0.06	0.06	0.00	0.00
AC	Vatnhlíðarvatn	0.00	0.11	**0.27**	0.00	**0.27**	0.02	0.00	0.03	**0.65**	0.00	0.00	0.00	0.00
	Thingvallavatn	0.19	**0.46**	0.00	0.01	0.01	0.04	0.04	0.05	0.16	**0.48**	0.00	0.00	0.00
	Iliamna Lake	**0.50**	**0.38**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Summit Lake	0.02	**0.29**	**0.22**	0.00	0.00	0.04	0.07	**0.42**	0.00	**0.78**	0.00	0.00	0.05
	Caribou Lake	0.08	**0.71**	**0.58**	0.00	0.00	0.04	0.13	0.00	0.00	0.00	0.00	0.00	0.00
	L. Tazimina Lake	0.00	**0.26**	0.09	0.00	0.00	**0.35**	0.00	0.04	0.00	0.09	0.00	0.00	0.00
AG	Caribou Lake	0.00	**0.36**	0.00	0.00	0.00	**0.36**	0.18	0.00	0.00	0.18	0.00	0.00	0.00
	L. Tazimina Lake	0.00	0.00	0.00	0.00	0.00	0.00	**0.25**	0.00	0.00	0.00	0.00	0.00	0.00
PW	Caribou Lake	0.00	0.00	0.00	0.00	0.00	**0.48**	0.00	0.00	**0.56**	0.00	0.00	0.00	0.00

Therefore, the average of these was used for the $\delta^{13}C$ base of the limnetic food chain, but only cladocerans were used for the $\delta^{15}N$ base. For lakes in which cladocerans could not be sampled, another species was needed for the $\delta^{15}N$ base. Therefore, average trophic positions of copepods or pea clams (actually small unionid mussels) were calculated across all lakes in which cladocerans were available as the $\delta^{15}N$ baseline. Their values and trophic positions (3.180 and 2.894 respectively) were then used as the limnetic $\delta^{15}N$ base values for lakes lacking cladoceran samples. Copepods were preferred because they had consistently lower $\delta^{13}C$ values than pea clams, suggesting that they were less influenced by benthic carbon sources (Fig. 5.1). In some instances, the maximum and minimum $\delta^{13}C$ values from invertebrates were not as extreme as values found for Arctic charr or stickleback, so we assumed that our invertebrate sampling was insufficient and instead used the extreme values for Arctic charr or stickleback.

Using these base values, with food chain 1 as benthic and food chain 2 as limnetic, we calculated TP and *a*, which reflects the proportion of carbon from the benthic food chain consumed (BFC), and used them to compare fish diets across lakes. Although fractionation of $\delta^{13}C$ values was assumed to be 0 in this procedure, the effect of this assumption being false was illustrated. Lines were drawn in figures to indicate the expected shifts in TP given BFC and a fractionation of 1‰ per trophic level when correcting for $\delta^{13}C$ after the calculation of TP. All statistical analyses were performed separately on Icelandic and Alaskan lakes using R v. 2.13.0 (R Development Core Team, 2011).

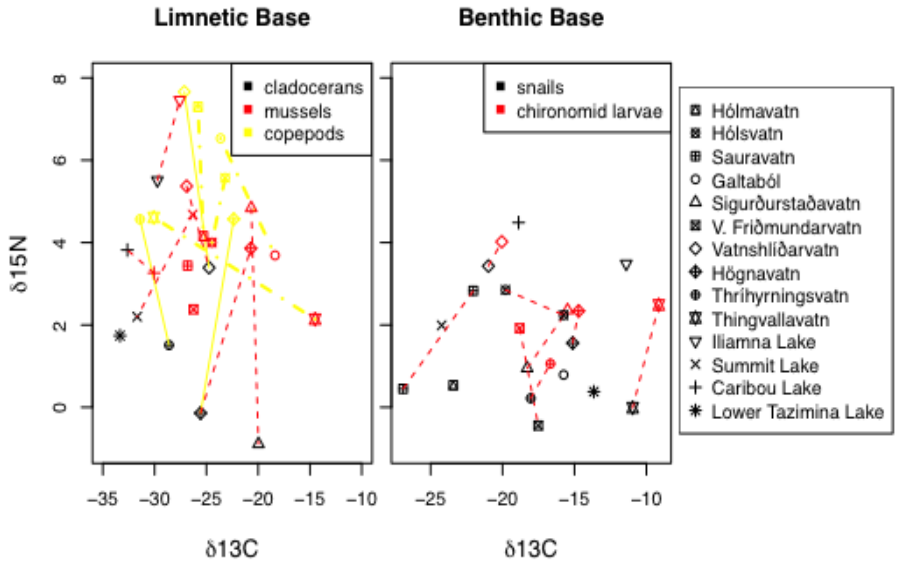


Figure 5.1. Potential baseline values for the limnetic and benthic food chains. Lines connect groups within lakes when > 1 group was available. Because three groups were considered on the left, three connections were possible: light grey solid lines connect copepods and cladocerans, dashed dark grey lines connect mussels and cladocerans, and light dash-dot lines connect copepods with mussels within lakes.

5.2.4. Variation in food web structure among lakes

Analyses of variance (ANOVA) were used to test whether variation attributable to lake, length, or their interaction could be detected in TP and BFC of Arctic charr, threespine stickleback, and Arctic grayling. Only lakes with more than three samples of a species were included. If the interaction was not significant, it was removed. Brown trout and

pygmy whitefish each only occurred in a single lake, so only length was tested.

To test for differences among species within lakes, species were first split into 3 size groups (< 20, [20, 30), or ≥ 30 cm) to account for allometric variation. Arctic charr were additionally split by assigned form. Linear models were used to predict TP and BFC based on species x form x size group. Large Arctic charr were used as the baseline for all lakes except Icelandic lakes with no stickleback present. As no large Arctic charr occurred in these lakes, the medium group was used as baseline. Coefficient values were compiled for comparison.

5.2.5. Effects of polymorphism, prey diet, and environment on Arctic charr dietary breadth

Range in BFC values was used to reflect Arctic charr dietary breadth, yielding a single value per lake. Arctic charr in the smallest size group were excluded to prevent ontogenetic niche changes from affecting results. Linear models were used to test whether Arctic charr a) BFC range and b) TP range were significantly affected by 1) the presence of overall polymorphism in Arctic charr, 2) the presence of growth rate differentiation as a type of polymorphism in Arctic charr, 3) the presence of morphological differentiation as another type of polymorphism in Arctic charr, 4) the presence of stickleback in the lake, 5) stickleback range in BFC, 6) stickleback mean BFC, and 4) environmental variables, transformed by log when necessary (log HVOL, log SA, log D, TNTP, ST, ALT, SH, MD).

5.3 Results

5.3.1. Variation in food web structure among lakes

In all cases, only a minimum shift in TP given BFC would have resulted when assuming a 1‰ $\delta^{13}C$ trophic fractionation, rather than 0‰ (Fig. 5.2). When a prey species was both frequently eaten and uncommon among lakes (Table 5.2), they were plotted with fish to aid in interpretation of fish stable isotope data (Fig. 5.2). Proportion of benthic food chain consumed (BFC) differed among lakes in all species for which it could be tested (ST: $F_{8,235} = 27.996$, $P<0.001$; AC: $F_{10,464} =$

19.688, P <0.001; AG: $F_{1,23}$ = 5.937, P = 0.0230). Length was significantly correlated with BFC in threespine stickleback ("stickleback" from here forward) and had an interactive effect with Lake in Arctic charr, indicating that the slope differed among lakes (ST: $F_{8,235}$ = 80.634, P < 0.001; AC length: $F_{1,464}$ = 3.122, P = 0.078; AC interaction: $F_{10,464}$ = 9.347, P < 0.001). These effects were significant in no other species (AG: $F_{1,23}$ = 0.105, P = 0.749, BT: $F_{1,11}$ = 0.5211, P = 0.485; PW: $F_{1,23}$ = 0.002, P = 0.970). Trophic position (TP) also differed among lakes in all species for which it could be tested (ST: $F_{8,235}$ = 80.634, P < 0.001; AC: $F_{10,474}$ = 38.635, P < 0.001; AG: $F_{1,23}$ = 83.385, P<0.001). Length was significantly correlated with TP for all species but the two smallest, stickleback and pygmy whitefish (TP: ST: $F_{1,235}$ = 0.00, P = 0.995; AC: $F_{1,474}$ = 157.449, P<0.001; AG: $F_{1,23}$ = 5.032, P = 0.035; BT: F1,11 = 10.734, P = 0.007; PW: $F_{1,23}$ = 0.037, P = 0.849).

In the linear models used to test for differences in proportion of benthic food chain consumed (BFC) among species x form x size bracket combinations, we found that differences among species were widespread, although some lakes showed no significance (Thingvallavatn: $F_{12,15}$ = 19.100, P < 0.001; Galtaból: $F_{5,77}$ = 1.862, P= 0.111; Sigurðurstaðavan: $F_{3,56}$ = 4.542, P = 0.006; Vatnshlíðarvatn: $F_{3,40}$ = 4.103, P = 0.013; Vestur Friðmundarvatn: $F_{3,60}$ = 12.7, P < 0.001; Högnavatn: $F_{2,45}$ = 1.354, P = 0.269; Thríhyrningsvatn: $F_{3,39}$ = 4.162, P = 0.012; Iliamna Lake: $F_{8,44}$ = 12.140, P < 0.001; Summit Lake: $F_{2,54}$ = 2.579, P = 0.085; Caribou Lake: $F_{6,66}$ = 12.260, P< 0.001; Tazimina Lake: $F_{5,27}$ = 28.610, P < 0.001). All linear models used to test for differences in trophic position (TP) among species x form x size bracket combinations were significant, except in lakes with only Arctic charr present (Thingvallavatn: $F_{12,159}$ = 10.580, P < 0.001; Galtaból: $F_{5,77}$ = 14.500, P < 0.001; Sigurðurstaðavatn: $F_{3,56}$ = 8.481, P < 0.001; Vestur Friðmundarvatn: $F_{3,60}$ = 36.740, P < 0.001; Vantshlíðarvatn: $F_{3,40}$ = 0.381, P = 0.767; Högnavatn: $F_{2,45}$ = 2.688, P = 0.079; Thríhyrningsvatn: $F_{3,39}$ = 2.062, P = 0.121; Iliamna Lake: $F_{8,44}$ = 11.49, P < 0.001; Summit Lake: $F_{2,54}$ = 8.063, P < 0.001; Caribou Lake: $F_{6,66}$ = 44.001, P < 0.001; Tazimina Lake: $F_{5,27}$ = 18.89, P = 0.451). Coefficients resulting from these models were used to interpret food web structure depicted by stable isotope data in Figure 5.2 (Table 5.2).

Over all Icelandic lakes, small or medium sized Arctic charr and stickleback were lower in trophic position than large piscivorous Arctic

charr (Table 5.3, Fig. 5.2). The similar coefficient values of small- and medium-sized Arctic charr to stickleback indicated similar trophic positions. Of the three Icelandic lakes that contained stickleback, Galtaból was the only polymorphic lake. The model to predict BFC was not significant, indicating minimal differences among groups (Table 5.3). Differences between species are likely minimal because both Arctic charr and stickleback consumed a wide range in BFC values (Fig. 5.2). The other two lakes with stickleback present (Sigurðurstaðavatn and Vestur Friðmundarvatn) also showed no difference between stickleback and piscivorous Arctic charr in BFC. The central position of *Gammarus* sp. beneath most Arctic charr in Sigurðurstaðavatn confirmed that this is an important prey, as indicated by high occurrence in the diet (Table 5.2). Both these lakes contain smaller individuals with limnetic signals, possibly indicating an ontogenetic shift.

Of the Icelandic lakes with no stickleback present (Table 5.3), two contained a second Arctic charr form that consumed more from the benthic food chain, especially at larger sizes (Vatnshlíðarvatn and Thríhyrningsvatn). The last lake (Högnavatn) contained a small form with a different growth curve (Chapter 3), but this form did not differ from larger fish in BFC. The central position of the tadpole shrimp beneath most Högnavatn Arctic charr also suggested that this species is an important component of the diet, as confirmed by the diet (Table 5.1). No groups differed in trophic position within these lakes (Table 5.2, Fig. 5.2).

In Thingvallavatn, four substantially differentiated Arctic charr morphs coexisted with stickleback and brown trout, which overall, consumed more benthic resources than the large piscivorous Arctic charr (Table 5.4). Stickleback caught in ~14 m versus ~1 – 2 m depth did not overlap in either BFC or TP: those caught deep had higher TP and lower BFC (Fig. 5.3). These differences appear to be transmitted to higher trophic positions in the fish that are most likely to consume them: piscivorous Arctic charr had lower BFC but higher TP than brown trout, which occur generally in littoral areas and were likewise confined to higher (more benthic) BFC values. As expected, the zooplanktivorous form fed more limnetically than the large piscivorous form, although results were only significant for the small size bracket. This is not surprising given that the piscivorous form is thought to develop from larger zooplanktivorous individuals (Skúlason et al. 1989), and that the large zooplanktivorous individuals are difficult to distinguish from

piscivorous forms. Medium and large piscivorous fish could not be distinguished by BFC, but all other groups except the zooplanktivorous groups fed more benthically (Fig. 5.2). Likewise, all other groups but the large brown trout and large zooplanktivorous form had lower trophic positions.

Stickleback and piscivorous Arctic charr in Iliamna Lake had a generally limnetic stable isotope signature (Table 5.5, Fig. 5.2). Sockeye fingerling, stickleback, and the small bracket of Arctic charr (fingerling, entirely < 4 cm) showed a similarly low TP, but BFC in Arctic charr fingerling was higher. Therefore, large Iliamna Arctic charr appeared to similarly specialize on stickleback, as diet data support (Table 5.2). Sculpin showed a highly benthic, middle trophic level signal, and rainbow trout showed a similar but slightly higher trophic level signal, potentially indicating a tendency toward piscivory through specialization on benthic prey. This mirrors the pattern found when Arctic charr co-occurred with brown trout in Thingvallavatn, although our samples are limited. Pike had a relatively high trophic level despite the lack of fish prey in their lake, but results should be interpreted with caution as baseline correction may be incorrect for this species. Iliamna Lake pygmy whitefish showed a high TP and low BFC value, but stomachs were not examined.

Lower Tazimina Lake contained Arctic charr of a relatively high trophic level, but in contrast with Iliamna Lake, these Arctic charr had a stronger benthic signal (Table 5.5, Fig. 5.2). Therefore, Arctic charr in L. Tazimina Lake more strongly resemble European Arctic charr that may consume some fish alongside their mainly benthic feeding habits, as is found in large benthic form in Thingvallavatn or Loch Rannoch and Loch Ericht in Scotland (Adams et al. 1998, Fraser et al. 1998). However, little was found in the stomachs of large Arctic charr to confirm this. Smaller fish of both forms in L. Tazimina Lake ate zooplankton (Chapter 4), although the limnetic form had a more extreme limnetic signal (Fig. 5.2).

Table 5.3. Coefficient value estimates, T statistics, and P-values for linear models with species x form x size groups used to predict either proportion of carbon from benthic food chain consumed (BFC) or trophic position (TP) in Icelandic lakes with stickleback present (Stick. Pres.) versus absent (Stick. Abs.). Values for intercepts (Int.) are shown as well as groups, designated by species (Arctic charr: AC; stickleback: ST), form (1- or 2-) and size bracket (S: < 20, M: [20, 30), L: ≥ 30 cm).

			Vatnshlíðarvatn			Högnavatn			Thríhyrningsvatn		
			Est.	T	P	Est.	T	P	Est.	T	P
BFC	Stick. Abs.	Int.	0.63	23.18	0.00	0.70	27.04	0.00	0.43	8.07	0.00
		AC 1-S	-0.12	-1.19	0.24	0.01	0.45	0.65	-0.18	-1.77	0.09
		AC 2-M	0.13	3.00	0.00	-	-	-	0.15	1.95	0.06
		AC 2-S	-0.04	-0.27	0.79	0.05	1.49	0.14	-0.13	-0.99	0.33
			Galtaból			Sigurðurstaðavatn			V. Friðmunarvatn		
	Stick. Pres.	Int.	0.40	7.64	0.00	0.60	18.86	0.00	0.86	42.91	0.00
		AC 1-M	0.08	0.89	0.37	-0.05	-1.00	0.32	-0.06	-1.88	0.06
		AC 1-S	0.10	1.21	0.23	-0.47	-3.62	0.00	-0.16	-5.47	0.00
		AC 2-M	0.06	0.59	0.56	-	-	-	-	-	-
		AC 2-S	0.19	2.56	0.01	-	-	-	-	-	-
		ST	0.16	2.56	0.01	-0.06	-1.42	0.16	-0.01	-0.29	0.77
			Vatnshlíðarvatn			Högnavatn			Thríhyrningsvatn		
TP	Stick. Abs.	Int.	3.28	109.8	0.00	3.60	60.15	0.00	3.45	66.51	0.00
		AC 1-S	-0.11	-1.01	0.32	-0.16	-2.13	0.04	-0.10	-0.97	0.34
		AC 2-M	-0.02	-0.50	0.62	-	-	-	0.09	1.19	0.24
		AC 2-S	-0.03	-0.23	0.82	-0.16	-2.09	0.04	-0.18	-1.35	0.18
			Galtaból			Sigurðurstaðavatn			V. Friðmunarvatn		
	Stick. Pres.	Int.	3.88	67.72	0.00	4.49	59.11	0.00	4.49	85.67	0.00
		AC 1-M	-0.56	-6.08	0.00	-0.38	-3.33	0.00	-0.58	-7.08	0.00
		AC 1-S	-0.60	-6.41	0.00	-0.27	-0.87	0.39	-0.73	-9.56	0.00
		AC 2-M	-0.49	-4.48	0.00	-	-	-	-	-	-
		AC 2-S	-0.55	-6.90	0.00	-	-	-	-	-	-
		ST	-0.49	-7.29	0.00	-0.47	-4.99	0.00	-0.58	-8.10	0.00

This pattern confirms both an ontogentic shift of the larger form and specialization by the limnetic form. Interestingly, stickleback do not appear to be prey in L. Tazimina Lake, as they had substantially lower BFC than the larger Arctic charr. Arctic grayling consumed a large

amount of terrestrial insects in both L. Tazimina Lake and Caribou Lake, but snails and zooplankton were additionally prominent in Caribou Lake, sometimes composing the majority of the gut contents (Table 5.2). This likely explains the much lower trophic level of Arctic grayling in Caribou Lake versus L. Tazimina Lake (Fig. 5.2). Arctic charr diets in Caribou Lake were entirely composed of snails, pea clams, caddisfly, or sculpin, thereby explaining the high BFC values (Table 5.2). In contrast, pygmy whitefish in Caribou Lake consumed entirely zooplankton and chironomid larvae, reflected by lower BFC values.

Table 5.4. Coefficient value estimates, T statistics, and P-values for linear models with species x form x size bracket groups used to predict either proportion of carbon from benthic food chain consumed (BFC) or trophic position (TP) in Thingvallavatn. Values for intercepts (Int.) are shown as well as groups, designated by species (Arctic charr: AC; stickleback: ST; brown trout: BT), form (1- or 2-) and size bracket (S: < 20; M: [20, 30); L: ≥ 30 cm).

		Thingvallavatn					
		Est.	T	P	Est.	T	P
BFC	Int.	0.57	9.32	0.00	4.66	44.27	0.00
	AC 1-M	0.14	1.65	0.10	-0.53	-3.54	0.00
	AC 2-M	0.31	2.79	0.01	-1.01	-5.25	0.00
	AC 2-S	0.27	4.05	0.00	-0.95	-8.14	0.00
	AC 3-L	-0.03	-0.19	0.85	-0.10	-0.34	0.73
	AC 3-M	-0.14	-1.79	0.08	-0.67	-5.03	0.00
	AC 3-S	-0.40	-5.17	0.00	-1.03	-7.68	0.00
	AC 4-L	0.25	3.21	0.00	-1.21	-9.15	0.00
	AC 4-M	0.26	3.31	0.00	-1.00	-7.46	0.00
	ST	0.23	3.57	0.00	-0.83	-7.52	0.00
	BT L	0.31	2.37	0.02	-0.40	-1.78	0.08
	BT M	0.29	2.88	0.00	-0.69	-3.98	0.00
	BT S	0.29	3.38	0.00	-0.89	-5.97	0.00

TP

Table 5.5. Coefficient value estimates, T statistics, and P-values for linear models with species x form x size bracket groups used to predict either proportion of carbon from benthic food chain consumed (BFC) or trophic position (TP) in Alaskan lakes. Values for intercepts (Int.) are shown as well as groups, designated by species (Arctic charr: AC; stickleback: ST; Arctic grayling: AG; northern pike: PI; pygmy whitefish: PW; rainbow trout: RT; sockeye fingerlings: SS; sculpin: SC), form (1- or 2-) and size bracket (S: < 20, M: [20, 30), L: ≥ 30 cm).

