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EXAMINATION OF THE ECOLOGICAL DIFFERENCES BETWEEN TWO
CLOSELY RELATED ENDEMIC WHITEFISH IN RELATION TO GROWTH
CONDITIONS AND PREDATION RISK

by

Benjamin M. Kennedy

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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2005

ABSTRACT

Examination of the Ecological Differences Between Two Closely Related
Endemic Whitefish in Relation to Growth Conditions and Predation Risk

by

Benjamin M. Kennedy, Master of Science

Utah State University, 2005

Major Professor: Dr. Chris Luecke

Department: Aquatic, Watershed, and Earth Resources

Benthic Bear Lake whitefish (*Prosopium abyssicola*) and Bonneville whitefish (*P. spilonotus*) are closely related, yet the extent of ecological separation remains poorly understood. We described their spring and summer distribution and diet in Bear Lake and examined how these were related to environmental growth conditions, and predation risk. In spring and summer, Bonneville whitefish dominated shallower depths (5-30 m), whereas Bear Lake whitefish dominated deeper depths (45-55 m). At intermediate depths (35-40 m), low numbers of both species occurred. Bonneville whitefish ate mostly Chironomidae, whereas Bear Lake whitefish ate mostly Ostracoda. Habitats occupied by Bonneville whitefish had better growth conditions, but higher predation risks compared to Bear Lake whitefish habitats. Avoided habitats had poor growth conditions and high predation risk. These data describe an

ecologically distinct, whitefish community in an ecoregion different from those studied before. Whitefish may maintain higher survival at shallow or deep but not middle depths.

(86 pages)

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Benjamin M. Kennedy

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CHAPTER 1

INTRODUCTION

Determining the degree of ecological separation among closely related species and understanding environmental factors associated with separation are central questions in ecology and crucial to the conservation of native communities (Schoener 1970, 1974). Ecologically similar species or groups that occupy analogous habitats and eat similar food items may have parallel habitat requirements, similar community roles, and potentially compete for limited resources. In contrast, ecologically different groups may have distinct requirements, diverse community roles, and not compete for resources (Brandt et al. 1980; Crowder et al. 1981). Most populations likely fall in between these extremes so understanding the degree of ecological overlap is essential. Once the degree of ecological separation is known it is important to know what environmental factors are associated with it. This knowledge is crucial to our understanding of processes that promote and maintain closely related species in addition to predicting how a species pair will respond to environmental changes.

Many factors influence the distribution and habitat use of a species and researchers can gain a more complete understanding of these factors by integrating data on environmental growth conditions and predation risk together instead of treating these topics independently (Godin 1997). Growth conditions are important to an individual because in general, higher growth is associated with higher survival and reproduction. A habitat with growth conditions that result

in high growth rates should have a high amount of food available, and a water temperature that allows for maximal growth. Predation is important to an individual because it can affect survival directly through mortality or indirectly through a change in habitat use. If predation risk is constant or non-existent across habitats, individuals may be distributed in relation to growth conditions only. If growth conditions are similar across habitats, individuals may be distributed in relation to predation risk only. Most often, growth conditions and predation risk will vary creating a complex set of trade-offs. Theory suggests that organisms should minimize the ratio of mortality to growth in order to maximize fitness from which individuals should use habitats with the best growth conditions and lowest predation risk (Werner and Gilliam 1984). The best way to assess these trade-offs is to examine these factors concurrently.

Lakes containing whitefish (subfamily Coregoninae) can be good systems for addressing ecological separation because some contain closely related yet ecologically distinct populations (Lindsey 1963; Fenderson 1964; Bodaly 1979; Bodaly et al. 1991). Typically, populations of sympatric ecotypes contain a benthic and a limnetic ecotype. The benthic ecotypes are relatively larger in body length and body depth and have fewer gill rakers that are shorter in length compared to limnetic ecotypes. These morphological differences are associated with differences in resource use (Bernatchez et al. 1999) where the benthic ecotype forages on the bottom and is more efficient at consuming benthic invertebrates compared to the limnetic ecotype which forages in the open water,

and is more efficient at foraging on zooplankton. These populations are thought to occur as the result of resource-based divergent natural selection leading to reproductive isolation and both sympatric speciation and allopatric speciation followed by secondary contact have been shown as modes of speciation depending on the system studied (Pigeon et al. 1997; Bernatchez et al. 1996; Lu and Bernatchez 1999; Douglas et al. 1999).