		Summit Lake			Caribou Lake			L. Tazimina Lake			Iliamna Lake		
		Est.	T	P	Est.	T	P	Est.	T	P	Est.	T	P
BFC	Int.	0.46	6.57	0.00	0.75	27.97	0.00	0.81	24.86	0.00	0.39	12.48	0.00
	AC 1-M	0.06	0.88	0.38	-0.10	-1.06	0.29	-0.31	-5.13	0.00	0.15	3.09	0.00
	AC 1-S	-	-	-	-	-	-	-	-	-	0.21	3.02	0.00
	AC 2-S	-	-	-	-	-	-	-0.60	-10.6	0.00	-	-	-
	AG L	-	-	-	-0.13	-2.03	0.05	-	-	-	-	-	-
	AG M	-	-	-	-0.11	-1.80	0.08	-	-	-	-	-	-
	AG S	-	-	-	-0.10	-2.33	0.02	-0.28	-4.22	0.00	-	-	-
	PI	-	-	-	-	-	-	-	-	-	-0.07	-0.80	0.43
	PW	-	-	-	-0.28	-7.56	0.00	-	-	-	0.08	0.83	0.41
	RT	-	-	-	-	-	-	-	-	-	0.33	3.53	0.00
	SS	-	-	-	-	-	-	-	-	-	-0.14	-1.74	0.09
	SC	0.29	2.25	0.03	0.21	2.28	0.03	0.08	1.21	0.24	0.46	7.67	0.00
	ST	-	-	-	-	-	-	-0.20	-2.36	0.03	-0.07	-1.15	0.26
TP	Int.	3.13	25.33	0.00	3.53	89.22	0.00	3.87	63.05	0.00	3.96	41.97	0.00
	AC 1-M	0.32	2.46	0.02	-0.63	-4.58	0.00	-0.03	-0.26	0.80	0.25	1.71	0.09
	AC 1-S	-	-	-	-	-	-	-	-	-	-0.72	-3.41	0.00
	AC 2-S	-	-	-	-	-	-	0.03	0.24	0.82	-	-	-
	AG L	-	-	-	-0.57	-6.18	0.00	-	-	-	-	-	-
	AG M	-	-	-	-0.57	-6.25	0.00	-	-	-	-	-	-
	AG S	-	-	-	-0.55	-8.33	0.00	0.03	0.24	0.81	-	-	-
	PI	-	-	-	-	-	-	-	-	-	0.34	1.19	0.24
	PW	-	-	-	0.27	4.93	0.00	-	-	-	0.65	2.31	0.03
	RT	-	-	-	-	-	-	-	-	-	0.01	0.04	0.97
	SS	-	-	-	-	-	-	-	-	-	-0.49	-2.07	0.04
	SC	-0.34	-1.47	0.15	-0.45	-3.25	0.00	0.04	0.34	0.73	-0.50	-2.75	0.01
	ST	-	-	-	-	-	-	0.34	2.09	0.05	-1.21	-6.69	0.00

Arctic charr in Summit Lake consumed a wide range of benthic and limnetic resources as well as terrestrial insects, showed no differences among sizes or species in BFC, and had trophic positions similar to those in lakes with no prey fish available in Iceland. However, the lower trophic positions of potential prey (sculpin and cinereus shrew) indicated that these Arctic charr may sometimes eat these vertebrates (Fig. 5.2, Table 5.2).

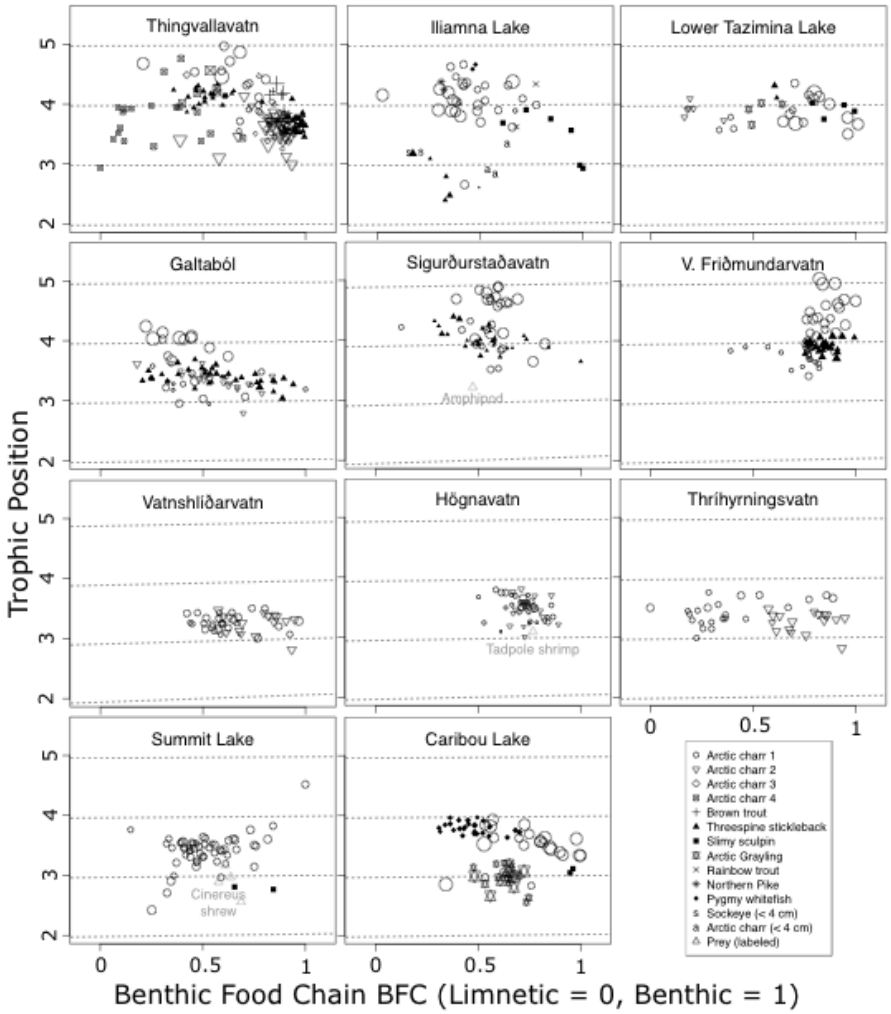


Figure 5.2. Food web structure of fish assemblages in Icelandic and Alaskan Lake as indicated by trophic position (TP) and proportion of carbon from the benthic food chain consumed (BFC). Size of points are proportional to individual sizes in all species represented by > 3 individuals in a lake. Arctic charr are split by form (1 – 4) and fingerlings (< 4 cm) are indicated. Lines indicate the shift in TP with BFC that would occur if $\delta^{13}C$ fractionation were assumed to be 1‰ instead of 0‰ and corrected after the described TP calculation.

5.3.2. Effects of prey diet, polymorphism, and environment on Arctic charr dietary breadth

The presence of stickleback did not affect the range of BFC for Arctic charr in either Iceland ($F_{1,5}$ = 0.041, P = 0.848) or Alaska ($F_{1,2}$ = 0.150, P = 0.736). When the effects of stickleback mean and range of BFC

were tested, neither were significant (mean BFC: $F_{1,2}$ = 0.321, P = 0.628; range BFC: $F_{1,2}$ = 1.549, P = 0.339). Polymorphism had no effect ($F_{1,5}$ = 1.559, P = 0.267), nor did growth rate differentiation ($F_{1,5}$ = 0.004, P = 0.953), but morphological differentiation yielded a significantly higher BFC range in Icelandic Arctic charr ($F_{1,5}$ = 7.19, P = 0.044).

The presence of stickleback affected Arctic charr TP range in Iceland ($F_{1,5}$ = 18.79, P = 0.007) but not Alaska ($F_{1,2}$ = 0.052, P = 0.841). Neither effects of stickleback mean nor range of BFC were significant (mean BFC: $F_{1,2}$ = 0.028, P = 0.884; range BFC: $F_{1,2}$ = 0.288, P = 0.645). Polymorphism had no effect ($F_{1,5}$ = 0.565, P = 0.486), and neither did growth rate differentiation ($F_{1,5}$ = 0.451, P = 0.532) nor morphological differentiation in Icelandic Arctic charr ($F_{1,5}$ = 0.043, P = 0.844).

In linear models predicting Arctic charr BFC range using environmental variables in Icelandic lakes, log HVOL ($F_{1,5}$ = 5.232, P = 0.071), log SA ($F_{1,5}$ = 1.737, P = 0.245), ALT ($F_{1,5}$ = 0.028, P = 0.873), TNTP ($F_{1,5}$ = 1.024, P = 0.36), and both the Shannon index and Margalef's D reflecting stone invertebrate diversity were not significant (SH: $F_{1,4}$ = 0.890, P = 0.400; MD: $F_{1,4}$ = 0.872, P = 0.403). However, log D ($F_{1,5}$ = 0.027, P = 0.027) and ST ($F_{1,5}$ = 19.64, P = 0.007) were significant. For Alaskan lakes, no correlations were found (log HVOL: $F_{1,2}$ = 0.000, P = 0.982; log SA: $F_{1,2}$ = 0.155, P = 0.732; ALT: $F_{1,2}$ = 1.049, P = 0.414;).

In linear models predicting Arctic charr TP range using environmental variables in Icelandic lakes, only log SA was significant ($F_{1,5}$ = 12.33, P = 0.017). All other variables were not, including log HVOL ($F_{1,5}$ = 0.071), D ($F_{1,5}$ = 1.155, P = 0.332), ALT ($F_{1,5}$ = 0.880, P = 0.391), ST ($F_{1,5}$ = 0.100, P = 0.764), TNTP ($F_{1,5}$ = 0.564, P = 0.487), and both stone invertebrate diversity indices (MD: $F_{1,4}$ = 0.153, P = 0.716; SH: $F_{1,4}$ = 0.223, P = 0.662). For Alaskan lakes, no correlations were found (log HVOL: $F_{1,2}$ = 0.230, P = 0.679; log SA: $F_{1,2}$ = 0.014, P = 0.917; ALT: $F_{1,2}$ = 1.121, P = 0.401).

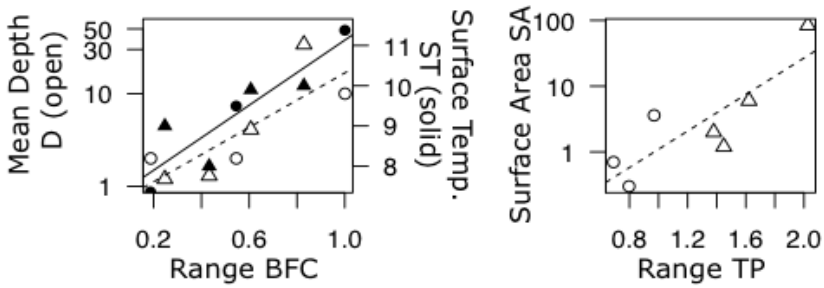


Figure 5.3. In Icelandic Lakes, range in proportion carbon from the benthic food chain consumed (BFC) was significantly correlated with mean depth (D) and surface temperature (ST). Range in trophic position (TP) was correlated with log surface area.

5.4 Discussion

The results revealed some important trends in how species interactions, resource polymorphism, and piscivory affect food web structure of subarctic lakes containing Arctic charr. First, trophic position and the proportion of carbon from the benthic food chain consumed by Arctic charr varied too much among lakes to permit species-wide generalizations. This was partially a result of variation due to resource polymorphism, but other species that were not polymorphic in these lakes (i.e., Arctic grayling) also exhibited extensive among-lake variation. Resource partitioning among species was apparent in many cases, as was partitioning among Arctic charr forms, although the latter appeared to be constrained by co-occurrence with other species. Second, the presence of threespine stickleback increased the trophic position of Arctic charr in Iceland and Alaska, but this was evident in the presence of other potential prey fish as well (i.e., sculpin in Alaska). In addition, the relative use of benthic carbon resources was transmitted up the food chain from stickleback to Arctic charr, indicating that diet diversity in the prey fish led to greater breadth of carbon sources received by the piscivore. Third, the range in proportion of benthic carbon consumed by Arctic charr was negatively related to surface temperature and mean depth in Iceland, whereas the range in trophic position increased with to lake surface area. Perhaps this indicates a dependence of expanded limnetic resource use on limnetic habitat availability, lake stratification, or increased run-off, and a dependence of trophic position breadth on prey availability through colonization opportunity or habitat diversity.

5.4.1. Effects of intraspecific variation on food webs

Our study places many of the dietary trends found in past studies of Arctic charr into a food web context. Medium-sized Arctic charr were not appreciably different in trophic position from stickleback, indicating that only the larger Arctic charr became piscivorous. This size falls within the realm of Arctic charr lengths indicated as the ontogenetic switch to piscivory, although this realm is quite large, including ~16 cm (L'Abée-Lund et al. 1992, Adams et al. 1998), ~20 cm (Malmquist et al. 1992b, Amundsen, 1994), and 35 – 40 cm (Hobson and Welch 1995, Guiguer et al. 2002). Icelandic brown trout switched toward piscivory at a larger size (~ 40 cm: Malmquist et al. 2002a, Jeppesen et al. 2002), indicating that our size range of brown trout might not fully represent piscivory in this species. However, growth rate divergence is not necessarily associated with differences in piscivory, trophic position, or range in limnetic carbon use, since Högnavatn had differentiated growth rates without stickleback present or any sign of cannabalism through increased trophic position. This type of divergence may instead be associated with differential resource use at a similar trophic level within the the benthic food chain, or it simply may not be associated with resource use. Similar divergence in growth rate with weak trophic divergence has been observed in other systems (Adams et al. 2003).

In addition, the lakes in which limnetic feeding dissipated at larger sizes showed an ontogenetic switch that has been well documented previously and may allow for resource partitioning among size classes within Arctic charr populations (Forseth et al. 1994, Byström and Andersson 2005). This switch was not as distinct in populations where morphological differentiation resulted in greater limnetic carbon consumption (i.e., Vatnshlíðarvatn, Thríhyrningsvatn, Thingvallavatn, L. Tazimina Lake). Instead, some individuals remain consuming limnetic resources at large sizes. Trophic position partitioning was also clearly confirmed in Galtaból and Thingvallavatn (Jónsson 2002, Wilson et al. 2004, Chapter 4).

5.4.2. Interspecific interactions

The great variability across lakes in Arctic grayling diets was not surprising, given that they utilize a wide range in resources from lakes in the region (Russell 1980). However, within lakes Arctic grayling

showed quite narrow ranges in resource use, indicating that this variation is more closely related to differences among lakes rather than individuals within lakes. Stickleback diets were likewise variable across lakes, but were also highly variable within populations that exhibitted resource polymorphim (Kristjánsson et al. 2002, Jónsson 2002). Pygmy whitefish, on the other hand, exhibited little variation within or among lakes, although sampling was minimal. Both stickleback and pygmy whitefish had surprisingly high trophic positions given their small sizes, although high stickleback trophic position has been reported previously (Jeppesen et al. 2002).

Although we can only speculate on the causes of differences among lakes in the expression of polymorphism, one hypothesis is apparent: resource polymorphism is constrained by resource partitioning between species. This idea conforms with the hypotheses regarding origins of resource polymorphism, which indicate low species diversity as an important factor (Griffiths 1994, Robinson and Wilson 1994, Skúlason & Smith 1995, Schluter 1996, Griffiths 2006). For example, Arctic grayling occupied a similar average trophic position to Arctic charr in L. Tazimina Lake, but used a proportion of the benthic food chain that was intermediate between the two forms, only overlapping with immature large forms in L. Tazimina Lake. In contrast, Caribou Lake Arctic charr overlapped with Arctic grayling extensively in range in proportion benthic food chain consumed, but trophic positions did not. Instead of a second Arctic charr form, pygmy whitefish occupied the position that might otherwise have been held by charr: greater consumption of limnetic carbon sources at higher trophic levels. Competition with more limnetic Arctic grayling and pygmy whitefish may have shifted Arctic charr into a more benthic role, so that piscivory by larger Arctic charr in L. Tazimina or Caribou Lakes generally occurs in benthic habitats. In addition, the lack of pygmy whitefish or other limnetic specialists may have promoted the development of a zooplanktivorous limnetic form in L. Tazimina Lake. This hypothesis is supported by past studies indicating that Arctic charr confine themselves to benthic or profundal habitats in the presence of European species that are close relatives and ecologically similar to pygmy whitefish and Arctic grayling in Alaska: lake whitefish and grayling (Amundsen et al. 2010, Sandlund et al. 2010). Competitive exclusion from lakes in Alaska by larger whitefish species has also been suggested (Russell 1980, Kreiner 2006). Other lakes that show piscivory in large

benthivorous Arctic charr forms also contain limnetic Arctic charr forms in addition to other species that could take intermediate roles at various stages, such as eels *Anguilla anguilla* or minnow *Phoxinus phoxinus* (Adams et al. 1998, Fraser et al. 1998). In contrast, the association between Arctic charr piscivory and a limnetic carbon signal in Iliamna Lake may be the result of co-occurrence with other piscivorous benthic species (i.e., rainbow trout among others). This pattern appears to occur whenever Arctic charr cohabitate with other salmonids and benthic piscivores (Langeland et al. 1991, Hesthagen et al. 1997, Jansen et al. 2002, Power et al. 2002, Forseth et al. 2003, Knudsen et al. 2010). It should be noted, however, that species interactions are not the only cause for greater piscivory to occur alongside greater limnetic resource use: Galtaból piscivores appeared to consume stickleback with a more limnetic signal despite the availability of stickleback with a benthic signal and no competing fish species. Also, cannibalistic Arctic charr in Canada were associated with limnetic feeding, possibly due to an ontogenetic shift from zooplanktivory (Arbour et al. 2011).

Thingvallavatn deserves special attention with regard to interspecific interactions and the development of piscivory in association with greater or lesser proportional use of the benthic food chain. Thingvallavatn Arctic charr exhibit both morphological and growth rate differentiation, and resources appear to be partitioned between Arctic charr and brown trout based on the availability of 2 stickleback forms (Kristjánsson et al. 2002): piscivorous Arctic charr mainly consume stickleback from the deeper *Nitella opaca* mud habitats, whereas brown trout are restricted to piscivory in rocky littoral zones. Although larger brown trout (> 38 cm) were not represented in our data set, our samples nonetheless had elevated trophic positions and past studies have indicating that brown trout specialize on littoral prey fish (Langeland et al. 1991, Hesthagen et al. 1997, Jansen et al. 2002, Forseth et al. 2003). Dietary differences between the 2 stickleback morphs correspond well with the observed differences in proportion consumed from the benthic food chain: the deeper form eat mostly copepods and cladocerans, whereas the shallower littoral form eat mostly chironomid larvae (Kristjánsson et al. 2002). However, deeper stickleback also have a higher trophic position, causing piscivorous Arctic charr in Thingvallavatn to be at least as high as brown trout in trophic position. There are two explanations for this apparent rise in trophic position: either 1) the deeper form of stickleback actually

consumed higher trophic level prey with a more limnetic signature, or 2) the base nitrogen levels have changed with depth due to anaerobic processes occurring in the hypolimnion or differences in inorganic nitrogen sources (Vander Zanden and Rasmussen 1999). Since the trophic positions of both deeply caught stickleback and piscivorous Arctic charr, which are thought to feed mostly in the *Nitella opaca* regions, are not substantially higher than those found in the shallow lake V. Friðmundarvatn, we believe that depth may not have a strong influence on these values. However, distinguishing these explanations would require further sampling of profundal zones.

5.4.3. Environmental trends with food webs

Trophic position breadth was only correlated positively with surface area, and likely reflects the greater extension of trophic position to higher levels. This supports the hypothesis that larger lakes yield greater availability of higher trophic-position prey due to the availability of habitats and greater colonization potential (Post et al. 2000). The positive correlation between range of carbon from the benthic food chain consumed by Arctic charr with mean depth supported the geometric hypothesis that greater consumption of limnetic resources occurs under conditions of greater relative limnetic habitat availability. Surface temperature was also correlated with this measure of dietary breadth in Arctic charr, possibly indicating greater runoff or stratification. Consistent stratification of dimictic lakes in arctic lakes of Alaska showed high levels of sub-surface algal production (LaPerriere et al. 2003), potentially yielding a stable and productive food source for abundant zooplankton populations. Alternatively, the greater range toward depleted $\delta^{13}C$ signal may be a side effect of greater sedimentation of limnetic resources to profundal areas and fixation of carbon from respired CO_2 or biogenic methane (Vander Zanden and Rasmussen 1999, Jeppesen et al. 2002, Hershey et al. 2006). However, the greater consumption of zooplankton in most of the deepest lakes (Thingvallavatn, Thríhyrningsvatn, L. Tazimina Lake) support the idea that this is not a side-effect: the greater range into limnetic $\delta^{13}C$ values results from the either the direct zooplankton consumption of Arctic charr ore consumption of zooplanktivorous prey fish.