Bear Lake is one of these rare ecosystems where multiple sympatric species exist. These species are the Bear Lake whitefish (*Prosopium abyssicola*), Bonneville whitefish (*P. spilontus*), and Bonneville cisco (*P. gemmifer*). They are closely related, but they are considered separate species (Bernatchez et al. 1991; Vuorinen et al. 1998; Toline et al. 1999). Available genetic evidence from Bonneville whitefish and Bonneville cisco indicates they are very similar, diverging relatively recently (< 35,000 years ago) and that gene flow does not occur presently. Additionally, these species are more related to *P. williamsoni* than other members of the genus. Additional phylogenetic studies including Bear Lake whitefish would be useful. In addition to genetic differences, these species are reproductively isolated, with Bonneville whitefish spawning in early December, Bonneville cisco spawning in early January, and Bear Lake whitefish spawning from mid-February to mid-March (White 1974). Bonneville cisco represent the limnetic ecotype and are separated from Bonneville whitefish and Bear Lake whitefish both morphologically and ecologically. Bonneville cisco have been studied intensively and data indicates that they occupy the pelagic

zone of the lake and eat zooplankton and like other systems with a limnetic ecotype, they have more gill rakers that are longer than the benthic species' (White 1974; Luecke and Wurtsbaugh 1993). Bear Lake and Bonneville whitefish are morphologically very similar and difficult to identify. White (1974) found that when multiple characteristics were examined together, Bear Lake whitefish tended to have a distinctly curved snout. However, a recent study found these differences to be small (Ward 2001). Difficulties in easily distinguishing between the species outside of spawning seasons have prevented ecological studies from being conducted. Fortunately, a recent study developed and validated a key to quickly identify all size classes of each species in the field (Ward 2001) thus providing the opportunity for more in-depth studies into the life history of each species.

The objectives of this study were to first test the hypothesis that Bear Lake whitefish and Bonneville whitefish are ecologically separated by distribution and diet. Since these species have coexisted for thousands of years we expected resource overlap to be low. Specifically, we predicted that associated with previously documented differences in morphology and genetics, Bear Lake whitefish and Bonneville whitefish would either have similar distributions but different diets, different distributions but similar diets, or both different distributions and different diets. We examined how catches in gill nets of each species varied with depth and season and how diets varied between species and season.

Secondly, we examined how distributions of Bonneville whitefish and Bear Lake whitefish were associated with differences in growth and predation risk conditions. Specifically, our objectives were to examine how food availability, water temperature, and predation risk varied with depth and season for both species. Typically, in large lakes that stratify like Bear Lake, the shallower depths will have the most food, the warmest temperatures, and the most predators. We assessed the degree to which both species associated with growth and predation loss by comparing the depth distribution of each whitefish species to distribution of temperature, food availability, and predation risk.

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CHAPTER 2

ECOLOGICAL DIFFERENCES BETWEEN TWO CLOSELY RELATED
MORPHOLOGICALLY SIMILAR BENTHIC WHITEFISH IN AN
ENDEMIC WHITEFISH COMPLEX¹

Abstract: Understanding the degree of ecological separation between two closely related species can contribute to our understanding of population divergence, community structure, and species conservation. Endemic Bear Lake whitefish (*Prosopium abyssicola*) and Bonneville whitefish (*P. spilontus*) are benthic, morphologically similar, and closely related, yet the extent of ecological separation remains poorly understood. To gain a better understanding of these processes, we described their seasonal distribution and diet in the lake. We used bottom-set gill nets to examine how catch of each species of whitefish varied in relation to depth and season (spring and summer). In both spring and summer Bonneville whitefish dominated the shallower depths (5-30 m), whereas Bear Lake whitefish dominated the deeper depths (45-55 m). Associated with large distributional differences, diets also varied between species. Bonneville whitefish ate a variety of benthic invertebrates, but mostly Chironomidae, whereas Bear Lake whitefish feed mostly on Ostracoda. These data describe a closely related morphologically similar, yet ecologically distinct group of whitefish in an ecoregion completely different from those studied before. Additionally,

¹Coauthored by Benjamin M. Kennedy and Chris Luecke.

these data indicate that each species has a very different role in the Bear Lake ecosystem. To conserve this unique fish assemblage, both habitats will need to be protected.