5.4.4. Conclusions

This study represents a rare opportunity to study the interplay between intraspecific variation and the development of food webs in subarctic lakes. Major differences between Iceland and Alaska appeared to be a result of species interactions with Arctic charr. Intraspecific variation in the form of morphological differentiation increased the range of benthic versus limnetic resources used, perhaps increasing food web stability by allowing Arctic charr to access and switch between resources (Romanuk et al. 2006, Rooney et al. 2008). The presence of prey caused greater trophic position breadth and body sizes, thereby potentially promoting resilience and stability in food webs by introducing intermediate pathways and body size variation linked to variation in energy flux rates (Rooney et al. 2008). Furthermore, this variation was linked with the physical and landscape in the form of environmental trends. Although we have provided an overview detailing trends in how food web structure varies with species interactions and environmental trends across subarctic lakes of Iceland and Alaska, much work is still left for the delineation of the mechanisms supporting these trends.

5.5 References cited

Åberg, J, Jansson, M., Karlsson, J., Nääs, K., and Jonsson, A. 207. Pelagic and benthic net production of dissolved inorganic carbon in an unproductive subarctic lake. Freshwater Biol. 52:549 – 560.

Adams, C., Fraser, D., McCarthy, I., Shields, S., Waldron, S., and Alexander, G. 2003. Stable isotope analysis reveals ecological segregation in a bimodal size polymorphism in Arctic charr from Loch Tay, Scotland. J. Fish Biol. 62: 474 – 481.

Adams, C.E., Fraser, D., Huntingford, F.A., Greer, R.B., Askew, C.M., and Walker, A.F. 1998. Trophic polymorphism amongst Arctic charr from Loch Rannoch, Scotland. J. Fish Biol. 52: 1259 – 1271.

Amundsen, P.A. 1994. Piscivory and cannibalism in Arctic charr. J. Fish Biol. 45 (Suppl. A): 181 – 189.

Amundsen, P.A., Knudsen, R., and Bryhni, H.T. 2010. Niche use and resource partitioning of Arctic charr, European whitefish and grayling in a subarctic lake. Hydrobiologia 650: 3 – 14.

Arbour, J.H., Hardie, D.C., and Hutchings, J.A. 2011. Morphometric and genetic analyses of two sympatric morphs of Arctic char

Salvelinus alpinus in the Canadian High Arctic. Can. J. Zool. 89: 19 – 30.

Ask, J. Karlsson, J., Persson, L., Ask, P. Byström, P., and Jansson, M. 2009. Whole-lake estimates of carbon flux through algae and bacteria in benthic and pelagic habitats of clear-water lakes. Ecology 90:1923 – 1932.

Bernatchez, L. & Wilson, C.C. (1998) Comparative phylogeography of Nearctic and Palearctic fishes. *Molecular Ecology*, 7, 431–452.

Byström, P., and Andersson, J. 2005. Size-dependent foraging capacities and intercohort competition in an ontogentic omnivore (Arctic char). Oikos 110: 523 – 536.

Cabana, G., and Rasmussen, J.B. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proc. Nat. Acad. Sci. of USA 93: 10844 - 10847.

Carpenter, S.R., Cole, J.J., Pace, M.L., Van de Bogert, M., Bade, D.L., Bastviken, D., Gille, C.M., Hodgson, J.R., Kitchell, J.F., and Kritzberg, E.S. 2005. Ecosystem subsidies: terrestrial support of food webs from $\delta^{13}C$ addition to contrasting lakes. Ecol. 86: 2737 – 2750.

Cole, J.J., Carpenter, S.R., Kitchell, J., Pace, M.L., Solomon, C.T., and Weidel, B. 2011. Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen. Proc. Nat. Acad. Sci….

Cole, J.J., Carpenter, S.R., Pace, M.L., Van de Bogert M.C., Kitchell, J.L., and Hodgson, J.R. 2006. Differential support of lake food webs by three types of terrestrial organic carbon. Ecol. Letters 9: 558 – 568.

Corrigan, L.J., Winfield, I.J., Hoelzel, A.R., and Lucas, M.C. 2011. Dietary plasticity in Arctic charr (*Salvelinus alpinus*) in response to long-term environmental change. Ecol. Freshwater Fish 20: 5 – 13.

Denton, K.P., Rich, H.B., Jr., Moore, J.W., and Quinn, T.P. 2010. The utilization of a Pacific salmon *Oncorhynchus nerka* subsidy by three populations of charr *Salvelinus* spp. J. Fish Biol. 77: 1006 - 1023.

Edmundson, J.A., Mazumder, A. 2002. Regional and hierarchical perspectives of thermal regimes in subarctic, Alaskan lakes. Freshwater Biol. 47: 1 – 17.

Finstad, A.G., Forseth, T., Jonsson, B., Bellier, E., Hesthagen, T., Jensen, A.J., Hessen, D.O., and Foldvik, A. 2011. Competitive exclusion along climate gradients: energy efficiency influences

the distribution of two salmonid fishes. Glob. Change Biol. 17: 1703 – 171.

Fraser, D., Adams, C.E., and Huntingford, F.A. 1998. Trophic polymorphism among Arctic charr *Salvelinus alpinus* L., from Loch Ericht, Scotland. *Ecol. Freshwater Fish 7:* 184-191.

Forseth, T., Ugedal, O., Jonsson, B. 1994. The energy budget, niche shift, reproduction and growth in a population of Arctic Charr *Salvelinus alpinus.* J. Anim. Ecol. 63: 116 – 126.

Forseth, T., Ugedal., O., Jonsson, B., and Fleming, I. 2003. Selection on Arctic charr generated by competition from brown trout. Oikos 101: 467 – 478.

Gannes, L.Z., Martínez del Rio, and Koch, P. 1998. Natural abundance variation in stable isotopes and their potential use in animal physiological ecology Comp. Biochem. And Physiol. 119A: 725 – 737.

Griffiths, D. 1994. The size structure of lacustrine Arctic charr (Pisces: Salmonidae) populations. Biol. J. Linn. Soc. 51: 337–357.

Griffiths, D. 2006. Pattern and process in the ecological biogeography of European freshwater fish. J. Anim. Ecol. 75: 734 – 751.

Guðbergsson, G., 2004. Arctic charr in Lake Myvatn: the centennial catch record in the light of recent stock estimates. Aquat. Ecol. 38: 271 – 285.

Guiguer, K.R.R.A., Reist, J.D., Power, M., and Babaluk, J.A., 2002. Using stable isotopes to confirm the trophic ecology of Arctic charr morphotypes from Lake Hazen, Nunavut, Canada. J. Fish Biol 60: 348 – 362.

Helland, I.P., Finstad, A.G., Forseth, T., Hesthagen, T., and Ugedal, O. 2011. Ice-cover effects on competitive interactions between two fish species. J. Anim. Ecol. 80: 539 – 547.

Hershey, A.E., Beaty, S., Fortino, K., Luecke, C., O'Brien, W.J., and Whalen, S.C. 2006. Stable isotope signatures of benthic invertebrates in arctic lakes indicate limited coupling to pelagic production. Limnol. Oceanogr. 51: 177 – 188.

Hesthagen, T., Jonsson, B., Ugedal, O., and Forseth, T. 1997. Habitat use and life history of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) in some low acidity lakes in central Norway. Hydrobiologia 348: 113 – 126.

Jansen, P.A., Slettvold, H., Finstad, A.G., and Langeland, A. 2002. Niche segregation between Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*): an experimental study of mechanisms. Can. J. Fish. Aquat. Sci. 59: 6 – 11.

Jeppesen, E., Landkildehus, F., Lauridsen, T.L., Jensen, J. P., Bjerring, R., Søndergaard, M., and Amsinck, S.L. 2002. Food web interactions in five Faroese lakes tracked by stable isotopes. Ann. Soc. Scient. Færoensis Suppl. 36: 114 – 125.

Jónasson, P.M. Jonsson, B., and Sandlund, O. 1998. Continental rifting and habitat formation: arena for resource polymorphism in Arctic charr. Ambio 27: 162 – 169.

Jónsson, B. 2002. Parallel sympatric segregation in Arctic charr and threespined stickleback in Lake Galtaból, Iceland. Fish. Sci. 68 (Supp. 1): 459 – 460.

Jonsson, B., and Jonsson, N. 2001. Polymorphism and speciation in Arctic charr. J. Fish Biol. 58: 605 – 638.

Jónsson, B., and Skúlason, S. 2000. Polymorphic segregation in Arctic charr *Salvinus alpinus* (L.) from Vatnshlíðarvatn, a shallow Icelandic lake. Biol. J. Linnean Soc. 69: 55 – 74.

Karlsson, J., Jonsson, A., Meili, M., and Jansson, M. 2004. $\delta^{15}N$ of zooplankton species in subarctic lakes in northern Sweden: effects of diet and trophic fractionation. 2004. Freshwater Biol. 49: 526 – 534.

Karst-Riddoch, T.L., Malmquist H.J. and Smol, J.P. 2009. Relationships between freshwater sedimentary diatoms and environmental variables in Subarctic Icelandic lakes. Fundament. and Appl. Limnol. 175, 1–28.

Kawaguchi, Y., and Nakano, S. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest adn grassland reaches of a headwater stream. Freshwater Biol. 46: 303 – 316.

Kelly, J.F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology Can. J. Of Zool. 78: 1 – 27.

Kiljunen, M., Grey, J. Sinisalo, T., Harrod, C., Immonen, H., and Jones, R.I. 2006. A revised model for lipid-normalizing $\delta^{13}C$ values from aquatic organisms with implications for isotope mixing models. J. Applied Ecol. 43: 1213 – 1222.

Klemetsen, A., Amundsen, P.A., Grotnes, P.E., Knudsen, R., Kristoffersen, R., and Svenning, M.A. 2002. Takvatn through 20 years: long-term effects of an experimental mass removal of Arctic charr, *Salvelinus slpinus*, from a subarctic lake. Environ. Biol. Fishes 64: 39 – 47.

Kline, T.C., Goering, J.J., Mathisen, O., and Poe, P.H. 1993. Recycling of elements transported upstream by runs of Pacific salmon: II. $\delta^{15}N$ and $\delta^{13}C$ evidence in the Kvichak river watershed, Bristol

Bay, southwestern Alaska. Can. J. Fish. Aquat. Sci. 50: 2350-2365.

Knudsen, R., Amundsen, P.A., and Klemetsen, A. 2010. Arctic char in sympatry with burbot: ecological and evolutionary consequences. Hydrobiologia 650: 43 – 54.

Kreiner, R. 2006. An investigation of Arctic char (*Salvelinus alpinus*) and lake trout (*Salvelinus namaycush*) in Lake Clark National Park. M.S. Thesis, University of Idaho. 76 pp.

Kristjánsson, B.K., Skúlason, S., and Noakes, D.L.G. 2002. Morphological segregation of Icelandic threespine stickleback (Gasterosteus aculeatus L.). Biol. J. Linnean Soc. 76: 247 – 257.

L'Abée-Lund, J.H., Langeland, A., and Sægrov, H. 1992. Piscivory by brown trout Salmon trutta L. and Arctic charr Salvelinus a*lpinus* L. in Norwegian lakes. J. Fish Biol. 41: 91 – 101.

L'Abée-Lund, J.H., Langeland, A., Jonsson, B., and Ugedal, O. 1993. Spatial segregation by age and size in Arctic charr: a trade-off between feeding possibility and risk of predation. J. Anim. Ecol. 62: 160 – 168.

Langeland, A., L'Abée-Lund, J.H., Jonsson, B., and Jonsson, N. 1991. Resource partitioning and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta.* J. Anim. Ecol. 60: 895 – 912.

LaPerriere, J.D., Jones, J.R., and Swanson, D.K. 2003. Limnology of lakes in Gates of the Arctic National Park and Preserve, Alaska. Lake and Reservoir Management 19: 108 – 121.

Levine, M.A., and Whalen, S.C. 2001. Nutrient limitation of phytoplankton production in Alaskan foothill lakes. Hydrobiologia 455: 189 – 2001.

Malmquist, H.J., Antonsson, T., Guðbergsson, G., Skúlason, S. & Snorrason, S.S. (2000) Biodiversity of macroinvertebrates on rocky substrate in the surf zone of Icelandic lakes. Verh. Int. Ver. Limnol., 27, 1–7.

Malmquist, H.J., Ingimarsson, F., Jóhannsdóttir, Gíslason, D., and Snorrason, S.S. 1992a. Biology of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) in four Faroese lakes. Ann. Soc. Sci. Færoensis Suppl. 36: 94 - 113.

Malmquist, H.J., Snorrason, S.S, Skúlason, S., Jonsson, B., Sandlund, O.T., and Jonasson, P.M. 1992b. Diet differentiation in polymorphic Arctic charr in Thingvallavatn, Iceland. Journal of Anim. Ecol. 61: 21 – 35.

Malmquist, H.J., Snorrason, S.S., Skúlason, S., Jónson, B., Sandlund, O.T., and Jónasson, P.M. 1992b. Diet differentiation in

polymorphic Arctic charr in Thingvallavatn, Iceland. J. Anim. Ecol. 61: 21 - 35.

Matthews, B., and Mazumder, A. 2004. A critical evaluation fo intrapopulation variation of $\delta^{13}C$ and isotopic evidence of individual specialization. Oecologia 140: 361 – 371.

Pienitz, R., Smol, J.P., and Lean, D.R.S. 1997. Physical and chemical limnology of 59 lakes located between the southern Yukon and the Tuktoyaktuk Peninsua, Northwest Territories (Canada). Can. J. Fish. Aquat. Sci. 54: 330 – 346.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: Models, methods and assumptions. Ecol. 823: 703 – 718.

Post, D.M., Pace, M.L., and Hairston, N.G., Jr. 2000. Ecosystem size determines food-chain length in lakes. Nature 405: 1047 – 1049.

Power, M., Power, G., Caron, F., Doucett, R.R., and Guiguer, K.R.A. 2002. Growth and dietary niche in *Salvelinus alpinus* and *Salvelinus fontinalis* as revealed by stable isotope analysis Environ. Biol. Fish. 64: 75 – 85.

Power, M., Power, G., Caron, F., Doucett, R.R., and Guiguer, K.R.A. 2002. Growth and dietary niche in *Salvelinus alpinus* and *Salvelinus fontinalis* as revealed by stable isotope analysis. Environ. Biol. Fish. 64: 75 – 85.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Rautio, M., and Vincent, W. 2007. Isotopic analysis of the sources of organic carbon for zooplankton in shallow subarctic and arctic waters. Ecography 30:77 – 87.

Robinson, B.W. & Schluter, D. (2000) Natural selection and the evolution of adaptive genetic radiation in northern freshwater fishes. *Adaptive Genetic Variation* (eds Mousseau, T.A., Sinervo, B. & Endler, J.), pp. 65–94. Oxford University Press, Oxford.

Romanuk, T.N., Beisner, B.E., Martine, N.D., and Kolasa, J. 2006. Non-omnivorous generality promotes population stability. Biol. Letters 2: 374 – 377.

Rooney, N., McCann, K.S., and Moore, J.C. 2008. A landscape theory for food web architecture. Ecol. Letters 11: 867 – 881.

Sandlund, O.T., Museth, J., Næsje, T.F., Rognerud, S., Saksgård, R., Hesthagen, T., and Borgstrøm, R. 2010. Habitat use and diet of sympatric Arctic charr (*Salvelinus alpinus*) and whitefish (*Coregonus lavaretus*) in five lakes in southern Norway: not

only interspecific population dominance? Hydrobiologia 650: 27 – 41.

Schielke, E.G., and Post, D.M. 2010. Size matters: comparing stable isotope ratios of tissue plugs and whole organisms. Limnol. Oceanogr.: Methods 8: 348 – 351.

Schindler, D.E., and Scheurell, M.D. 2002. Habitat coupling in lake ecosystems. Oikos 98:177 – 189.

Schluter, D. 1996. Ecological speciation in postglacial fishes. Phil. Trans. Roy. Soc. B: Biological Sciences 351: 807–814.

Sierszen, M.E., McDonald, M.E., and Jensen, D.A. 2003. Benthos as the basis for arctic lake food webs. Aquatic Ecol. 37: 437 – 445.

Skúlason, S. & Smith, T.B. 1995. Resource polymorphisms in vertebrates. Trends in Ecol. and Evol., 10, 366–370.

Skúlason, S., Noakes, D.L.G., and Snorrason, S.S. 1989. Ontogeny of trophic morphology in four sympatric morphs of arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. Biol. J. Linn. Soc. 38: 281 - 301.

Snorrason, S.S. & Skúlason, S. 2004. Adaptive Speciation in northern freshwater fishes. *Adaptive Speciation* (eds, Dieckmann, U., Doebeli, M., Metz, J.A.J. & Tautz, D.), pp. 210–228. Cambridge University Press, Cambridge.

Vadeboncoeur, Y., Jeppesen, E., Vander Zanden, M.J., Scheirup, H.H., Christoffersen, K., and Lodge, D.M. From Greenland to green lakes: cultural eutrophication and the loss of benthic pathways in lakes. Limnol. Oceanogr. 48: 1408 – 1418.

Vander Zanden, M.J., and Rasmussen, J.B. 1999. Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecol. 80: 1395 – 1404.

Vander Zanden, M.J., and Rasmussen, J.B. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. Limnol. Oceanogr. 46: 2061 – 2066.

Vander Zanden, M.J., Chandra, S., Allen, B.C., Reuter, J.E., and Goldman, C.R. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) Basin. Ecosystems 6: 274 – 288.

Ventura, M., and Jeppesen, E. 2009. Effects of fixation on freshwater invertebrate carbon and nitrogen isotope composition and its arithmetic correction. Hydrobiologia 632: 297 – 308.

Wetzel, R.G. 1990. Land-water interfaces: Metabolic and limnological regulators. Int. Ver. Für Theor. Angew. Limnol. 24: 6 - 24.

Wilson, A.J., Gíslason, D., Skúlason, S., Snorrason, S., Adams, C.E., Alexander, G., Danzmann, R.G., and Ferguson, M.M. 2004. Population genetic structure of Arctic charr *Salvelinus alpinus* from northwest Europe on large and small spatial scales. Mol. Ecol. 13: 1129 - 1142.

Synthesis and conclusions

From this dissertation, it is apparent that foraging behavior and polymorphism in Arctic charr is at least partially predictable using physical and chemical characteristics of the landscape. In addition, ecological variability in the species forms a link between these limnological characteristics and food web structure by facilitating pathways of limnetic and benthic food chain use and increasing trophic positions. The first three chapters of this dissertation examined broad trends across Iceland and developed methods that can be used to compare study systems in a standard manner. The last two chapters used this information to test for polymorphism in a relatively unexplored region, southwestern Alaska, to determine whether trends observed there correspond with those in Iceland, and to place these patterns in an ecosystem context of food webs.

Each chapter was built from knowledge gained in the previous chapter. Forming prey categories that reflected habitat-associated feeding behavior in the first chapter paved the way for further analyses showing how morphology may be related to resource acquisition when analyzed across a wide variety of ecological circumstances (Iceland, Chapter 2). The third chapter used morphological variables defined in Chapter 2 along with length-at-age data to determine whether polymorphism could be detected in a standard test across lakes in Iceland. Polymorphism was detected in many more lakes than expected, indicating either that 1) polymorphism is more common than previously thought or 2) temporary bimodal patterns were detectable. Both patterns are important in understanding how polymorphism develops. The resulting categorization of lakes as polymorphic was then used to determine which environmental variables were best at predicting this state, and to determine whether they were related to hypotheses regarding the origin of polymorphism. The fourth chapter used the categorization methods of Chapter 3 to determine whether polymorphism was present in four proximate lakes in Alaska, after which ecological differences within and among lakes were further explored. Finally, the fifth chapter compared food webs across 4

Alaskan and 7 Icelandic lakes containing Arctic charr to determine how food web structure in subarctic lakes changes with the inclusion of polymorphism, species interactions among fish, and environmental characteristics.