Introduction

Quantitative data on the presence and extent of ecological separation between closely related species inhabiting the same environment can elucidate relationships between each species and their roles in the surrounding ecosystem, thus increasing our ability to understand the evolution of species pairs and create sound conservation plans (Scott and Angermeier 1998; Mauritzen et al. 2002; Foster et al. 2003; Wood 2003). Ecologically similar species or groups that occupy analogous habitats and eat similar food items may have parallel habitat requirements, similar community roles, and potentially compete for limiting resources. In contrast, ecologically different groups may have distinct requirements, diverse community roles, and not compete for resources (Brandt et al. 1980; Crowder et al. 1981). Most populations likely fall in between these extremes so understanding the degree of ecological overlap is essential (Schoener 1970, 1974). This information can then be integrated with morphology and genetic data to determine if phenotypically and genotypically different species differ in ecology, a key requirement to the ecological theory of adaptive radiation (Bernatchez et al. 1999), which is the evolution of ecological

and phenotypic diversity through divergent natural selection within a rapidly multiplying lineage (Schluter 2000).

Fish populations occupying northern temperate lakes during the last 15,000 years have very diverse life histories and in special cases contain closely related sympatric ecotypes (Lindsey 1963; Fenderson 1964; Bodaly 1979; Bodaly et al. 1991). Typically, populations of sympatric ecotypes contain a benthic and a limnetic ecotype. The benthic ecotypes are relatively larger in body length and body depth and have fewer gill rakers that are shorter in length compared to limnetic ecotypes. These morphological differences are associated with differences in resource use (Bernatchez et al. 1999) where the benthic ecotype forages on the bottom and is more efficient at consuming benthic invertebrates compared to the limnetic ecotype which forages in the open water, and is more efficient at foraging on zooplankton. These populations are thought to occur as the result of resource-based divergent natural selection leading to reproductive isolation and both sympatric speciation and allopatric speciation followed by secondary contact have been shown as modes of speciation depending on the system studied (Bernatchez et al. 1996; Pigeon et al. 1997; Lu and Bernatchez 1999; Douglas et al. 1999).

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(Bernatchez et al 1991; Vuorinen et al. 1998; Toline et al. 1999). Available genetic evidence from Bonneville whitefish and Bonneville cisco indicates they are very similar, diverging relatively recently ($< 35,000$ years ago) and that gene flow does not occur presently. Additionally, these two species are more related to *P. williamsoni* than other members of the genus. Additional phylogenetic studies with the inclusion of Bear Lake whitefish would be useful. In addition to genetic differences, these species are reproductively isolated, with Bonneville whitefish spawning in early December, Bonneville cisco spawning in early January, and Bear Lake whitefish spawning from mid-February to mid-March (White 1974). Bonneville cisco represent the limnetic ecotype and are separated from Bonneville whitefish and Bear Lake whitefish both morphologically and ecologically. Bonneville cisco have been studied intensively and data indicates that they occupy the pelagic zone of the lake and eat zooplankton and like other systems with a limnetic ecotype, they have more gill rakers that are longer than the benthic species' (White 1974; Luecke and Wurtsbaugh 1993). Bear Lake and Bonneville whitefish are morphologically very similar and difficult to identify. White (1974) found that when multiple characteristics were examined together, Bear Lake whitefish tended to have a distinctly curved snout. However, a recent study found these differences to be small (Ward 2001). Difficulties in easily distinguishing between the species outside of spawning seasons have prevented ecological studies from being conducted. Fortunately, a recent study developed and validated a key to quickly identify all size classes of each species in the field

(Ward 2001) thus providing the opportunity for more in-depth studies into the life history of each species.

The objective of this study was to test the hypothesis that Bear Lake whitefish and Bonneville whitefish are ecologically separated by distribution and diet. Since these species are morphologically different and have co-existed for thousands of years, we expected resource overlap to be low. Specifically, we predicted Bear Lake whitefish and Bonneville whitefish would either have similar distributions but different diets, different distributions but similar diets, or both different distributions and different diets. We examined how catches in gill nets of each species varied with depth and season and how diets varied between species and season. Management and conservation of these fishes will depend on the amount and type of resource divergence between the two species.

Materials and Methods

Study Area

Bear Lake is an oligotrophic lake located at 42°N, 111°20'W and straddles the northeast Utah-Idaho boarder (Lamarra et al. 1986; Wurtsbaugh and Hawkins 1990). At full pool, the lake covers 282 km² at an elevation of 1,805 m above sea level. Bear Lake has a maximum depth of 62 m and a mean depth of 28 m. In approximately three out of every 4 years the lake will ice over. The watershed geology consists mostly of limestone and other soft sedimentary rocks, causing the lake to be alkaline with calcite precipitation that strips

phosphorus from the water. The substrate is dominated by fine marl sediments with limited areas of rock, sand, and snail shells from an extinct species of gastropod. Bear Lake is dimictic, cold, and contains dissolved oxygen concentrations greater than 5 mg/L throughout the water column throughout the year (Fig. 2-1). Epilimnetic mid-summer chlorophyll-*a* concentrations are near 0.5 µg/L and zooplankton communities are dominated by the copepod *Epischura nevadensis* and *Bosmina lacustris*, with *Daphnia pulex* and *Daphnia galeata* occasionally present. Benthic invertebrate biomass (0.34 g dry wt/m²) is among the lowest recorded for mid-latitude lakes (Wurtsbaugh and Hawkins 1990). The Bear Lake fish assemblage contains 13 fish species including nine that are native, four of which are endemic. The dominant piscivores in the system are native Bonneville cutthroat trout (*Oncorhynchus clarki utah*) and non-native lake trout (*Salvelinus namaycush*), both of which are maintained primarily by stocking. Currently, the top 6.5 m of water in Bear Lake is managed as an irrigation storage reservoir where water is diverted into the lake during spring and pumped out throughout the summer and fall.

Species Identification

We classified whitefish as Bonneville whitefish or Bear Lake whitefish according to a key developed by Ward (2001). Ward (2001) used Bonneville whitefish caught in December and Bear Lake whitefish caught in February and progeny from both species reared in the laboratory to examine morphological differences between each species. He found that the two species differed at all

size classes in the number of scales along the lateral line. Bonneville whitefish had 80 scales on average and never had less than 75 scales whereas Bear Lake whitefish had 70 scales on average and never had more than 75 scales. Ward (2001) could correctly classify 99% of fish of all size classes by counting lateral line scales.

Spatial Distribution and Analyses

We measured whitefish distribution using the number of fish caught in gill nets set overnight. Gill net catch per net night (CPUE) was measured in July 2000, August 2000, 2001, 2002, and 2003 and May 2001, 2002, and 2003. This time frame enabled us to collect samples during summer stratification and near spring isothermal conditions and in years when the lake was at full pool and when the lake was 5 m lower during drought conditions. For each sample period, we set experimental sinking gill nets for approximately 12 to 14 hours from dusk to dawn to capture both crepuscular periods. In 2000 and 2001, we placed gill nets in a stratified random design to ensure sampling coverage throughout the entire area and depth of the lake. In 2002, gill nets were placed at depths of 15, 20, 25, 30, 35, and 40 m along four randomly chosen transects starting at the deepest part of the lake and extending to each shore (north, south, east, west). At 50 m and 55 m depths, gill nets were placed along two randomly selected transects from the original four (ex. north and west). In May and August 2003, gill nets were placed at 5 m and 10 m along the four transects. We used gill nets that consisted of 10 panels of different mesh size that were 4.6 m in length. The

panels started at 1.27 cm stretch mesh and increased by 0.65 cm increments up to 5.08 cm stretch, then mesh size increased by 1.27 cm up to 8.89 cm. The numerous panels were included in an effort to catch a wide range of fish sizes.

We examined a set of candidate models in a model averaging framework to describe whitefish distribution and estimate the mean and 95% confidence interval of CPUE for each species at each depth in spring and summer. An information-theoretic approach using Akaike's Information Criterion (AIC) works better than traditional statistical approaches in these situations because of its ability to simultaneously rank and select good approximating models that explain the data while balancing bias and precision (Burnham and Anderson 2002). In addition, model averaging using AIC avoids the disadvantages of using arbitrary α -levels and comparing models two at a time. For example, the information-theoretic approach can provide an unbiased method to determine if a linear function is a more appropriate model for describing whitefish distributions than a log or polynomial function. Five models representing biological hypotheses about possible whitefish distributions in relation to depth were chosen as candidates (Table 2-1) to be simultaneously compared given our gill net data using AIC values with a small sample bias adjustment (AIC_c ; Burnham and Anderson 2002). Models were ranked and compared using AIC_c differences (Δ_i) and normalized weights (w_i). The models with the lowest AIC_c differences and the highest weights represent the best models for the data provided. Typically, more than one model may be appropriate, so to account for this model

uncertainty and estimate distribution patterns more robustly, we used all models in a model averaging framework. The final estimate of CPUE was the weighted average of CPUE from all models adjusted by how likely a given model represented the best model (w_i) so that the best approximating models contributed the most to the final estimate. Model-averaged 95% confidence intervals included model-selection uncertainties so that confidence intervals expanded if uncertainty existed in which models were best. All analyses were performed using a generalized linear model (PROC GENMOD; SAS 2001) with a negative binomial link function to account for overdispersion in the count data (White and Bennetts 1996).