There are a few broad conclusions that can be drawn from this study, as well as open questions that remain. First, both prey acquisition and polymorphism conclusively varied with environmental variables. This explains why polymorphism is common only in certain regions, such as northern temperate freshwater lakes (Robinson and Wilson 1994, Skúlason and Smith 1995). Within these regions, further patterns became clearer in this dissertation through the studies of how foraging, the occurrence of polymorphism, and food web structure varied with physical and chemical characteristics of the lake environment (Chapters 1, 3, and 5, respectively). However, these patterns were analyzed by comparing environmental characteristics as they varied in space, as opposed to time, and attempted to reduce temporal variation by using samples collected during the same time span (late summer, early fall). Although temporal patterns are more directly related to the development of frequency dependence, few studies have managed to include a temporal aspect (but see Schluter 1994; Rundle, Vamosi & Schluter 2003; Schluter 2003; Bolnick 2004; Langerhans et al. 2004; Svanbäck & Bolnick 2007). Therefore, future studies would likely gain the most by including the traditional experimental method of 1) perturb and 2) observe to understand temporal patterns, although simply observing natural fluctuations of population abundances with foraging habits would also prove enlightening. In addition, there is now enough information available on geographical patterns across regions that study systems may be chosen carefully for comparative studies.

Similarly, few studies have addressed the issue of understanding how polymorphism affects ecosystem properties directly using experimental methods (but see Harmon et al. 2009). Some first steps have been presented in this study through the description and comparison of food webs under similar ecological circumstances across regions. However, this topic likewise requires a temporal aspect, at least on a seasonal scale and ideally with experimentation, to link effects of polymorphism to dynamical properties of food webs. Understanding how these patterns are linked to food web stability and resilience requires carefully designed studies that address temporal issues such as seasonal abundances of food and ontogenetic shifts. Once this has been

done, the spatial patterns observed in this dissertation will likely become even clearer. For example, similarities in diet among lakes captured in Chapter 1 may indicate similarities in population dynamical mechanisms related to the environment or seasonality. Only then can these patterns be fully integrated and interpreted through a landscape theory (Rooney et al. 2008).

References cited

Bolnick, D.I. 2004. Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. Evolution 58: 608 – 618.

Harmon, L.J., Matthews, B., Des Roches, S., Chase, J.M., Shurin, J.B., and Schluter D. 2009. Evolutionary diversification in stickleback affects ecosystem functioning. Nature 458: 1167 – 1170.

Langerhans, R.B., Layman, C.A., Shokrollahi, A.M., and DeWitt, T.J. 2004. Predator-driven phenotypic diversification in *Gambusia affinis*. Evolution 58: 2305 – 2318.

Robinson, B.W., and Wilson, D.S. 1994. Character release and displacement in fishes: a neglected literature. Am. Nat. 144: 596 – 627.

Rooney, N., McCann, K.S., and Moore, J.C. 2008. A landscape theory for food web architecture. Ecol. Letters 11: 867 – 881.

Rundle, H.D., Vamosi, S.M. & Schluter, D. 2003. Experimental test of predation's effect on divergent selection during character displacement in sticklebacks. Proc. Nat. Acad. Sci. 100, 14943 – 14948.

Schluter, D. 1994. Experimental evidence that competition promotes divergence in adaptive radiation. Science 266: 798 – 801.

Schluter, D. 2003. Frequency dependent natural selection during character displacement in sticklebacks. Evolution 57: 1142 – 1150.

Skúlason, S., and Smith, T.B. 1995. Resource polymorphisms in vertebrates. Trends Ecol. Evol. *10:* 366 – 370.

Svanbäck, R. & Bolnick, D.I. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proc. Roy. Soc. B: 839–844.

References

Abrams, P.A., and Vos, M. 2003. Adaptation, density dependence, and the responses of trophic level abundances to mortality. Evol. Ecol. Res. 5: 1113-1132.

Adams, C.E., Wilson, A.J., and Ferguson, M.M. 2008. Parallel divergence of sympatric genetic and body size forms of Arctic charr, *Salvelinus alpinus*, from two Scottish lakes. Biol. J. Linnean Soc. 95: 748-757.

Alekseyev, S.S., Mina, M.V., Smirina, E.M., and Sokolov, A.A. 2009. Late ontogeny growth acceleration and size form transformations in Transbaikalian Arctic charr, *Salvelinus alpinus* complex: evidence from fin ray cross section growth layers. Environ. Biol. Fish. 86: 487 – 505.

Araújo, M.S., Bolnick, D.I., Machado, G., Giaretta, A.A., and dos Reis, S.F. 2007. Using δ13C stable isotopes to quantify individual-level variation. Oecologia 152: 643 – 654.

Bednekoff, P.A. 2007. Foraging in the face of danger. In: Foraging Behavior and Ecology. Stephens, D.W., Brown, J.S., and Ydenberg, R.C., eds. University of Chicago Press, Chicago. 608 pp.

Bolker, B.M. 2008. Ecological Models and Data in R. Princeton University Press, Princeton. 408. pp.

Carlsson, N.O.L., Sarnelle, O., and Strayer, D.L. 2009. Native predators and exotic prey – an acquired taste? Front. Ecol. Environ. 7: 525-532.

Caut, S., Roemer, G.W., Donlan, C.J., & Courchamp, F. 2006. Coupling stable isotopes with bioenergetics to estimate interspecific interactions. Ecol. App. 16: 1893-1900.

Cohen, Y., Pastor, J., and Vincent, T.L. 2000. Evolutionary strategies and nutrient cycling in ecosystems. Evol. Ecol. Res. 2: 719-743.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition. Am. Nat. 122: 661 – 696.

Coyne, J.A., and Orr, H.A. 2004. Speciation. Sinauer Associates, Sunderland, MA. 545 pp.

Friesen, M.L., Saxer, G., Travisano, M., and Doebeli, M. 2004. Experimental evidence for sympatric ecological diversification

due to frequency-dependent competition in Escherichia coli. Evolution 58: 245 – 260.

Funk, D.J. 2009. Investigating ecological speciation. In: Speciation and Patterns of Diversity. Butlin, R., Bridle, J., and Schluter, D., eds. Cambridge University Press, Cambridge. 333 pp.

Gavrilets, S. 2004. Genetic theories of allopatric and parapatric speciation. In: Adaptive Speciation. Cambridge University Press, Cambridge. 460 pp.

Geritz, S.A.H, Kisdi, É., Meszéna, G. ,and Metz, J.A.J. 2004. Adaptive dynamics of speciation: ecological underpinnings. In: Adaptive speciation. Cambridge University Press, Cambridge. 460 pp.

Gray, S.M., and Robinson, B.W. 2002. Experimental evidence that competition between stickleback species favours adaptive character divergence. Ecol. Lett. 5: 264 – 272.

Hairston, N.G., Ellner, S.P., Geber, M.A., Yoshida, T., and Fox, J.A. 2005. Rapid evolution and the convergence of ecological and evolutionary time. Ecol. Letters 8: 1114 – 1127.

Harvey, C.J., Hanson, P.C., Essington, T.E., & Kitchell, J.F. 2002. Using bioenergetics models to predict stable isotope ratios in fishes. Can. J. Fish. Aquat. Sci. 59:115-124.

Hendry, A.P. 2009. Ecological speciation! Or the lack thereof? Can. J. Fish. Aquat. Sci. 66: 1383 – 1398.

Hendry, A.P., and Kinnison, M.T. 1999. The pace of modern life: measuring rates of contemporary microevolution. Evolution 53: 1637 – 1653.

Hendry, A.P., Bolnick, D.I., Berner, D., and Peichel, C.L. 2009. Along the speciation continuum in sticklebacks. Journal of Fish Biology 75: 2000 – 2036.

Hodgson JR and Kitchell JF. 1987. Opportunistic foraging by large-mouth bass (*Micropterus salmoides*). Am. Midl. Nat. 118: 323 – 336.

Holt, R.D., and Kimbrell, T. 2007. Foraging and population dynamics. pp. 365 – 396 in Foraging Behavior and Ecology. Eds. D.W. Stephens, J.S. Brown, and R.C. Ydenberg.

Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton. 448 pp.

Hudson, A.G., Vonlanthen, P., and Seehausen, O. 2011. Rapid parallel adaptive radiations from a single hybridogenic ancestral population. Proc. R. Soc. Lond. B Biol. Sci. 278: 58 – 66.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 415 – 427.

Jepsen, D.B., & Winemiller, K.O. 2007. Basin geochemistry and isotopic ratios of fishes and basal production sources in four neotropical rivers. Ecol. Freshwater Fish 16: 267-281.

Kahilainen, K., and Lehtonen, H. 2003. Piscivory and prey selection of four predator species in a whitefish dominated subarctic lake. J. Fish Biol. 63: 659-672.

Kinnison, M.T., and Hendry, A.P. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. Genetica: 145 – 164.

Kinnison, M.T., Unwin, M.J., Hendry, A.P., and Quinn, T.P. 2001. Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. Evolution 55: 1656 – 1667.

Kotler, B.P., and Brown, J.S. 2007. Community Ecology pp. 397-436 in Foraging Behavior and Ecology. Eds. D.W. Stephens, J.S. Brown, and R.C. Ydenberg.

Layman, C.A., et al. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88: 42-48.

Losos, J.B., Warheit, K.I., and Schoener, T.W. 1997. Adaptive differentiation following experimental island colonization in Anolis lizards. Nature 387: 70 – 73.

MacArthur, R.H., and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Nat. 101: 377 – 385.

MacArthur, R.H., and Pianka, E.R. 1966. An optimal use of a patchy environment. Am. Nat. 100: 603 – 609.

Magurran, A.E. 1999. Population differentiation without speciation. In: Evolution of Biological Diversity. Magurran, A.E., and May, R.M., eds. Oxford University Press, Oxford. 329 pp.

Mallet, J. 2009. Rapid speciation, hybridization and adaptive radiation. In: Speciation and Patterns of Diversity. Butlin, R., Bridle, J., and Schluter, D., eds. Cambridge University Press, Cambridge. 333 pp.

Mayr, E. 1963. Animal species and evolution. Belknap Press, Cambridge.

Mori, S., and Takamura, N. 2004. Changes in morphological characteristics of an introduced population of the threespine stickleback *Gasterosteus aculeatus* in Lake Towada, northern Japan. Ichthy. Res. 51: 295 – 300.

Nash, C.E. 2003. Interactions of Atlantic salmon in the Pacific Northwest VI. A synopsis of the risk and uncertainty. Fisheries Res. 62: 339 – 347.

Nosil, P., and Harmon, L. 2009. Niche dimensionality and ecological speciation. In: Speciation and Patterns of Diversity. Butlin, R., Bridle, J., and Schluter, D., eds. Cambridge University Press, Cambridge. 333 pp.

Pfennig, D.W., and Murphy, P.J. 2002. How fluctuating competition and phenotypic plasticity mediate species divergence. Evolution 56: 1217 – 1228.

Post, D.M., Kitchell, J.F., and Hodgson, J.R. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. Can. J. Fish. Aquat. Sci. 55: 2588 – 2600.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., and Paine, R.T. 1995. Challenges in the quest for keystones. BioScience 46: 609 – 620.

Price, T. 1999. Sexual selection and natural selection in bird speciation. In: Evolution of Biological Diversity. Magurran, A.E., and May, R.M., eds. Oxford University Press, Oxford. 329 pp.

Pyke GH, Pulliam, HR, and Charnov EL. 1977. Optimal foraging: a selective review of theory and test. Q Rev Biol. 52: 137 – 154.

Quinn, T.P. 2005. The Behavior and Ecology of Pacific Salmon and Trout. University of Washington Press, Seattle. 378 pp.

Quinn, T.P., Doctor, K., Kendall, N., and Rich, H.B. 2009. Diadromy and the life history of sockeye salmon: nature, nurture, and the hand of man. AFS Symposium 69: 23 – 42.

Quinn, T.P., Kinnison, M.T., and Unwin, M.J. 2001. Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. Genetica 112 – 113: 493 – 513.

Quinn., T.P. 1999. Revisiting the stock concept in Pacific salmon: insights from Alaska and New Zealand. Northwest Sci. 73: 312 – 324.

Reimchen, T.E. 1994. Predators and morphological evolution in threespine stickleback, pp. 240 – 276 in The Evolutionary Biology or the Threespine Stickleback. Bell, M.A., and Foster, S.A., eds. Oxford University Press, Oxford.

Reznick, D.N., Bryga, H., and Endler, J.E. 1990. Experimentally induced life-history evolution in a natural population. Nature 346: 357 – 359.

Rooney, N., McCann, K., Gellner, G., and Moore, J.C. 2006. Structural asymmetry and the stability of diverse food webs. Nature 442: 265-269.

Rouse, W.R., Douglas, M.S.V., Heckey, R.E., Hershey, A.E., Kling, G.W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B.J., Roulet, N.T., and Smol, J.P. 1997. Effects of climate change on the waters of arctic and subarctic North America. Hydrol. Proc. 11: 873-902.

Rundle, H.D. 2002. A test of ecologically dependent postmating isolation between sympatric sticklebacks. Evoluion 56: 322 – 329.

Sakai, M., and Espinos A. 1994. Repeat homing and migration of rainbow trout to the inlet and outlet spawning streams in a patagonian lake, Argentina. Fisheries Sienc 60: 137 – 142.

Schemske, D.W. 2009. Biotic interactions and speciation in the tropics. In: Speciation and Patterns of Diversity. Butlin, R., Bridle, J., and Schluter, D., eds. Cambridge University Press, Cambridge. 333 pp.

Schluter, D. 1981. Does the theory of optimal diets apply in complex environments? Am. Nat. 118: 139 – 147.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford University Press, Oxford. 288 pp.

Schluter, D. 2009. Evidence for ecological speciation and its alternative. Science 323: 737 – 741.

Schoener. T.W. 1983. Field experiments on interspecific competition. Am. Nat. 122: 240 – 285.

Seehausen, O. 2006. Conservation: Losing biodiversity by reverse speciation. Current Biol. 16: R334 – R337.

Seehausen, O. 2009. Progressive levels of trait divergence along a 'speciation transect' in the Lake Victoria cichlid fish Pundamilia. In: Speciation and Patterns of Diversity. Butlin, R., Bridle, J., and Schluter, D., eds. Cambridge University Press, Cambridge. 333 pp.

Skúlason, S., Snorrason, S.S., Noakes, D.L.G., and Ferguson, M.M. 1996. Genetic basis of life history variations among sympatric morphs of Arctic char, *Salvelinus alpinus*. Can. J. Fish. Aquat. Sci. 53: 1807 – 1813.

Smith, T.B., and Skúlason, S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. Ann. Rev. Ecol. Syst. 27: 111 – 133.

Snorrason, S.S., and Skúlason, S. 2004. Adaptive speciation in northern freshwater fishes. In: Adaptive Speciation. Cambridge University Press, Cambridge. 460 pp.

Stearns, S.C. 1983. A natrual experiment in differences in life-history traits among six populations of mosquitofish (*Gambusia affinis*) to Hawaii. Evolution 37: 601 – 617.

Stearns, S.C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford. 249 pp.

Taylor, B.W., Flecker, A.S., and Hall, R.O. 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. Science 5788: 833-836.

Taylor, E.B., Boughman, J.W., and Groenenboom, M., Sniatynski, M., Schluter, D., and Gow, J.L. 2006. Speciation in reverse: morphological and genetic evidence of the collapse of a three-spined stickleback (*Gasterosteus aculeatus*) species pair. Mol. Ecol. 15: 343 – 355.

Turner, G.F. 1999. Explosive speciation of African cichlid fishes. In: Evolution of Biological Diversity. Magurran, A.E., and May, R.M., eds. Oxford University Press, Oxford. 329 pp.

Tyerman, J., Havard, N., Saxer, G., Travisano, M., and Doebeli, M. 2005. Unparallel diversification in bacterial microcosms. Proc. Roy. Soc. B 272: 1393 – 1398.

Venables, W.N., and Ripley, B.D. 2002. Modern Applied Statistics with S. Fourth edition. Springer, New York. 495 pp.

Vila-Gispert, A., Fox, M.G., Zamora, L., Moreno-Amich, R. 2007. Morphological variation in pumpkinseed *Lepomis gibbosus* introduced into Iberian lakes and reservoirs; adaptations to habitat type and diet? J. Fish Biol. 71: 163 – 181

Walters, C. and Juanes, F. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Can. J. Fish. Aquat. Sci. 50: 2058 – 2070.

Walters, C. and Kitchell, J.F. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. Can. J. Fish. Aquat. Sci. 58: 39 – 50.

Waples, R.S. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. Amer. Fish. Soc. Symp. 17: 8 – 27.

Weiher, E. and Keddy, P., eds, 1999. Ecological Assembly Rules: Perspectives, advances, retreats. Cambridge University Press, Cambridge. 430 pp.

Werner, E.E., and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15: 393 – 425.

Werner, E.E., and Peacor, S.D. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84: 1083 – 1100.

Wolf, J.B., and Brodie, E.D. III 1998. The coadaptation of parental and offspring characters. Evolution 52: 299 – 308.

Wolinska, J., Bittner, K., Ebert, D., Spaak, P. 2006. The coexistence of hybrid and parental Daphnia: the role of parasites. Proc. Roy. Soc. B 273: 1977 – 1983.

Woods, P.J., Müller, R., and Seehausen, O. 2009. Intergenomic epistasis causes asynchronous hatch times in whitefish hybrids, but only when parental ecotypes differ. Journal of Evolutionary Biology 22: 2305 – 2319.

Ydenberg, R.C., Brown, J.S., and Stephens, D.W. 2007. Foraging: an overview. In: Foraging Behavior and Ecology. Stephens, D.W., Brown, J.S., and Ydenberg, R.C., eds. University of Chicago Press, Chicago. 608 pp.

Appendix 1

Table A1.1 Coefficient values for the categorical Lake predictor estimated in GLMs fit to presence/absence or biomass indicator data. The intercept is the first row; other rows refer to lakes (Table 1.1). Each column reflects a separate model of the type indicated to predict the prey categories snail (S), tadpole shrimp (T), pea clam (P), Bosmina *(B), chironomid pupae (C), and fish (F).*

	Presence / Absence						Biomass indicator					
	SD	TD	PD	BD	CD	FD	SG	TG	PG	BG	CG	FG
Int.	-0.103	-2.554	-1.622	-3.861	-0.062	-1.412	-0.279	3.226	-1.148	0.725	-2.340	-0.337
1	-1.976	21.120	1.399	-16.705	-2.018	-18.154	-3.119	-5.813	-3.245	-	-3.802	-
2	0.968	4.303	2.152	-16.705	-18.504	-18.154	0.423	-9.372	-0.711	-	-	-
3	-0.890	0.698	4.050	0.999	0.445	-18.154	-0.677	-8.662	-0.334	-2.465	-0.775	-
4	0.663	-16.012	-15.944	-16.705	-18.504	1.972	-1.411	-	-	-	-	1.043
6	-2.409	1.455	3.356	1.348	1.448	-18.154	-1.535	-7.587	-0.030	-2.108	0.234	-
7	-17.463	21.120	1.009	2.219	0.558	-18.154	-	-6.365	-1.922	-3.516	-0.393	-
8	-17.463	1.401	2.566	-16.705	1.448	-1.030	-	-5.940	-0.259	-	-0.694	-0.525

(Continued)

Table A1.1 (Continued). Coefficient values for the categorical Lake predictor estimated in GLMs fit to presence/absence or biomass indicator data. The intercept is the first row; other rows refer to lakes (Table 1.1). Each column reflects a separate model of the type indicated to predict the prey categories snail (S), tadpole shrimp (T), pea clam (P), Bosmina *(B), chironomid pupae (C), and fish (F).*

9	-3.922	3.495	-0.191	-16.705	-0.257	0.948	-2.700	-6.346	-4.124	-	-1.388	0.072
10	-0.260	1.034	3.142	-16.705	-18.504	-0.757	-1.046	-11.918	1.042	-	-	0.096
11	-2.325	2.057	2.757	-16.705	2.172	0.124	-0.827	-4.649	1.295	-	0.928	-0.783
13	-3.264	3.401	2.469	1.222	-18.504	-18.154	-2.848	-5.771	-0.599	-5.783	-	-
14	-1.318	3.653	0.200	0.305	-2.771	2.368	-0.734	-10.095	-2.617	-8.493	0.474	-0.313
15	17.669	-16.012	-15.944	-16.705	-18.504	-18.154	-0.093	-	-	-	-	-
17	-0.590	2.378	1.231	-16.705	1.281	-0.728	0.149	-3.457	0.665	-	0.490	-0.325
19	0.796	3.401	0.610	-16.705	-0.206	-18.154	0.149	-4.415	-3.204	-	-0.346	-
20	-1.437	2.258	2.101	-16.705	-0.960	-1.360	-1.436	-5.208	-0.286	-	-0.040	-0.374
21	-3.032	1.219	19.188	1.463	-18.504	-18.154	-3.753	-8.883	0.600	-7.608	-	-
22	-17.463	1.088	0.684	-16.705	-0.876	1.792	-	-7.464	-0.054	-	0.564	-0.449
23	-1.113	21.120	1.216	0.334	0.350	-18.154	-0.964	-6.255	-0.182	-4.468	-0.820	-
24	-2.571	0.905	4.296	-16.705	-18.504	-0.821	-1.149	-10.266	2.310	-	-	0.534
28	-0.025	1.796	0.436	-16.705	1.646	-1.273	0.433	-6.895	-2.501	-	0.275	1.259
29	0.663	1.330	1.622	1.558	0.430	-18.154	0.176	-8.034	-0.500	-3.238	-0.736	-
30	-0.064	-16.012	0.735	2.251	-0.105	-18.154	-0.764	-	-3.326	-1.114	-0.723	-
31	2.766	-16.012	1.448	-16.705	-1.219	-0.939	0.835	-	-0.748	-	-0.354	2.426