Diet Collection and Analyses

In 2002 and 2003, stomachs from each species were removed and preserved in 95% ethanol soon after capture. For both seasons, 10 fish between 100 mm and 300 mm (total length) of each species from each depth were randomly selected for diet analysis. Only Bonneville whitefish grow to a size larger than 300 mm, and individuals that large have been documented to become piscivorous and eat exclusively sculpin, so they were excluded from this study (Thompson 2003). Fish less than 100 mm were not caught in our nets. If 10 or less fish were caught at a given depth, then all the fish were used. In spring, all Bear Lake whitefish were used for diet analysis due to a small number of fish caught then.

Food items from each fish stomach were separated into groups, counted, and each individual was measured (nearest 0.1 mm) with a dissecting microscope at 10X magnification. If a fish did not have any food items in its stomach the fish was removed and a replacement was selected. Groups consisted of Chironomidae, Ostracoda, Pisidae, terrestrial (Homoptera and Hymenoptera), Oligochaeta, and Amphipoda. Length-to-dry weight equations from Wurtsbaugh and Hawkins (1990) were used to estimate dry weight biomass of each group. Head capsules of partially digested Chironomidae were measured at 30X and converted to undigested length using a regression equation (undigested length (mm) = head capsule width (mm) * 10.47 + 2.58, $r^2 = 0.67$, $P < 0.0001$) developed from a sample of 178 chironomids. The percent of dry weight biomass for each food group contributing greater than 5% of the total diet was described between species and season by visually assessing percentages of dry weights in stomachs. We then used logistic regression (PROC GENMOD) to relate the presence or absence of each food group in a stomach to fish species, season, and fish length (total length). Separate analyses were performed for each food group. Logistic regression was used instead of linear regression due to highly non-normal distributions of diet proportions. Estimates of effect size and precision were used to evaluate the importance of each factor.

Results

Spatial Distribution

Bonneville whitefish and Bear Lake whitefish had very different benthic distributions in both spring and summer (Fig. 2-2; Table 2-2; Table A-1). In spring, average Bonneville whitefish abundance was highest at 5 m and decreased gradually with depth to 35 m (Fig. 2-2; Table A-1). Below 35 m, in the deep profundal zone, few Bonneville whitefish were caught. Bear Lake whitefish abundance had the opposite pattern. Few Bear Lake whitefish were caught until 40 m and abundance increased rapidly from 45 m with the highest abundance being at 55 m. Given the data, there were two models that were better than the others at describing Bonneville whitefish distribution and one model that best described Bear Lake whitefish distribution. These models were the random-linear model and the polynomial model ($\Delta AIC_c < 2$, highest weights; Table 2-2). These models were characterized by properties that allowed for areas of abundance increase or decrease in addition to areas where abundance did not change. This contrasts with other models like the linear model where abundance would have had to change at a constant rate throughout every depth or the pseudothreshold model, which also assumed a constant change in abundance. The random model, which described a random relationship between numbers caught and depth, was ranked last with a ΔAIC_c value greater than 10 indicating no support for this model.

In summer, Bonneville whitefish abundance was low at 5 m, then increased to a maximum at 15 m, and then decreased to 35 m. Like spring, few Bonneville whitefish were caught deeper than 35 m in the deep profundal zone (Fig. 2-2; Table A-1). Unlike Bonneville whitefish, Bear Lake whitefish abundance had a similar pattern as spring. Bear Lake whitefish abundance was low until 40 m, and then increased rapidly with depth to 55 m. The model that best described Bonneville whitefish and Bear Lake whitefish distribution in this season was the polynomial model (Table 2-2). The polynomial model fit the Bonneville whitefish distribution well because of its ability to describe the maximum levels of CPUE reached at middle depths, and it fit the Bear Lake whitefish distribution well because of its ability to describe the rapid increase of CPUE at the deeper depths. The random model was again ranked last with high ΔAIC_c values indicating no support for this model.