(Continued)

Table A1.1 (Continued). Coefficient values for the categorical Lake predictor estimated in GLMs fit to presence/absence or biomass indicator data. The intercept is the first row; other rows refer to lakes (Table 1.1). Each column reflects a separate model of the type indicated to predict the prey categories snail (S), tadpole shrimp (T), pea clam (P), Bosmina *(B), chironomid pupae (C), and fish (F).*

32	2.706	-0.778	-0.211	-16.705	-1.771	-1.920	0.328	-6.314	0.416	-	-1.153	0.044
33	2.406	-16.012	0.789	-16.705	-1.919	-0.310	0.307	-	-1.214	-	-1.338	-0.207
34	-1.283	1.542	-15.944	-16.705	0.755	-18.154	-1.143	-11.078	-	-	0.112	-
35	-0.276	0.285	-15.944	-16.705	0.187	0.474	-1.087	-8.558	-	-	0.672	1.759
36	0.663	0.573	1.561	-16.705	0.123	-0.890	0.931	-5.016	-0.664	-	1.122	3.277
37	0.181	3.892	3.041	-16.705	-2.842	-2.918	-0.436	-0.849	1.054	-	-1.459	-0.998
39	-2.248	1.586	4.171	3.716	-0.260	-18.154	-1.106	5.420	0.822	-3.404	-0.610	-
41	0.375	1.820	-1.962	-16.705	-0.672	-0.043	0.044	-4.518	-3.279	-	0.262	0.097
42	0.796	2.249	0.929	-16.705	0.001	-2.053	0.882	-4.581	-0.034	-	-0.446	-1.172
43	-0.022	1.281	1.873	1.592	-1.404	0.474	-1.209	-6.038	0.897	-1.297	0.418	-0.466
44	-2.224	21.120	0.929	2.849	-18.504	-18.154	-3.855	-0.625	-2.495	-4.066	-	-
46	1.019	0.762	-0.170	-16.705	-1.730	-18.154	0.150	-10.942	-1.440	-	-4.149	-
47	-2.700	2.497	3.670	1.057	1.123	-18.154	0.575	-6.044	0.054	-2.307	0.596	-
48	-0.539	0.394	1.829	-16.705	-2.098	0.770	-0.820	-5.289	1.485	-	-2.535	0.691
49	1.672	-16.012	-0.981	0.529	-1.507	-18.154	0.669	-	-3.915	-2.638	-0.593	-
50	0.347	0.708	-0.101	-16.705	0.688	-1.632	-0.163	-6.391	-1.966	-	1.374	0.567
51	-0.359	2.554	1.622	1.246	-0.306	0.054	0.289	-6.132	0.264	-1.628	0.393	0.642
52	-2.094	21.120	2.027	1.664	-18.504	-18.154	-3.681	-2.320	-2.620	-8.522	-	-

(Continued)

Table A1.1 (Continued). Coefficient values for the categorical Lake predictor estimated in GLMs fit to presence/absence or biomass indicator data. The intercept is the first row; other rows refer to lakes (Table 1.1). Each column reflects a separate model of the type indicated to predict the prey categories snail (S), tadpole shrimp (T), pea clam (P), Bosmina *(B), chironomid pupae (C), and fish (F).*

53	0.103	0.819	2.241	-16.705	-18.504	-0.785	0.323	-6.014	0.381	-	-	-0.077
54	-3.155	3.604	1.997	3.935	-18.504	-0.337	-4.680	-4.563	1.682	-4.004	-	-1.356
57	-1.631	2.148	19.188	0.916	-1.673	-18.154	0.269	-2.793	0.983	-6.478	-0.994	-
58	-1.283	2.364	-1.503	3.882	0.601	0.590	0.151	-5.750	-3.736	-0.627	1.093	0.548
59	0.914	1.974	2.976	3.168	0.532	-2.225	0.055	-10.845	-0.102	-1.016	0.088	-0.689
60	-1.843	2.353	1.421	0.916	3.725	-2.251	-0.005	-3.963	-1.315	-1.717	1.741	-1.172
61	-2.462	0.762	3.742	-16.705	-0.373	-18.154	-1.466	-8.559	0.378	-	0.162	-
62	0.742	0.783	4.899	-16.705	-1.570	-18.154	0.519	-3.967	0.641	-	-2.478	-
64	-1.091	2.979	2.246	1.270	-0.666	-2.325	-0.667	-4.827	1.457	-5.422	-0.119	-0.419
65	-0.431	1.273	0.795	3.686	-0.472	-18.154	0.096	11.242	0.493	-0.986	-1.531	-
67	-17.463	1.573	2.181	2.357	2.364	-18.154	-	-4.179	-0.689	-3.484	0.631	-

Table A1.2. Standard errors for coefficient values (Table A1.1) of the categorical Lake predictor estimated in GLMs fit to presence/absence or biomass indicator data. The intercept is the first row; other rows refer to lakes (Table 1.1). Each column reflects a separate model of the type indicated to predict the prey categories snail (S), tadpole shrimp (T), pea clam (P), Bosmina *(B), chironomid pupae (C), and fish (F).*

	Presence/Absence						Biomass indicator					
	SD	TD	PD	BD	CD	FD	SG	TG	PG	BG	CG	FG
Int.	0.203	0.392	0.274	0.715	0.203	0.256	0.166	0.590	0.395	1.024	0.216	0.196
1	0.568	1087.107	0.433	2955.062	0.568	1792.336	0.587	0.645	0.558	-	0.771	-
2	0.468	0.669	0.483	3412.211	1255.282	2069.611	0.307	0.674	0.550	-	-	-
3	0.422	0.621	0.662	1.019	0.392	1767.949	0.393	0.914	0.479	1.448	0.382	-
4	0.488	1390.631	843.461	3780.128	1390.631	0.512	0.344	-	-	-	-	0.300
6	0.634	0.536	0.521	0.933	0.444	1700.359	0.671	0.769	0.479	1.322	0.339	-
7	650.392	1072.315	0.440	0.842	0.395	1767.949	-	0.643	0.590	1.182	0.377	-
8	791.236	0.611	0.523	3546.074	0.540	0.780	-	0.868	0.543	-	0.395	0.634
9	1.029	0.491	0.469	2348.445	0.337	0.373	1.138	0.638	0.684	-	0.371	0.267
10	0.384	0.573	0.499	2839.131	1044.458	0.587	0.327	0.834	0.484	-	-	0.469
11	0.636	0.519	0.471	2914.855	0.567	0.474	0.671	0.722	0.495	-	0.336	0.359
13	1.037	0.559	0.483	1.023	1190.865	1963.405	1.138	0.681	0.524	1.448	-	-
14	0.468	0.550	0.502	1.241	0.755	0.452	0.457	0.662	0.716	1.773	1.069	0.257
15	2797.442	4612.202	2797.44	12537.265	4612.202	7604.236	0.813	-	-	-	-	-
17	0.347	0.474	0.384	2348.445	0.375	0.502	0.307	0.664	0.514	-	0.311	0.399

(Continued)

Table A1.2 (Continued). Standard errors for coefficient values (Table A1.1) of the categorical Lake predictor estimated in GLMs fit to presence/absence or biomass indicator data. The intercept is the first row; other rows refer to lakes (Table 1.1). Each column reflects a separate model of the type indicated to predict the prey categories snail (S), tadpole shrimp (T), pea clam (P), Bosmina (B), chironomid pupae (C), and fish (F).

19	0.341	0.483	0.400	2288.981	0.330	1388.337	0.243	0.637	0.558	-	0.362	-
20	0.378	0.463	0.370	2150.123	0.342	0.575	0.365	0.657	0.464	-	0.410	0.469
21	1.042	0.638	807.552	1.028	1331.428	2195.154	1.138	0.914	0.510	1.448	-	-
22	699.361	0.599	0.479	3134.316	0.443	0.442	-	0.868	0.658	-	0.539	0.277
23	0.451	1102.527	0.440	1.241	0.397	1817.760	0.431	0.646	0.578	1.773	0.395	-
24	0.759	0.626	0.781	3184.469	1171.500	0.659	0.813	0.914	0.492	-	-	0.530
28	0.356	0.502	0.440	2586.240	0.438	0.649	0.292	0.714	0.619	-	0.321	0.530
29	0.374	0.532	0.407	0.886	0.368	1621.228	0.270	0.769	0.519	1.254	0.362	-
30	0.457	1331.428	0.526	0.900	0.457	2195.154	0.378	-	0.716	1.254	0.496	-
31	0.631	961.711	0.403	2614.201	0.411	0.582	0.239	-	0.524	-	0.516	0.469
32	0.761	1.091	0.604	3292.447	0.576	1.049	0.273	1.668	0.883	-	0.771	0.875
33	0.639	1135.446	0.467	3086.461	0.571	0.549	0.264	-	0.637	-	0.771	0.428
34	0.677	0.703	1021.48	4577.962	0.584	2776.674	0.671	0.978	-	-	0.516	-
35	0.413	0.722	699.361	3134.316	0.408	0.469	0.354	1.077	-	-	0.419	0.345
36	0.415	0.662	0.443	3086.461	0.403	0.657	0.297	0.978	0.558	-	0.419	0.530
37	0.306	0.483	0.397	2020.563	0.552	1.039	0.243	0.623	0.443	-	0.771	0.875

(Continued)

Table A1.2 (Continued). Standard errors for coefficient values (Table A1.1) of the categorical Lake predictor estimated in GLMs fit to presence/absence or biomass indicator data. The intercept is the first row; other rows refer to lakes (Table 1.1). Each column reflects a separate model of the type indicated to predict the prey categories snail (S), tadpole shrimp (T), pea clam (P), Bosmina (B), chironomid pupae (C), and fish (F).

39	0.473	0.476	0.539	0.754	0.317	1294.631	0.489	0.690	0.442	1.055	0.350	-
41	0.389	0.527	1.050	2914.855	0.406	0.492	0.297	0.742	1.628	-	0.479	0.377
42	0.422	0.527	0.460	3086.461	0.403	1.047	0.292	0.722	0.619	-	0.429	0.875
43	0.408	0.580	0.449	0.937	0.496	0.469	0.335	0.834	0.543	1.322	0.642	0.345
44	0.562	972.338	0.418	0.790	972.338	1603.114	0.587	0.634	0.568	1.106	-	-
46	0.861	1.149	1.114	6701.450	1.099	4064.635	0.530	1.668	1.628	-	1.496	-
47	0.554	0.460	0.465	0.881	0.341	1285.350	0.587	0.648	0.443	1.254	0.298	-
48	0.440	0.725	0.463	3292.447	0.643	0.467	0.393	1.077	0.558	-	0.882	0.333
49	0.532	1211.224	0.782	1.243	0.532	1996.970	0.283	-	1.185	1.773	0.696	-
50	0.321	0.532	0.439	2182.458	0.329	0.644	0.249	0.786	0.637	-	0.312	0.530
51	0.370	0.495	0.407	0.932	0.368	0.453	0.320	0.677	0.519	1.322	0.410	0.345
52	1.074	2062.639	0.701	1.273	2062.639	3400.718	1.138	0.769	0.756	1.773	-	-
53	0.491	0.739	0.543	3964.631	1458.506	0.788	0.393	1.077	0.590	-	-	0.634
54	1.039	0.589	0.478	0.812	1255.282	0.599	1.138	0.685	0.558	1.094	-	0.469
57	0.658	0.602	884.629	1.250	0.658	2404.670	0.671	0.808	0.530	1.773	0.882	-
58	0.327	0.443	0.580	0.743	0.294	0.339	0.307	0.636	0.883	1.045	0.288	0.252

(Continued)

Table A1.2 (Continued). Standard errors for coefficient values (Table A1.1) of the categorical Lake predictor estimated in GLMs fit to presence/absence or biomass indicator data. The intercept is the first row; other rows refer to lakes (Table 1.1). Each column reflects a separate model of the type indicated to predict the prey categories snail (S), tadpole shrimp (T), pea clam (P), Bosmina (B), chironomid pupae (C), and fish (F).

59	0.402	0.515	0.482	0.791	0.387	1.045	0.273	0.722	0.486	1.100	0.371	0.875
60	0.520	0.505	0.419	1.018	1.033	1.045	0.530	0.695	0.543	1.448	0.321	0.875
61	0.761	0.668	0.669	3350.725	0.437	2032.317	0.813	0.978	0.506	-	0.496	-
62	0.349	0.548	0.771	2390.763	0.417	1450.071	0.251	0.808	0.451	-	0.539	-
64	0.414	0.501	0.421	0.932	0.384	1.044	0.393	0.664	0.495	1.322	0.451	0.875
65	0.367	0.531	0.421	0.773	0.367	1585.593	0.320	0.769	0.578	1.071	0.419	-
67	1192.833	0.782	0.684	1.059	1.068	3242.457	-	1.077	0.716	1.448	0.516	-

(Continued)

Appendix 2

Table A2.1. Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict snail consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model:*
$d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

	Logistic						Log					
	L only		optimum		simult. optimum		L only		optimum		simult. optimum	
	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
$ß_0$	-0.12	0.20	-1.17	1.63	1.38	1.50	-0.28	0.17	3.36	1.44	2.66	1.43
L1	-1.87	0.65	-1.41	0.67	-2.29	0.67	-3.27	0.69	-3.16	0.65	-3.57	0.68
L2	1.57	0.59	1.82	0.62	0.85	0.63	0.52	0.33	0.52	0.32	0.21	0.36
L3	-0.88	0.49	-0.07	0.52	-1.12	0.56	-0.84	0.47	-0.75	0.45	-1.01	0.50
L4	0.71	0.59	0.98	0.63	0.55	0.63	-1.58	0.42	-1.24	0.41	-1.64	0.44
L6	-2.65	0.76	-1.96	0.78	-2.61	0.78	-1.25	0.83	-0.80	0.77	-1.16	0.82
L7	-17.4	1142	-16.8	1123	-17.5	1127	-	-	-	-	-	-
L8	-17.4	1057	-17.3	1022	-17.5	1042	-	-	-	-	-	-
L9	-17.4	960	-16.8	941	-17.8	938	-	-	-	-	-	-
L10	0.12	1.43	0.90	1.48	-0.37	1.47	-2.05	1.16	-1.75	1.08	-2.41	1.15
L11	-2.28	1.06	-2.24	1.13	-2.93	1.09	0.01	1.16	0.21	1.08	-0.03	1.15
L13	-3.01	1.04	-2.42	1.05	-3.12	1.06	-2.85	1.16	-2.55	1.08	-2.92	1.14
L14	-0.76	0.49	-0.24	0.53	-1.04	0.52	-0.73	0.47	-0.53	0.44	-0.77	0.47
L17	-1.67	0.79	-1.09	0.81	-1.65	0.80	0.22	0.83	0.67	0.77	0.35	0.82
L19	-0.01	0.42	0.75	0.45	-0.15	0.45	-0.74	0.35	-0.49	0.34	-0.84	0.37
L20	-1.06	0.45	-0.39	0.48	-1.35	0.51	-1.56	0.44	-1.31	0.42	-1.72	0.46
L21	-2.71	1.05	-2.42	1.07	-3.14	1.07	-3.76	1.16	-3.52	1.08	-3.95	1.14
L22	-17.4	1142	-17.2	1133	-18.0	1116	-	-	-	-	-	-
L23	-0.86	0.71	-0.56	0.73	-1.62	0.75	-0.46	0.69	-0.44	0.64	-0.82	0.69
L24	-17.4	1319	-16.7	1308	-16.9	1316	-	-	-	-	-	-
L28	0.03	0.36	0.87	0.40	0.29	0.38	0.47	0.30	0.84	0.29	0.62	0.31

(Continued)

Table A2.1 (Continued). Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict snail consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model:*

$d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

L29	0.97	0.45	1.28	0.48	1.18	0.47	0.18	0.30	0.28	0.30	0.13	0.32
L30	0.22	0.48	1.13	0.52	0.29	0.51	-0.76	0.39	-0.41	0.37	-0.77	0.40
L31	3.52	1.04	4.17	1.05	3.79	1.04	0.85	0.27	1.03	0.27	0.89	0.28
L32	2.32	0.77	3.02	0.81	2.58	0.79	0.23	0.32	0.56	0.32	0.24	0.33
L33	1.51	0.82	1.88	0.83	1.55	0.84	0.49	0.44	0.39	0.42	0.37	0.44
L34	-1.18	0.68	-0.88	0.70	-1.54	0.71	-1.14	0.69	-1.00	0.64	-1.37	0.69
L35	0.12	0.57	0.60	0.60	0.02	0.59	-1.46	0.47	-1.28	0.44	-1.56	0.47
L36	1.00	0.57	1.97	0.61	1.23	0.59	0.64	0.37	0.93	0.35	0.72	0.38
L37	0.33	0.33	1.49	0.41	0.93	0.44	-0.45	0.26	-0.26	0.27	-0.58	0.29
L39	-0.57	0.58	-0.28	0.61	-0.53	0.60	-1.08	0.54	-0.82	0.51	-1.24	0.54
L42	0.62	0.43	1.22	0.46	0.43	0.47	0.93	0.32	0.82	0.32	0.72	0.34
L43	0.05	0.44	0.45	0.46	-0.28	0.46	-1.25	0.36	-1.15	0.35	-1.35	0.37
L44	-1.18	0.68	-0.70	0.70	-1.93	0.73	-3.68	0.69	-3.30	0.64	-3.75	0.69
L47	-2.47	0.63	-1.84	0.65	-2.29	0.65	-0.19	0.69	-0.02	0.63	-0.39	0.68
L48	-0.79	0.52	-0.70	0.59	-1.15	0.56	-1.04	0.50	-0.95	0.50	-1.13	0.52
L49	1.83	0.58	2.34	0.61	1.29	0.61	0.63	0.30	0.72	0.29	0.40	0.33
L50	0.50	0.33	1.34	0.38	0.49	0.36	-0.17	0.26	-0.01	0.25	-0.30	0.28
L51	-0.09	0.38	0.74	0.44	-0.05	0.41	0.29	0.33	0.36	0.32	0.35	0.34
L53	-17.4	2797	-16.6	2784	-17.1	2797	-	-	-	-	-	-
L54	-1.82	1.09	-1.72	1.19	-2.01	1.12	-4.69	1.16	-3.59	1.17	-4.18	1.25
L57	-2.52	1.05	-2.62	1.09	-3.09	1.08	-2.14	1.16	-3.12	1.13	-2.11	1.14
L58	-1.18	0.38	-0.41	0.42	-1.20	0.40	0.19	0.37	0.12	0.35	0.01	0.38
L59	1.22	0.48	2.02	0.53	1.17	0.51	0.14	0.30	0.27	0.30	0.01	0.32
L60	-2.15	0.64	-1.67	0.74	-2.03	0.65	-1.81	0.69	-1.61	0.66	-1.78	0.69
L61	-2.44	0.76	-1.82	0.90	-2.23	0.77	-1.47	0.83	-1.28	0.77	-1.56	0.82
L62	0.36	0.45	1.13	0.48	0.70	0.48	0.01	0.35	0.23	0.33	0.18	0.35
L64	-1.21	0.54	-0.55	0.57	-1.18	0.56	-0.44	0.54	-0.10	0.50	-0.38	0.53
L65	0.06	0.41	0.64	0.44	0.60	0.43	0.05	0.34	0.23	0.33	0.02	0.34
L67	-17.4	1399	-16.5	1385	-17.1	1397	-	-	-	-	-	-

(Continued)

Table A2.1 (Continued). Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict snail consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model:*

$d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

$ß_{10}$	-	-	-0.17	0.21	-0.30	0.19	-	-	-0.55	0.19	-0.42	0.19
$ß_{20}$	-	-	0.01	0.01	0.02	0.01	-	-	0.02	0.01	0.02	0.01
$ß_{30}$	-	-	0.00	0.00	0.00	0.00	-	-	0.00	0.00	0.00	0.00
$ß_{40}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{01}$	-	-	-1.00	0.36	-2.42	0.61	-	-	-0.54	0.24	0.13	0.07
$ß_{02}$	-	-	2.86	0.58	-	-	-	-	0.20	0.05	-	-
$ß_{03}$	-	-	0.30	0.09	-	-	-	-	-0.06	0.03	-	-
$ß_{11}$	-	-	0.03	0.01	0.21	0.05	-	-	0.03	0.01	-	-
$ß_{12}$	-	-	-0.23	0.05	-	-	-	-	-	-	-	-
$ß_{13}$	-	-	-0.01	0.00	-	-	-	-	-	-	-	-
$ß_{21}$	-	-	-	-	0.00	0.00	-	-	-	-	-	-
$ß_{31}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{22}$	-	-	0.00	0.00	-	-	-	-	-	-	-	-

Table A2.2. Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict tadpole shrimp consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model:*

$d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

	Logistic						Log					
	L only		optimum		simult. optimum		L only		optimum		simult. optimum	
	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
$ß_0$	-2.56	0.39	-1.98	0.53	-2.05	0.50	0.81	0.59	1.54	1.06	1.57	0.63
L1	21.13	1305	21.32	1225	21.93	1293	-3.49	0.67	-3.34	0.69	-3.23	0.66
L2	4.82	0.84	5.97	0.93	6.35	0.92	-6.89	0.69	-6.23	0.71	-6.11	0.69
L3	0.08	0.83	0.17	0.85	0.80	0.88	-7.33	1.26	-7.31	1.18	-7.19	1.18
L4	-16.00	1743	-14.99	1699	-15.16	1683	-	-	-	-	-	-
L6	1.69	0.54	1.87	0.57	2.14	0.58	-5.17	0.77	-5.28	0.77	-5.21	0.76
L7	21.13	1883	21.14	1848	21.57	1866	-4.97	0.75	-4.64	0.74	-4.47	0.72
L8	0.77	0.86	0.90	0.88	1.27	0.88	-2.83	1.26	-3.26	1.17	-3.18	1.17
L9	3.17	0.64	3.88	0.69	4.10	0.69	-4.37	0.76	-3.97	0.75	-3.85	0.73
L10	2.56	1.47	3.21	2.45	3.78	1.58	-11.22	1.68	-11.34	1.53	-11.24	1.53
L11	1.47	0.77	1.68	0.80	2.41	0.81	-4.74	1.08	-4.60	1.02	-4.52	1.01
L13	3.45	0.60	3.82	0.62	3.93	0.61	-3.31	0.70	-3.01	0.71	-2.88	0.69
L14	3.66	0.61	4.42	0.67	4.61	0.66	-7.55	0.70	-6.77	0.70	-6.66	0.69
L17	2.28	0.67	2.37	0.72	2.66	0.69	-2.38	0.87	-2.01	0.82	-1.99	0.82
L19	4.76	0.72	4.68	0.74	5.32	0.75	-1.63	0.67	-1.58	0.68	-1.48	0.66
L20	1.96	0.53	2.07	0.56	2.77	0.59	-2.53	0.75	-2.73	0.74	-2.68	0.73
L21	1.31	0.69	1.92	0.74	2.03	0.72	-6.27	0.98	-4.64	0.95	-4.53	0.95
L22	1.47	0.77	1.82	0.82	2.32	0.81	-5.54	1.08	-5.45	1.02	-5.35	1.01
L23	21.13	1967	21.85	1953	22.56	1913	-4.02	0.76	-3.20	0.76	-3.09	0.74
L24	0.49	1.13	0.88	1.15	0.40	1.13	-10.74	1.68	-10.26	1.52	-10.13	1.51
L28	1.70	0.51	2.12	0.55	1.76	0.52	-4.40	0.74	-3.69	0.71	-3.80	0.71
L29	1.38	0.58	1.95	0.62	1.62	0.60	-5.80	0.84	-4.84	0.84	-4.72	0.83
L30	-16.00	1423	-15.67	1415	-15.72	1404	-	-	-	-	-	-
L31	-16.00	1172	-15.46	1166	-15.87	1164	-	-	-	-	-	-
L32	-0.38	1.10	0.31	1.12	-0.12	1.11	-3.90	1.68	-3.48	1.54	-3.29	1.54
L33	-16.00	2063	-15.38	2056	-15.59	2004	-	-	-	-	-	-

(Continued)

Table A2.2 (Continued). Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict tadpole shrimp consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model:*

$d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

L34	1.27	0.76	1.90	0.79	1.89	0.78	-8.96	1.08	-8.19	1.03	-8.06	1.01
L35	0.00	1.11	0.43	1.13	0.44	1.12	-6.60	1.68	-5.89	1.53	-5.74	1.52
L36	1.02	0.75	1.32	0.77	1.23	0.76	-2.32	1.08	-2.23	1.01	-2.38	1.01
L37	3.81	0.50	4.07	0.57	4.05	0.57	1.47	0.64	1.31	0.67	1.29	0.67
L39	1.55	0.70	1.26	0.74	1.88	0.72	-2.11	0.98	-1.83	0.93	-1.74	0.92
L42	2.22	0.54	2.65	0.58	2.80	0.57	-2.20	0.75	-1.82	0.73	-1.72	0.72
L43	1.31	0.61	1.76	0.64	2.00	0.63	-3.47	0.87	-3.24	0.85	-3.15	0.83
L44	21.13	1743	21.54	1639	22.38	1682	1.73	0.73	2.12	0.74	2.31	0.72
L47	2.52	0.50	2.81	0.53	2.81	0.53	-3.64	0.68	-3.89	0.68	-3.85	0.68
L48	0.31	0.84	1.43	0.89	1.22	0.87	-2.77	1.26	-2.48	1.16	-2.40	1.15
L49	-16.00	1279	-15.48	1270	-15.08	1253	-	-	-	-	-	-
L50	0.85	0.53	1.31	0.57	1.24	0.55	-3.97	0.79	-3.77	0.76	-3.72	0.75
L51	2.35	0.51	2.83	0.55	2.93	0.53	-3.52	0.70	-3.56	0.70	-3.47	0.68
L53	-16.00	4612	-15.64	4608	-15.89	4612	-	-	-	-	-	-
L54	3.66	0.91	4.53	0.96	5.28	1.08	-2.51	0.87	-1.78	0.85	-1.76	0.84
L57	2.70	0.65	4.14	0.99	3.70	0.71	-0.37	0.81	0.88	0.80	1.01	0.79
L58	2.85	0.48	3.29	0.51	3.15	0.49	-3.18	0.65	-2.50	0.62	-2.40	0.61
L59	2.28	0.55	2.93	0.59	2.95	0.58	-8.61	0.75	-7.73	0.73	-7.59	0.71
L60	2.44	0.53	2.46	0.62	2.68	0.54	-1.66	0.72	-1.28	0.75	-1.07	0.73
L61	0.77	0.67	0.97	0.73	0.84	0.68	-6.16	0.98	-5.22	0.91	-5.47	0.91
L62	0.57	0.73	0.86	0.75	0.62	0.74	-1.44	1.08	-1.60	1.00	-1.57	1.00
L64	2.90	0.57	3.37	0.61	3.18	0.59	-2.92	0.73	-2.14	0.70	-2.04	0.69
L65	0.66	0.66	0.92	0.69	0.46	0.67	-0.94	0.98	-1.27	0.97	-1.17	0.96
L67	1.47	0.91	1.58	0.92	1.47	0.91	-3.69	1.26	-2.83	1.14	-2.65	1.13

(Continued)

Table A2.2 (Continued). Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict tadpole shrimp consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for* ß *values). Coefficient labels refer to a model:*

$d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

$ß_{10}$	-	-	-0.04	0.02	-0.04	0.01	-	-	0.00	0.07	-	-
$ß_{20}$	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00
$ß_{30}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{40}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{01}$	-	-	-2.01	0.39	0.21	0.27	-	-	1.30	0.30	1.35	0.30
$ß_{02}$	-	-	0.75	0.22	-	-	-	-	-1.07	0.18	-0.62	0.10
$ß_{03}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{11}$	-	-	0.07	0.01	-0.03	0.01	-	-	-0.05	0.01	-0.05	0.01
$ß_{12}$	-	-	-0.02	0.01	-	-	-	-	0.04	0.01	-	-
$ß_{13}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{21}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{31}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{22}$	-	-	-	-	-	-	-	-	-	-	0.00	0.00

Table A2.3. Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict pea clam consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model:* $d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

	Logistic						Log					
	L only		optimum		simult. optimum		L only		optimum		simult. optimum	
	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
$ß_0$	-1.63	0.27	-1.83	0.33	-1.35	0.28	-1.15	0.37	6.24	2.37	3.60	2.04
L1	1.23	0.49	1.21	0.51	1.35	0.49	-2.96	0.60	-2.00	0.66	-1.11	0.65
L2	2.12	0.53	2.83	0.56	2.48	0.54	-0.65	0.56	1.18	0.62	1.43	0.63
L3	3.67	0.67	3.96	0.69	3.53	0.67	-0.15	0.49	0.82	0.56	1.14	0.60
L4	-15.93	1057	-15.07	1029	-15.46	1041	-	-	-	-	-	-
L6	3.39	0.56	3.66	0.58	3.23	0.56	-0.31	0.47	0.69	0.54	1.03	0.54
L7	1.30	0.65	1.56	0.66	1.29	0.65	-2.27	0.77	-1.21	0.79	-0.70	0.78
L8	3.43	0.81	3.83	0.83	3.40	0.81	-0.04	0.57	0.86	0.61	1.35	0.62
L9	-1.14	1.07	-0.52	1.08	-0.99	1.07	-3.37	1.54	-1.98	1.50	-1.83	1.49
L10	1.63	1.44	1.68	1.45	1.90	1.47	1.11	1.54	2.29	1.51	2.55	1.49
L11	3.24	0.82	3.79	0.84	3.33	0.82	1.46	0.60	3.08	0.64	3.02	0.65
L13	2.52	0.53	2.96	0.55	2.52	0.53	-0.68	0.52	0.70	0.58	0.90	0.58
L14	-0.31	0.68	0.42	0.70	-0.05	0.68	-4.29	0.94	-1.98	0.95	-1.99	0.95
L17	1.05	0.62	1.38	0.65	1.08	0.63	0.38	0.77	1.50	0.80	2.22	0.80
L19	1.09	0.47	1.37	0.49	1.03	0.47	-2.96	0.59	-1.70	0.63	-1.46	0.63
L20	2.51	0.47	2.97	0.50	2.54	0.47	-0.59	0.48	0.77	0.54	0.90	0.57
L21	19.20	932	20.15	920	19.65	923	0.75	0.51	2.11	0.58	2.38	0.58
L22	0.02	0.82	0.52	0.84	0.21	0.83	0.45	1.12	1.98	1.11	2.06	1.11
L23	1.07	0.68	1.94	0.72	1.44	0.70	-1.94	0.84	-0.07	0.90	0.20	0.87
L24	3.71	1.10	4.12	1.11	3.68	1.10	2.68	0.65	3.76	0.69	4.29	0.69
L28	0.41	0.45	0.65	0.47	0.33	0.45	-2.45	0.60	-1.46	0.64	-1.10	0.63
L29	1.50	0.46	1.92	0.49	1.75	0.47	-0.45	0.55	1.03	0.60	1.22	0.61
L30	0.47	0.58	0.82	0.60	0.39	0.58	-3.79	0.77	-2.62	0.79	-2.27	0.79
L31	1.70	0.45	2.16	0.48	1.76	0.45	-0.55	0.53	0.54	0.58	1.10	0.59
L32	-0.10	0.68	0.50	0.71	0.13	0.69	0.70	0.94	1.76	0.94	2.46	0.93
L33	2.48	0.74	3.19	0.77	2.71	0.75	-1.07	0.68	0.36	0.71	0.73	0.71
L34	-15.93	1057	-15.33	1053	-15.73	1055	-	-	-	-	-	-
L35	-15.93	1057	-15.42	1054	-15.83	1055	-	-	-	-	-	-

(Continued)

Table A2.3 (Continued). Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict pea clam consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model:*

$d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

L36	1.75	0.56	2.00	0.58	1.58	0.56	-2.39	0.62	-1.74	0.66	-1.30	0.63
L37	2.88	0.42	3.17	0.49	2.68	0.42	1.09	0.44	2.04	0.53	2.42	0.53
L39	3.51	0.81	3.68	0.82	3.47	0.81	1.03	0.56	2.24	0.59	2.55	0.59
L42	0.84	0.49	1.29	0.51	0.86	0.49	-0.33	0.62	1.43	0.67	1.35	0.67
L43	1.71	0.47	2.31	0.51	1.86	0.48	0.94	0.55	2.41	0.60	2.71	0.60
L44	1.63	0.60	1.83	0.61	1.75	0.61	-3.18	0.68	-1.99	0.71	-1.54	0.72
L47	3.91	0.59	4.26	0.61	3.82	0.59	0.13	0.44	1.13	0.50	1.53	0.51
L48	1.54	0.52	2.36	0.57	2.04	0.54	1.68	0.60	3.27	0.65	3.75	0.65
L49	-0.85	0.79	-0.30	0.80	-0.70	0.79	-3.93	1.12	-2.47	1.11	-2.41	1.11
L50	0.04	0.44	0.41	0.47	0.01	0.44	-1.97	0.60	-0.74	0.64	-0.62	0.64
L51	1.95	0.43	2.65	0.47	2.18	0.44	0.26	0.49	1.67	0.54	1.95	0.55
L53	19.20	2797	19.57	2796	19.08	2797	0.23	1.12	1.29	1.11	1.60	1.10
L54	1.12	0.78	2.11	0.83	1.60	0.81	-0.35	0.94	0.53	0.95	1.30	0.95
L57	19.20	1021	19.25	956	19.60	1016	0.77	0.54	2.19	0.64	2.68	0.59
L58	-1.66	0.77	-1.31	0.79	-1.73	0.77	-4.61	1.12	-2.68	1.12	-2.73	1.11
L59	3.16	0.56	3.92	0.62	3.41	0.58	-0.06	0.49	1.23	0.54	1.59	0.54
L60	1.63	0.45	2.26	0.49	1.80	0.46	-2.22	0.53	-0.98	0.57	-0.75	0.57
L61	3.75	0.67	3.95	0.69	3.55	0.67	0.38	0.48	0.91	0.52	1.13	0.50
L62	19.20	791	19.58	788	19.15	789	0.47	0.48	1.77	0.53	2.02	0.54
L64	2.14	0.50	2.57	0.53	2.11	0.50	1.65	0.54	2.76	0.57	3.07	0.57
L65	1.04	0.46	1.15	0.48	1.05	0.47	0.71	0.59	1.73	0.63	2.33	0.64
L67	2.73	0.86	3.03	0.88	2.60	0.86	-0.61	0.72	0.63	0.72	0.92	0.73

(Continued)

Table A2.3 (Continued). Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict pea clam consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model:*

$d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

$ß_{10}$	-	-	-	-	-	-	-	-	-1.00	0.33	-0.75	0.29
$ß_{20}$	-	-	-	-	-	-	-	-	0.04	0.01	0.03	0.01
$ß_{30}$	-	-	0.00	0.00	0.00	0.00	-	-	0.00	0.00	0.00	0.00
$ß_{40}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{01}$	-	-	-	-	-	-	-	-	-5.12	2.13	-4.86	1.81
$ß_{02}$	-	-	0.18	0.06	-	-	-	-	-1.50	0.56	-	-
$ß_{03}$	-	-	-0.07	0.02	-	-	-	-	0.05	0.02	-	-
$ß_{11}$	-	-	-	-	-	-	-	-	0.75	0.29	0.63	0.26
$ß_{12}$	-	-	-	-	-	-	-	-	0.14	0.05	-	-
$ß_{13}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{21}$	-	-	-	-	-	-	-	-	-0.03	0.01	-0.03	0.01
$ß_{31}$	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00
$ß_{22}$	-	-	-	-	-	-	-	-	0.00	0.00	-	-

Table A2.4 Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict cladoceran consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model with:*

$d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

	Logistic						Log					
	L only		optimum		simult. optimum		L only		optimum		simult. optimum	
	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
$ß_0$	-3.87	0.71	-3.37	0.78	-38.99	19.08	0.72	0.81	24.59	11.78	31.59	22.05
L1	-16.69	3546	-15.13	3487	-15.60	5670	-	-	-	-	-	-
L2	-16.69	3869	-14.51	3820	-15.39	5815	-	-	-	-	-	-
L3	1.39	1.03	3.38	1.15	3.52	1.27	-2.47	1.14	-2.67	1.27	-2.85	1.43
L4	-16.69	4739	-14.36	4508	-14.87	6978	-	-	-	-	-	-
L6	0.37	1.24	1.57	1.30	1.36	1.35	-1.92	1.39	-2.43	1.24	-2.33	1.38
L7	2.26	1.05	2.96	1.11	3.22	1.18	-8.28	1.14	-10.35	1.14	-9.59	1.25
L8	-16.69	4739	-15.21	4495	-16.56	7482	-	-	-	-	-	-
L9	-16.69	4300	-15.32	4130	-15.50	6583	-	-	-	-	-	-
L10	-16.69	12537	-15.64	11888	-15.76	19059	-	-	-	-	-	-
L11	-16.69	5118	-14.78	5048	-15.18	8012	-	-	-	-	-	-
L13	0.74	1.25	1.77	1.29	2.05	1.34	-8.09	1.39	-5.97	1.46	-9.22	1.53
L14	0.74	1.25	2.35	1.31	2.71	1.34	-8.76	1.39	-10.96	1.43	-10.02	1.51
L17	-16.69	4739	-15.98	4502	-17.38	7325	-	-	-	-	-	-
L19	-16.69	3237	-15.71	3170	-16.06	5190	-	-	-	-	-	-
L20	-16.69	3041	-15.50	2841	-15.63	2619	-	-	-	-	-	-
L21	1.04	1.25	3.17	1.35	2.88	1.39	-7.63	1.39	15.30	3.38	2.03	2.27
L22	-16.69	5118	-14.97	4970	-15.81	7983	-	-	-	-	-	-
L23	-16.69	5346	-14.45	5272	-15.15	7860	-	-	-	-	-	-
L24	-16.69	5910	-16.87	5750	-18.16	9584	-	-	-	-	-	-
L28	-16.69	2673	-16.78	2489	-17.71	4201	-	-	-	-	-	-
L29	1.23	1.02	2.68	1.09	2.02	1.12	-5.30	1.14	-4.08	1.20	-1.37	1.27
L30	1.62	1.03	1.89	1.08	2.26	1.10	-1.76	1.14	-2.32	1.11	-2.41	1.20
L31	-16.69	3184	-16.74	2860	-17.50	4846	-	-	-	-	-	-

(Continued)

Table A2.4 (Continued). Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict cladoceran consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model with:*

$d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

L32	-16.69	3965	-16.05	3577	-17.35	5817	-	-	-	-	-	-
L33	-16.69	5607	-15.60	5157	-17.18	8114	-	-	-	-	-	-
L34	-16.69	4739	-15.86	4118	-16.40	7174	-	-	-	-	-	-
L35	-16.69	4739	-15.49	4608	-16.22	7575	-	-	-	-	-	-
L36	-16.69	4300	-16.28	4160	-17.46	6927	-	-	-	-	-	-
L37	-16.69	2328	-16.19	2182	-17.74	3724	-	-	-	-	-	-
L39	3.47	0.89	4.84	0.98	4.45	1.03	-3.28	0.93	-5.46	0.88	-4.04	1.01
L42	-16.69	3292	-15.74	3168	-16.32	5110	-	-	-	-	-	-
L43	0.61	1.24	2.10	1.30	2.41	1.35	-1.91	1.39	-2.91	1.26	-1.82	1.38
L44	3.28	0.91	5.08	1.04	5.34	1.12	-3.77	0.95	-4.74	1.05	-4.98	1.24
L47	0.85	1.02	1.51	1.06	1.09	1.15	-2.12	1.14	-2.46	1.01	-2.33	1.15
L48	-16.69	3869	-14.59	3577	-15.20	5705	-	-	-	-	-	-
L49	-16.69	3477	-15.18	3359	-15.65	5344	-	-	-	-	-	-
L50	-16.69	2308	-16.70	2049	-16.96	3539	-	-	-	-	-	-
L51	0.26	1.24	0.65	1.27	1.14	1.30	-1.88	1.39	-2.04	1.32	-2.75	1.43
L53	-16.69	12537	-16.48	12456	-17.62	20615	-	-	-	-	-	-
L54	2.77	1.08	4.77	1.21	5.06	1.25	-8.78	1.14	-12.45	1.29	-9.90	1.36
L57	1.23	1.26	2.08	1.51	2.69	1.38	-6.51	1.39	11.61	2.82	-2.59	1.80
L58	3.73	0.76	3.80	0.81	4.08	0.83	-0.83	0.84	-0.66	0.75	-1.02	0.84
L59	3.12	0.82	4.39	0.91	4.45	0.96	-1.00	0.89	-2.13	0.90	-2.07	1.00
L60	1.16	1.02	0.78	1.08	1.14	1.09	-1.72	1.14	-2.98	1.10	-1.24	1.17
L61	-16.69	3351	-17.82	3114	-17.69	5356	-	-	-	-	-	-
L62	-16.69	3546	-16.75	3390	-18.07	5472	-	-	-	-	-	-
L64	0.74	1.25	0.45	1.31	0.64	1.29	-5.17	1.39	-5.54	1.29	-5.25	1.39
L65	3.41	0.80	4.08	0.88	3.28	0.89	-1.36	0.87	-0.23	0.95	-0.46	0.98
L67	2.77	1.08	2.30	1.14	2.36	1.14	-3.49	1.14	-3.44	1.00	-3.20	1.10

(Continued)

Table A2.4 (Continued). Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict cladoceran consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model with:*

$d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

$ß_{10}$	-	-	-	-	7.02	3.50	-	-	-3.68	1.79	-5.95	4.18
$ß_{20}$	-	-	0.00	0.00	-0.50	0.23	-	-	0.18	0.09	0.43	0.29
$ß_{30}$	-	-	-	-	0.01	0.01	-	-	0.00	0.00	-0.01	0.01
$ß_{40}$	-	-	-	-	0.00	0.00	-	-	-	-	0.00	0.00
$ß_{01}$	-	-	-1.74	0.37	8.18	2.49	-	-	-37.33	10.57	0.96	0.54
$ß_{02}$	-	-	-	-	-	-	-	-	-3.01	1.93	-3.51	2.41
$ß_{03}$	-	-	-	-	-	-	-	-	-0.34	0.08	-0.19	0.07
$ß_{11}$	-	-	-	-	-0.89	0.24	-	-	6.61	1.67	-	-
$ß_{12}$	-	-	-	-	-	-	-	-	0.61	0.19	0.46	0.24
$ß_{13}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{21}$	-	-	0.00	0.00	0.02	0.01	-	-	-0.35	0.08	0.00	0.00
$ß_{31}$	-	-	-	-	-	-	-	-	0.01	0.00	-	-
$ß_{22}$	-	-	-	-	-	-	-	-	-0.03	0.00	-0.02	0.01

Table A2.5. Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict chironomid pupae consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model:*

$d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

	Logistic						Log					
	L only		optimum		simult. optimum		L only		optimum		simult. optimum	
	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
$ß_0$	-0.08	0.20	-6.05	2.56	-6.61	2.70	-2.34	0.20	-3.75	1.83	-4.29	1.94
L1	-1.58	0.58	-1.71	0.61	-1.57	0.61	-3.85	0.71	-2.95	0.67	-2.64	0.67
L2	-17.48	863	-17.19	841	-17.24	846						
L3	0.55	0.45	0.78	0.53	0.72	0.55	-0.95	0.39	-0.59	0.40	-0.67	0.42
L4	-17.48	1057	-17.14	998	-17.03	1009						
L6	2.10	0.57	2.11	0.61	2.01	0.61	0.23	0.32	0.39	0.33	0.40	0.34
L7	1.18	0.70	0.85	0.72	0.95	0.72	-0.57	0.49	0.13	0.47	0.24	0.47
L8	1.38	0.68	1.47	0.72	1.37	0.72	-0.38	0.46	-0.36	0.44	-0.27	0.44
L9	-0.27	0.53	-0.18	0.58	-0.15	0.58	-1.73	0.55	-0.44	0.53	-0.42	0.53
L10	-17.48	2797	-17.35	2654	-17.28	2721						
L11	1.69	0.80	1.82	0.83	1.77	0.83	1.34	0.47	2.16	0.46	2.14	0.46
L13	-17.48	808	-17.82	802	-17.75	805						
L14	-3.05	1.04	-3.01	1.06	-2.90	1.06	0.92	1.37	1.13	1.28	1.48	1.27
L17	1.87	0.79	1.97	0.84	2.05	0.83	0.47	0.44	0.35	0.42	0.51	0.42
L19	0.08	0.42	-0.25	0.46	-0.18	0.46	-0.87	0.40	-0.33	0.39	-0.27	0.40
L20	-0.79	0.43	-1.10	0.50	-0.96	0.50	-0.31	0.47	0.61	0.48	0.77	0.50
L21	-17.48	932	-17.51	895	-17.60	882						
L22	-0.61	0.64	-0.51	0.68	-0.51	0.68	-1.18	0.71	-0.11	0.67	-0.01	0.67
L23	0.26	0.64	0.76	0.69	0.65	0.69	-0.87	0.59	0.47	0.57	0.60	0.57
L24	-17.48	1319	-17.99	1318	-17.92	1317						
L28	1.59	0.44	1.28	0.46	1.40	0.46	0.26	0.30	-0.05	0.29	0.04	0.29
L29	0.49	0.42	0.31	0.46	0.40	0.46	-1.04	0.38	-0.31	0.36	-0.22	0.36
L30	-0.01	0.48	-0.27	0.51	-0.20	0.51	-1.02	0.47	-0.66	0.45	-0.64	0.45
L31	-0.97	0.46	-1.38	0.48	-1.29	0.48	-0.28	0.52	-0.26	0.49	-0.26	0.49
L32	-1.65	0.66	-1.77	0.68	-1.66	0.68	-1.35	0.81	-1.31	0.75	-1.16	0.75

(Continued)

Table A2.5 (Continued). Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict chironomid pupae consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model:*

$d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

L33	-1.30	0.82	-1.37	0.84	-1.34	0.84	-0.90	0.98	-1.03	0.91	-1.05	0.91
L34	1.00	0.63	1.11	0.65	1.14	0.65	0.11	0.47	1.28	0.45	1.37	0.45
L35	0.67	0.59	0.49	0.62	0.57	0.62	-0.10	0.49	0.69	0.47	0.68	0.47
L36	-0.04	0.53	-0.14	0.56	-0.14	0.56	0.06	0.52	-0.09	0.50	0.07	0.50
L37	-3.25	0.75	-3.32	0.82	-3.51	0.83	-1.09	0.98	-0.74	0.93	-0.78	0.94
L39	-0.05	0.56	-0.29	0.58	-0.22	0.58	-0.02	0.55	-0.39	0.52	-0.19	0.52
L42	0.01	0.42	-0.19	0.46	-0.18	0.46	-0.42	0.41	0.54	0.40	0.61	0.40
L43	-1.67	0.58	-1.69	0.61	-1.66	0.61	0.78	0.71	2.10	0.67	2.07	0.67
L44	-17.48	1057	-17.30	1046	-17.39	1050						
L47	1.28	0.41	1.19	0.46	1.13	0.45	0.55	0.31	1.05	0.31	1.13	0.31
L48	-2.91	1.04	-2.76	1.09	-2.45	1.07	-4.22	1.37	-3.23	1.31	-2.73	1.32
L49	-1.35	0.54	-1.32	0.57	-1.32	0.57	-0.59	0.64	0.35	0.60	0.45	0.60
L50	0.60	0.34	0.60	0.37	0.63	0.37	1.27	0.30	1.51	0.30	1.54	0.30
L51	-0.46	0.39	-0.57	0.43	-0.42	0.43	0.35	0.41	0.42	0.40	0.50	0.40
L53	-17.48	2797	-18.01	2793	-17.88	2794						
L54	-17.48	1399	-17.19	1332	-17.14	1360						
L57	-17.48	1021	-17.18	1002	-17.10	1001						
L58	0.83	0.35	0.84	0.37	0.90	0.37	1.20	0.30	0.90	0.29	0.96	0.29
L59	0.83	0.45	1.14	0.51	1.13	0.51	0.18	0.37	1.02	0.36	1.15	0.37
L60	3.52	1.04	3.67	1.08	3.58	1.07	1.69	0.31	2.32	0.31	2.19	0.31
L61	-0.35	0.44	-0.41	0.47	-0.33	0.47	0.16	0.46	0.03	0.45	0.00	0.44
L62	-1.58	0.58	-1.88	0.60	-1.89	0.60	-2.56	0.71	-1.78	0.67	-1.87	0.66
L64	-0.25	0.46	-0.43	0.48	-0.39	0.48	-0.21	0.47	0.33	0.44	0.25	0.44
L65	-0.24	0.42	-0.52	0.46	-0.68	0.46	-1.45	0.43	-1.42	0.40	-1.40	0.41
L67	17.65	1399	17.16	1393	17.27	1393	0.55	0.52	0.55	0.49	0.71	0.49

(Continued)

Table A2.5 (Continued). Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict chironomid pupae consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model:*

$d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

$ß_{10}$	-	-	0.74	0.33	0.80	0.35	-	-	0.43	0.23	0.46	0.24
$ß_{20}$	-	-	-0.03	0.01	-0.03	0.01	-	-	-0.03	0.01	-0.03	0.01
$ß_{30}$	-	-	0.00	0.00	0.00	0.00	-	-	0.00	0.00	0.00	0.00
$ß_{40}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{01}$	-	-	3.30	1.79	5.13	2.25	-	-	-0.24	0.07	-3.33	1.48
$ß_{02}$	-	-	0.82	0.53	1.21	0.47	-	-	-1.54	0.33	-1.08	0.30
$ß_{03}$	-	-	0.07	0.03	-	-	-	-	-	-	-	-
$ß_{11}$	-	-	-0.48	0.24	-0.69	0.31	-	-	-	-	0.40	0.18
$ß_{12}$	-	-	-0.10	0.05	-0.13	0.04	-	-	0.14	0.03	0.10	0.03
$ß_{13}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{21}$	-	-	0.02	0.01	0.03	0.01	-	-	-	-	-0.02	0.01
$ß_{31}$	-	-	0.00	0.00	0.00	0.00	-	-	-	-	0.00	0.00
$ß_{22}$	-	-	0.00	0.00	0.00	0.00	-	-	0.00	0.00	0.00	0.00

Table A2.6. Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict fish consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model:* $d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

	Logistic						Log					
	L only		optimum		simult. optimum		L only		optimum		simult. optimum	
	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
$ß_0$	-1.43	0.26	-9.05	2.01	-7.84	2.07	-0.34	0.20	-10.03	5.27	2.68	1.56
L1	-19.14	3546	-20.11	3454	-19.74	3478	-	-	-	-	-	-
L2	-19.14	3869	-20.77	3723	-20.66	3744	-	-	-	-	-	-
L3	-19.14	3477	-18.85	3394	-18.72	3448	-	-	-	-	-	-
L4	2.01	0.61	0.61	0.70	0.71	0.69	1.11	0.35	1.18	0.29	1.16	0.32
L6	-19.14	3041	-18.27	2940	-18.39	3010	-	-	-	-	-	-
L7	-19.14	5118	-19.40	5026	-19.18	5020	-	-	-	-	-	-
L8	-0.37	0.81	-0.10	0.94	-0.25	0.89	-0.53	0.64	-0.88	0.59	-0.61	0.60
L9	1.54	0.55	0.54	0.62	1.06	0.62	-0.23	0.35	-0.29	0.29	-0.25	0.34
L10	1.43	1.44	0.20	1.67	0.60	1.81	0.12	0.88	0.44	0.72	0.16	0.83
L11	-0.18	0.82	-0.77	0.87	-0.59	0.89	-0.43	0.64	-0.69	0.63	-0.46	0.61
L13	-19.14	3619	-19.53	3577	-19.21	3606	-	-	-	-	-	-
L14	2.52	0.54	1.39	0.61	1.70	0.58	-0.45	0.28	-0.52	0.24	-0.40	0.27
L17	0.51	0.64	0.37	0.84	0.50	0.79	-0.42	0.47	-0.93	0.40	-1.23	0.45
L19	-19.14	3237	-19.26	3179	-18.89	3209	-	-	-	-	-	-
L20	-19.14	3041	-21.06	2171	-24.70	2254	-	-	-	-	-	-
L21	-19.14	4179	-20.91	3970	-20.38	4029	-	-	-	-	-	-
L22	2.12	0.66	1.25	0.75	1.45	0.72	-0.72	0.36	-0.43	0.31	-0.77	0.35
L23	-19.14	5346	-20.83	5118	-20.71	5140	-	-	-	-	-	-
L24	-0.65	1.09	-0.68	1.13	-0.55	1.13	-0.46	0.88	-0.54	0.74	-0.72	0.80
L28	-1.19	0.65	-0.78	0.76	-0.61	0.71	1.26	0.54	0.33	0.47	0.13	0.52
L29	-19.14	3237	-20.19	2962	-19.99	3113	-	-	-	-	-	-
L30	-19.14	3869	-19.30	3685	-18.81	3732	-	-	-	-	-	-
L31	-19.14	3184	-19.88	3054	-19.42	3053	-	-	-	-	-	-
L32	-1.52	1.06	-3.00	1.10	-2.65	1.11	0.04	0.88	-0.07	0.72	0.10	0.80
L33	0.58	0.74	-0.50	0.82	-0.20	0.78	-0.13	0.54	0.10	0.44	0.03	0.49
L34	-19.14	4739	-20.32	4502	-20.03	4643	-	-	-	-	-	-

(Continued)

Table A2.6 (Continued). Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict fish consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model:* $d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

L35	0.13	0.70	-0.72	0.74	-0.42	0.73	0.67	0.54	0.61	0.44	0.52	0.49
L36	-19.14	4300	-17.91	4135	-17.95	4193	-	-	-	-	-	-
L37	-2.62	1.04	-2.81	1.41	-2.25	1.36	-1.00	0.88	-1.40	0.74	-1.57	0.81
L39	-19.14	4578	-18.86	4001	-18.93	4324	-	-	-	-	-	-
L42	-1.91	1.05	-2.52	1.07	-2.08	1.07	-1.17	0.88	-1.62	0.72	-1.50	0.80
L43	0.73	0.48	-0.23	0.53	0.14	0.53	-0.47	0.35	-0.56	0.28	-0.45	0.33
L44	-19.14	4739	-20.28	4476	-19.81	4496	-	-	-	-	-	-
L47	-19.14	2704	-19.10	2418	-18.84	2532	-	-	-	-	-	-
L48	0.94	0.52	-0.77	0.60	-0.51	0.60	0.90	0.36	0.55	0.31	1.14	0.34
L49	-19.14	3477	-20.33	3371	-19.84	3414	-	-	-	-	-	-
L50	-1.50	0.65	-2.13	0.69	-1.66	0.69	0.57	0.54	0.41	0.47	0.61	0.53
L51	0.25	0.46	-0.80	0.57	-0.38	0.56	0.64	0.35	-0.22	0.36	0.58	0.36
L53	-19.14	12537	-18.65	11877	-18.37	12353	-	-	-	-	-	-
L54	0.91	0.77	-0.93	0.89	-1.07	1.07	-1.44	0.54	-1.04	0.49	-1.27	0.56
L57	-19.14	4578	-20.64	4351	-20.51	4428	-	-	-	-	-	-
L58	0.42	0.40	0.59	0.51	0.98	0.50	0.15	0.30	-0.10	0.26	-0.16	0.30
L59	-1.87	1.05	-4.76	2.12	-3.07	1.13	-0.69	0.88	-0.27	0.91	-0.40	0.82
L60	-2.01	1.05	-3.71	1.26	-2.74	1.09	-1.17	0.88	-0.88	0.73	-0.73	0.82
L61	-19.14	3351	-18.45	3111	-17.42	3248	-	-	-	-	-	-
L62	-19.14	3546	-19.21	3344	-18.95	3396	-	-	-	-	-	-
L64	-1.71	1.05	-2.09	1.10	-1.67	1.08	-0.42	0.88	-0.81	0.73	-0.69	0.80
L65	-19.14	3184	-19.32	2731	-19.03	2904	-	-	-	-	-	-
L67	-19.14	6269	-18.24	6148	-18.13	6153	-	-	-	-	-	-

(Continued)

Table A2.6 (Continued). Estimated coefficient values and standard errors for terms in logistic and log GLMs to predict fish consumption with 1) only a lake categorical factor included (L only), 2) an optimization with morphology allowed to vary among models (optimum), and 3) an optimization with morphology constrained to be the same among all models for all resources (simult. optimum). These results correspond with model comparison results in Table 2.1, and morphologies used in the models are defined by the coefficients for c *reported in that table. Any coefficient with no value indicates that it was unavailable (for the lake categorical factor) or removed during model reduction (for ß values). Coefficient labels refer to a model:* $d = ß_0 + L + ß_{10}s + ß_{20}s^2 + ß_{30}s^3 + ß_{40}s^4 + ß_{01}m + ß_{02}m^2 + ß_{03}m^3 + ß_{04}m^4 + ß_{11}sm + ß_{12}sm^2 + ß_{13}sm^3 + ß_{21}s^2m + ß_{31}s^3m + ß_{22}s^2m^2$

$ß_{10}$	-	-	0.47	0.14	0.36	0.15	-	-	1.68	0.74	-0.15	0.11
$ß_{20}$	-	-	-0.01	0.00	0.00	0.00	-	-	-0.09	0.04	0.00	0.00
$ß_{30}$	-	-	-	-	-	-	-	-	0.00	0.00	-	-
$ß_{40}$	-	-	-	-	-	-	-	-	0.00	0.00	-	-
$ß_{01}$	-	-	4.50	1.90	4.63	1.95	-	-	23.59	6.59	-2.99	0.95
$ß_{02}$	-	-	-0.46	0.17	-	-	-	-	0.13	0.08	-	-
$ß_{03}$	-	-	0.21	0.08	-	-	-	-	-0.09	0.04	-	-
$ß_{11}$	-	-	-0.27	0.12	-0.36	0.15	-	-	-2.45	0.69	0.18	0.05
$ß_{12}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{13}$	-	-	-	-	-	-	-	-	-	-	-	-
$ß_{21}$	-	-	0.00	0.00	0.01	0.00	-	-	0.08	0.02	0.00	0.00
$ß_{31}$	-	-	-	-	-	-	-	-	0.00	0.00	-	-
$ß_{22}$	-	-	-	-	-	-	-	-	-	-	-	-

*Table A2.7. Estimates of the means, standard deviations, and correlations coefficients for morphology (*m*) and size (*s*) of the bivariate normal probability density functions (P_1(m, s), P_2(m, s)) of each data set corresponding with the indicated model. These were used in the correction function C(m, m, s) (Eq. 2.7.)*

		m mean		*s* mean		*m* σ		*s* σ		*ρ*		*r*
		Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.
Snail	Logistic	0.000	0.028	23.431	0.208	0.990	0.020	7.331	0.147	0.121	0.028	-
	Log	0.000	0.029	23.430	0.208	1.005	0.020	7.331	0.147	-0.343	0.025	0.893
Tadpole shrimp	Logistic	0.000	0.028	23.431	0.208	1.000	0.020	7.331	0.147	-0.460	0.022	-
	Log	0.000	0.029	23.431	0.208	1.005	0.020	7.331	0.147	0.090	0.028	0.513
Pea clam	Logistic	0.000	0.028	23.431	0.208	0.998	0.020	7.331	0.147	-0.327	0.025	-
	Log	0.000	0.029	23.431	0.208	1.007	0.020	7.331	0.147	-0.380	0.024	0.491
Cladoceran	Logistic	0.000	0.028	23.431	0.208	1.002	0.020	7.331	0.147	-0.017	0.028	-
	Log	0.000	0.028	23.431	0.208	1.003	0.020	7.331	0.147	-0.037	0.028	1.043
Chironomid pupae	Logistic	0.000	0.029	23.431	0.208	1.007	0.020	7.331	0.147	-0.073	0.028	-
	Log	0.000	0.029	23.431	0.208	1.004	0.020	7.331	0.147	-0.126	0.028	0.513
Fish	Logistic	0.000	0.028	23.431	0.208	0.991	0.020	7.331	0.147	0.038	0.028	-
	Log	0.000	0.028	23.431	0.208	0.996	0.020	7.331	0.147	0.254	0.027	0.630
Simul-taneous	-	0.000	0.029	23.431	0.208	1.006	0.020	7.331	0.147	-0.028	0.028	-

Appendix 3

Table A3.1. Estimated parameters and standard errors of Von Beralanffy growth curve models per lake. When the best model contained 2 or more components (K = 2), parameters for each growth curve were given under a different morph designation (M). For two-curve models, the estimated mixture proportion p *is given for M = 1, or 1 -* p *for M = 2. For three-curve models,* p_1 *is given for M = 1,* p_2 *for M = 2, and 1 –* p_1 *–* p_2 *for M = 3.*

Lake	M	$L\infty$	κ	σ	$L\infty$	κ	σ	p
1	1	26.31	1.00	0.69	0.53	0.08	0.16	0.09
1	2	32.07	0.74	1.60	0.73	0.05	0.25	0.91
2	1	42.46	0.33	1.86	1.58	0.02	0.18	-
3	1	23.76	0.29	1.54	1.48	0.04	0.14	-
4	1	21.19	0.99	2.72	0.95	0.59	0.49	0.61
4	2	60.38	0.23	2.25	10.51	0.07	0.50	0.39
6	1	17.91	0.51	0.52	0.29	0.04	0.09	0.54
6	2	22.72	0.33	0.96	0.82	0.04	0.16	0.46
7	1	25.83	0.49	2.10	1.34	0.07	0.24	-
8	1	54.16	0.07	4.53	18.41	0.03	0.43	-
9	1	58.34	0.17	2.37	20.67	0.08	0.29	0.86
9	2	72.00	0.19	1.08	10.08	0.04	0.46	0.14
10	1	41.47	0.62	2.50	1.64	0.05	0.41	0.64
10	2	53.47	0.27	1.01	4.39	0.03	0.24	0.36
11	1	25.86	0.54	1.31	0.92	0.06	0.23	0.44
11	2	39.08	0.21	1.48	1.75	0.02	0.26	0.56
13	1	24.41	0.52	1.42	0.57	0.07	0.16	-
14	1	46.05	0.22	3.57	5.14	0.04	0.37	-
17	1	15.98	0.67	0.63	0.31	0.06	0.15	0.27
17	2	23.19	0.35	2.46	1.36	0.07	0.44	0.45
17	3	44.56	0.16	3.60	8.34	0.06	0.82	0.28
19	1	21.94	0.72	0.40	-	-	-	0.26
19	2	53.90	0.17	2.53	7.76	0.04	0.44	0.38
19	3	28.01	0.29	1.04	1.46	0.03	0.19	0.36
20	1	22.65	0.34	2.75	1.45	0.05	0.35	0.66

(Continued)

Table A3.1 (Continued). Estimated parameters and standard errors of Von Beralanffy growth curve models per lake. When the best model contained 2 or more components (K = 2), parameters for each growth curve were given under a different morph designation (M). For two-curve models, the estimated mixture proportion p *is given for M = 1, or 1 -* p *for M = 2. For three-curve models,* p_1 *is given for M = 1,* p_2 *for M = 2, and 1 –* p_1 *–* p_2 *for M = 3.*

20	2	66.64	0.08	3.80	23.92	0.04	0.64	0.34
21	1	54.45	0.20	2.06	4.73	0.03	0.28	-
22	1	31.82	0.31	2.04	1.26	0.03	0.21	0.74
22	2	50.89	0.13	1.16	5.16	0.02	0.35	0.26
23	1	37.84	0.30	0.74	1.75	0.03	0.18	0.49
23	2	86.94	0.11	3.31	36.90	0.06	0.58	0.51
24	1	28.02	0.39	1.48	1.06	0.03	0.15	-
28	1	18.43	0.50	1.61	0.56	0.07	0.17	0.76
28	2	44.48	0.34	3.87	7.35	0.10	0.75	0.24
29	1	25.29	0.47	0.40	0.28	0.02	0.11	0.22
29	2	72.04	0.08	2.42	15.45	0.02	0.30	0.78
30	1	28.96	0.31	1.84	1.48	0.03	0.21	-
31	1	37.78	0.33	2.78	3.22	0.05	0.30	-
32	1	58.41	0.11	1.00	5.88	0.02	0.21	0.32
32	2	83.77	0.08	1.42	14.06	0.02	0.22	0.68
33	1	44.09	0.12	1.59	7.16	0.03	0.42	0.52
33	2	56.73	0.10	2.65	9.46	0.03	0.49	0.48
34	1	30.78	0.43	1.03	0.38	0.02	0.15	-
35	1	28.59	0.65	1.29	0.66	0.05	0.29	0.78
35	2	34.56	0.42	3.86	7.15	0.20	1.01	0.22
36	1	16.64	0.47	1.29	1.09	0.17	0.35	-
37	1	13.45	0.35	0.40	0.41	0.04	NA	0.30
37	2	125.90	0.03	4.40	71.91	0.02	1.19	0.16
37	3	15.11	0.85	2.26	1.01	2.07	0.25	0.54
39	1	28.70	0.25	0.83	1.76	0.03	0.15	0.35
39	2	38.88	0.20	2.20	3.92	0.03	0.24	0.65
41	1	52.10	0.28	4.18	9.05	0.10	1.23	0.48
41	2	76.49	0.17	0.69	3.13	0.01	0.13	0.52
42	1	27.85	0.37	3.03	1.51	0.07	0.28	-
43	1	32.37	0.25	1.95	1.71	0.03	0.30	0.73
43	2	50.35	0.16	1.97	7.97	0.04	0.51	0.27
44	1	200.00	0.04	4.10	199.07	0.04	0.45	-

(Continued)

Table A3.1 (Continued). Estimated parameters and standard errors of Von Beralanffy growth curve models per lake. When the best model contained 2 or more components (K = 2), parameters for each growth curve were given under a different morph designation (M). For two-curve models, the estimated mixture proportion p *is given for M = 1, or 1 -* p *for M = 2. For three-curve models,* p_1 *is given for M = 1,* p_2 *for M = 2, and 1 –* p_1 *–* p_2 *for M = 3.*

47	1	32.17	0.22	3.14	6.98	0.07	0.45	0.82
47	2	200.00	0.03	5.45	105.16	0.02	1.68	0.18
48	1	34.41	0.39	0.40	0.52	0.01	NA	0.27
48	2	84.79	0.11	4.00	32.32	0.05	0.62	0.37
48	3	44.45	0.32	0.49	0.68	0.01	0.10	0.36
49	1	26.27	0.47	1.00	0.96	0.08	0.26	0.26
49	2	36.01	0.30	2.22	2.43	0.05	0.30	0.74
50	1	17.44	0.67	1.51	0.53	0.09	0.33	0.40
50	2	31.00	0.38	4.33	2.26	0.08	0.71	0.60
51	1	70.32	0.19	2.26	8.72	0.03	0.28	0.77
51	2	62.66	0.15	2.21	4.86	0.03	0.76	0.23
53	1	49.70	0.14	0.89	2.75	0.01	0.14	0.74
53	2	56.03	0.14	5.36	12.54	0.05	0.97	0.26
54	1	24.82	0.62	0.41	0.29	0.02	0.09	0.33
54	2	97.04	0.06	2.86	38.12	0.03	0.45	0.35
54	3	32.09	0.31	0.84	0.94	0.02	0.18	0.31
57	1	59.03	0.27	2.91	13.88	0.10	0.46	-
58	1	17.17	0.61	0.93	0.55	0.06	0.11	0.58
58	2	74.38	0.10	4.65	60.27	0.11	0.57	0.42
59	1	36.20	0.16	3.13	4.54	0.03	0.48	0.44
59	2	67.45	0.10	3.51	12.45	0.02	0.42	0.56
60	1	49.67	0.15	3.20	8.87	0.06	1.42	0.17
60	2	36.63	0.18	2.05	2.72	0.02	0.24	0.83
61	1	18.50	0.30	0.88	1.25	0.04	0.20	0.60
61	2	27.19	0.19	1.16	5.27	0.06	0.29	0.40
62	1	24.33	0.69	1.64	0.95	0.07	0.22	0.75
62	2	48.88	0.20	2.97	19.47	0.12	0.64	0.25
64	1	21.55	0.22	0.53	1.99	0.04	0.20	0.27
64	2	70.44	0.06	3.27	33.90	0.04	0.42	0.73
65	1	62.16	0.10	2.78	6.64	0.01	0.25	-
67	1	23.01	0.46	0.66	0.68	0.04	0.13	-

Table A3.2. Estimated parameters for bivariate models of morphological variables m_1, m_2, *and* m_3 for each lake (L). *When the best model was unimodal, the means, variances and covariances among all variables are given. When the best model contained a bimodal mixture of 2 bivariate normal distributions, parameters for each distribution are given under a different morph designation (M), and the estimated mixture proportion* p *is given for M = 1, or 1 –* p *for M = 2. The bivariate combinations for which bimodal models give the best fit are in bold. The value for the variable not included in the model is given as the mean value across all individuals in the lake, but variances and covariances are not given as they depend on the samples included.*

		Mean			**Variance**			**Covariance**			
L	**M**	**m_1**	**m_2**	**m_3**	**m_1**	**m_2**	**m_3**	**m_1- m_2**	**m_2- m_3**	**m_1-m_3**	***p***
1	1	-1.55E-02	-2.89E-03	-2.24E-02	1.10E-04	5.87E-05	5.14E-05	-4.14E-05	5.14E-05	-9.48E-06	-
2	1	-9.28E-04	8.28E-03	-1.67E-02	2.13E-04	1.36E-04	5.13E-05	-2.96E-05	5.13E-05	-4.49E-05	-
3	1	1.66E-02	1.49E-02	-7.01E-03	1.85E-04	1.05E-04	6.84E-05	-1.71E-05	6.84E-05	4.26E-06	-
4	1	6.72E-03	7.70E-03	-5.90E-03	2.65E-04	2.62E-04	8.47E-05	7.67E-05	8.47E-05	2.21E-05	-
6	1	1.95E-02	6.25E-03	-9.09E-04	1.07E-04	1.27E-04	8.42E-05	-2.72E-06	8.42E-05	-2.50E-05	-
7	1	-9.25E-03	-3.03E-03	-6.31E-03	1.78E-04	6.84E-05	4.89E-05	-1.76E-05	4.89E-05	-9.78E-06	-
8	1	2.38E-02	-2.39E-03	-3.65E-03	4.42E-04	1.29E-04	9.41E-05	-6.09E-05	9.41E-05	-9.43E-05	-
9	1	-3.02E-03	5.59E-03	-1.27E-03	2.20E-04	1.08E-04	5.63E-05	-6.94E-05	5.63E-05	-9.23E-06	-
10	1	-2.36E-02	4.30E-04	-1.95E-02	1.28E-04	3.79E-05	7.26E-05	-3.50E-05	7.26E-05	-1.17E-05	-
11	1	1.23E-02	5.77E-03	-1.01E-02	2.49E-04	8.84E-05	3.01E-05	-3.97E-05	3.01E-05	-8.19E-07	-
13	1	-4.80E-04	-2.40E-04	1.27E-03	1.19E-04	1.32E-04	4.81E-05	-1.29E-05	4.81E-05	-7.61E-07	-
14	1	-1.37E-02	3.71E-03	-2.84E-03	2.25E-04	1.22E-04	5.63E-05	-1.96E-05	5.63E-05	-2.13E-06	-

(Continued)

Table A3.2 (Continued).. Estimated parameters for bivariate models of morphological variables m_1, m_2, *and* m_3 for each lake (L). *When the best model was unimodal, the means, variances and covariances among all variables are given. When the best model contained a bimodal mixture of 2 bivariate normal distributions, parameters for each distribution are given under a different morph designation (M), and the estimated mixture proportion* p *is given for M = 1, or 1 –* p *for M = 2. The bivariate combinations for which bimodal models give the best fit are in bold. The value for the variable not included in the model is given as the mean value across all individuals in the lake, but variances and covariances are not given as they depend on the samples included.*

17	1	-3.60E-03	-4.16E-03	-3.27E-03	1.60E-04	7.81E-05	7.70E-05	-1.00E-05	7.70E-05	6.81E-06	-
19	1	-5.71E-03	-1.56E-03	-1.56E-02	2.22E-04	7.20E-05	1.06E-04	-2.34E-05	1.06E-04	-1.45E-06	-
20	1	5.34E-03	1.31E-02	-1.00E-02	2.66E-04	3.05E-04	1.06E-04	7.77E-05	1.06E-04	-5.89E-05	-
21	1	-4.05E-03	2.33E-03	3.85E-03	3.43E-04	9.16E-05	6.74E-05	-2.81E-05	6.74E-05	-8.37E-05	-
22	1	7.49E-03	-2.37E-03	-1.10E-02	1.46E-04	5.40E-05	5.70E-05	2.87E-06	5.70E-05	-2.70E-05	-
23	1	-3.28E-03	5.54E-05	-9.01E-03	2.51E-04	1.22E-04	3.64E-05	4.95E-06	3.64E-05	2.37E-05	-
24	1	-1.34E-02	-1.24E-02	1.07E-02	1.84E-04	2.36E-05	3.29E-05	-2.27E-05	3.29E-05	-3.24E-05	-
28	1	**7.52E-03**	-8.38E-03	**1.41E-02**	3.19E-05	-	5.72E-05	-	-	-3.78E-05	0.35
28	2	**9.03E-03**	-8.38E-03	**2.71E-03**	3.42E-04	-	8.58E-05	-	-	6.72E-05	0.65
29	1	1.77E-03	-1.46E-02	-3.89E-03	3.09E-04	7.96E-05	4.83E-05	-4.59E-05	4.83E-05	8.27E-06	-
30	1	-4.99E-03	-1.69E-03	3.99E-03	1.82E-04	1.51E-04	6.05E-05	-5.14E-06	6.05E-05	-3.57E-05	-
31	1	-6.66E-03	-6.17E-03	5.42E-03	2.53E-04	8.25E-05	7.38E-05	1.09E-05	7.38E-05	-3.13E-05	-
32	1	**-5.57E-03**	-9.83E-03	**5.82E-04**	1.05E-04	-	1.08E-04	-	-	2.87E-08	0.83
32	2	**2.47E-03**	-9.83E-03	**1.83E-02**	2.13E-04	-	2.50E-05	-	-	7.29E-05	0.17
33	1	1.25E-03	-5.96E-03	1.14E-02	1.84E-04	6.61E-05	1.13E-04	-2.67E-05	1.13E-04	-5.88E-05	-

(Continued)

Table A3.2 (Continued). Estimated parameters for bivariate models of morphological variables m_1, m_2, *and* m_3 for each lake (L). *When the best model was unimodal, the means, variances and covariances among all variables are given. When the best model contained a bimodal mixture of 2 bivariate normal distributions, parameters for each distribution are given under a different morph designation (M), and the estimated mixture proportion* p *is given for M = 1, or 1 –* p *for M = 2. The bivariate combinations for which bimodal models give the best fit are in bold. The value for the variable not included in the model is given as the mean value across all individuals in the lake, but variances and covariances are not given as they depend on the samples included.*

34	1	1.81E-03	-2.95E-03	-1.45E-03	1.22E-04	1.31E-04	6.00E-05	-6.65E-05	6.00E-05	-2.33E-05	-
35	1	-6.82E-03	-3.54E-03	1.46E-03	2.45E-04	7.60E-05	8.27E-05	-5.33E-05	8.27E-05	-4.65E-05	-
36	1	1.23E-02	1.08E-03	5.63E-03	2.10E-04	1.08E-04	4.90E-05	3.27E-05	4.90E-05	-2.04E-05	-
37	1	1.04E-02	1.71E-02	1.06E-02	1.79E-04	2.32E-04	9.92E-05	9.84E-05	9.92E-05	-4.48E-05	-
39	1	**1.36E-02**	**-1.54E-02**	-5.58E-03	2.48E-04	8.94E-05	-	-7.77E-05	-	-	0.76
39	2	**2.23E-02**	**-8.59E-03**	-5.58E-03	9.71E-05	6.38E-06	-	2.25E-05	-	-	0.24
42	1	4.28E-03	2.38E-03	2.27E-03	2.06E-04	1.22E-04	1.20E-04	-1.93E-05	1.20E-04	-7.08E-05	-
43	1	6.41E-04	3.33E-04	-9.13E-04	1.97E-04	7.63E-05	4.87E-05	-2.67E-06	4.87E-05	-1.54E-05	-
44	1	-6.77E-03	3.07E-03	-2.18E-02	1.28E-04	5.69E-05	1.55E-04	-9.35E-06	1.55E-04	-1.62E-05	-
47	1	8.86E-03	2.13E-03	7.87E-04	2.10E-04	1.19E-04	9.43E-05	1.37E-05	9.43E-05	-3.10E-05	-
48	1	-1.17E-02	3.32E-03	-4.97E-03	2.80E-04	1.11E-04	1.36E-04	-4.63E-05	1.36E-04	6.25E-06	-
49	1	-2.93E-03	8.64E-03	-3.02E-03	1.54E-04	1.22E-04	9.41E-05	-2.70E-05	9.41E-05	-3.65E-06	-
50	1	9.45E-04	4.72E-03	4.28E-03	2.43E-04	1.28E-04	1.07E-04	2.02E-05	1.07E-04	2.67E-05	-
51	1	-9.07E-03	**4.81E-03**	**2.24E-03**	-	7.30E-05	2.19E-05	-	3.98E-05	-	0.18
51	2	-9.07E-03	**1.16E-03**	**-3.64E-03**	-	1.23E-04	6.09E-05	-	-2.98E-05	-	0.82

(Continued)

Table A3.2 (Continued). Estimated parameters for bivariate models of morphological variables m_1, m_2, *and* m_3 for each lake (L). *When the best model was unimodal, the means, variances and covariances among all variables are given. When the best model contained a bimodal mixture of 2 bivariate normal distributions, parameters for each distribution are given under a different morph designation (M), and the estimated mixture proportion* p *is given for M = 1, or 1 –* p *for M = 2. The bivariate combinations for which bimodal models give the best fit are in bold. The value for the variable not included in the model is given as the mean value across all individuals in the lake, but variances and covariances are not given as they depend on the samples included.*

53	1	-7.52E-03	4.06E-03	5.56E-04	1.16E-04	5.74E-05	5.00E-05	-2.83E-05	5.00E-05	-7.18E-06	-
54	1	-1.37E-02	**4.25E-04**	**4.23E-03**	-	2.31E-05	4.21E-05	-	-1.53E-06	-	0.79
54	2	-1.37E-02	**1.32E-02**	**-7.68E-03**	-	2.18E-04	8.12E-06	-	-4.17E-05	-	0.21
57	1	-2.34E-02	-4.38E-03	-2.29E-02	4.47E-04	1.88E-04	1.89E-04	-1.13E-04	1.89E-04	7.60E-06	-
58	1	2.03E-03	-2.44E-03	6.21E-03	1.74E-04	1.39E-04	9.32E-05	9.53E-06	9.32E-05	-2.10E-05	-
59	1	-4.12E-04	2.56E-03	-2.33E-03	2.14E-04	2.07E-04	2.09E-04	-3.16E-05	2.09E-04	-6.40E-05	-
60	1	**-1.23E-02**	4.69E-03	**2.39E-02**	2.31E-04	-	4.83E-05	-	-	3.07E-05	0.82
60	2	**2.84E-03**	4.69E-03	**8.90E-03**	6.66E-06	-	2.45E-05	-	-	-1.20E-05	0.18
61	1	2.64E-03	5.93E-03	1.64E-02	2.19E-04	1.04E-04	8.73E-05	-4.11E-05	8.73E-05	-4.06E-05	-
62	1	**9.58E-03**	-1.14E-02	**-9.03E-03**	2.17E-04	-	4.37E-05	-	-	8.97E-05	0.11
62	2	**-7.03E-03**	-1.14E-02	**7.45E-03**	1.37E-04	-	3.09E-05	-	-	-1.65E-05	0.89
64	1	3.14E-03	-2.11E-03	1.23E-02	2.09E-04	1.45E-04	5.25E-05	-5.79E-05	5.25E-05	1.54E-06	-
65	1	**-8.01E-03**	**-2.69E-02**	4.90E-03	3.17E-04	6.52E-05	-	-6.87E-05	-	-	0.62
65	2	**1.91E-02**	**1.36E-03**	4.90E-03	1.43E-04	1.00E-04	-	-2.62E-05	-	-	0.38

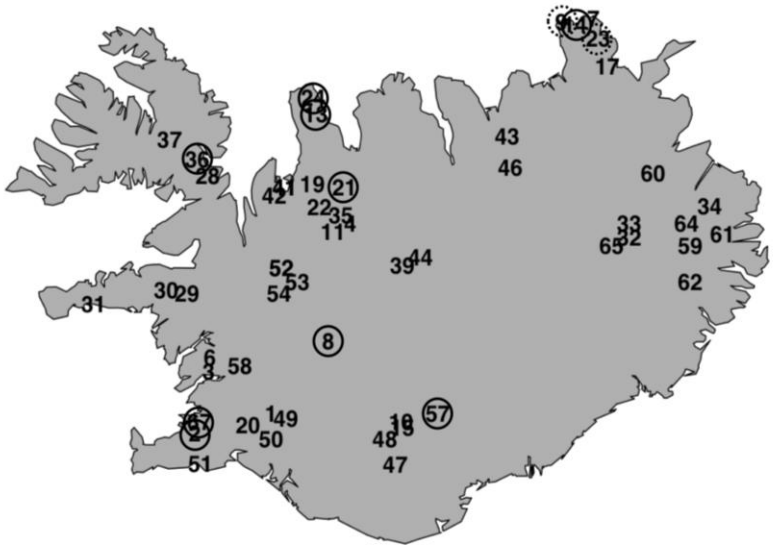


Figure A3.1. Map of Iceland showing lake geographic locations and random forest misclassifications. Lake numbers are in Table 3.1. Dashed circles indicate polymorphic lakes erroneously characterized as monomorphic, and solid circles indicate monomorphic lakes erroneously characterized as polymorphic.