Diet

Associated with distribution differences were large diet differences between the species. In spring, Chironomidae, Ostracoda, Pisidae, and terrestrial insects contributed at least 5% each to the total diet of whitefish. Bonneville whitefish had all of these food items in their stomachs, but Chironomidae were the dominant food group followed by Pisidae. At a given depth, Chironomidae were present in most Bonneville stomachs (Table A-2) and made up between 50% and 85% of the biomass on average for an individual fish (Fig. 2-3). Unlike Chironomidae, Pisidae were present in few stomachs, but they

made up a high percentage of the biomass when present (Table A-2). Ostracoda and terrestrials were present in few diets and made up small percentages of the diet when present (Table A-2). In contrast to Bonneville whitefish, spring diets of Bear Lake whitefish consisted of mostly Ostracoda with Chironomidae contributing to the weight of a couple of stomachs at shallower depths (Fig. 2-3). At the depths with the highest abundance (50 m and 55 m) of Bear Lake whitefish, Ostracoda averaged between 85% and 95% of their diet. Chironomidae were present in a small percentage and Pisidae and terrestrial groups were found in very small percentages. At depths where Bonneville and Bear Lake whitefish overlapped in low numbers (35 m and 40 m), diets were still different. However, a few Bear Lake whitefish diets were similar to Bonneville whitefish. Lastly, some Bear Lake whitefish collected at depths dominated by Bonneville whitefish had diets similar to Bonneville whitefish while some were more similar to the majority of Bear Lake whitefish.

In summer, large diet differences continued to exist between species and diets within a species were similar between seasons. In most Bonneville whitefish stomachs, Chironomidae continued to make up very high percentages of the biomass (Fig. 2-3), and Pisidae continued to comprise a high percentage of the biomass in some stomachs (Table A-2). Also, Ostracoda and terrestrial insects were found at low percentages, similar to spring. In contrast to Bonneville whitefish, but again similar to spring, Bear Lake whitefish diets were dominated by Ostracoda at deeper depths. However, in this season Ostracoda

also dominated diets of the few Bear Lake whitefish found at depths with high abundances of Bonneville whitefish.

Diet- Presence and Absence

Fish species had a large effect on the presence or absence of a prey group while season and fish length had lesser effects. For most food groups, logistic regression models with species, season, and fish length effects fit the data well (Table 2-3). For each model, the deviance divided by the degrees of freedom values were slightly less than one. The effect of species was large on the presence of Chironomidae, Ostracoda, and Pisidae with Bonneville whitefish having a much higher probability of having Chironomidae and Pisidae food groups present in their stomach than Bear Lake whitefish and Bear Lake whitefish having a much higher probability of having Ostracoda in their stomach. The effect of season was important for Chironomidae and potentially important for Ostracoda with these food groups having a higher probability of being present in spring, although the 95% confidence interval for the season parameter estimate overlapped with zero in the Ostracoda model. The effect of length was important for Pisidae and terrestrial groups with larger fish having a slightly higher probability of having these food groups present in their diet.

Discussion

Our results support the idea that the two benthic whitefish in Bear Lake are ecologically very different. First, these species inhabited different depths,

with Bonneville whitefish dominating the upper strata and Bear Lake whitefish dominating the deep profundal zone. Second, these species had very different diets even at depths where the species overlapped, with Bonneville whitefish eating a variety of benthic invertebrates, but mostly Chironomidae, and Bear Lake whitefish eating mostly Ostracoda. These patterns were evident in both spring and summer seasons. Although, CPUE of gill nets has been shown to vary with water temperature and fish body shape, which could bias our results, we think our results are robust to these effects. The two species in Bear Lake have almost the exact same body shape (Ward 2001), so their retention in the net should be equal for both species. Additionally, differences in swimming performance in relation to water temperature are similar for closely related salmonids (Myrick and Cech 2000), and whitefish are known to be active in water temperatures as cold as 4°C (Rudstam et al. 1994).

Given these distributions, Bonneville whitefish occupy a much larger benthic area than Bear Lake whitefish. Assuming Bonneville whitefish actively occupy depths of 5 m to 30 m in spring and 10 m to 30 m in summer they would inhabit an area of 120 km² and 90 km² respectively when the lake is at full pool (282 km²; Fig. 2-1). If Bear Lake whitefish actively occupy depths of 45 m to 55 m, they would inhabit an area of only 50 km². At 5 m shallower than full pool, which can occur during drought conditions, Bonneville would occupy an area of 110 km² in spring and 90 km² in summer and Bear Lake whitefish would

occupy an area of only 30 km² in both seasons (Fig. 2-1). This would be one third less area than they occupied when the lake was at full pool.

Furthermore, these distributions indicate that Bonneville whitefish and Bear Lake whitefish occupy very different thermal regimes (Fig. 2-1). In spring, Bonneville whitefish were associated with the highest temperature found in the lake (7°C). In summer, high numbers of Bonneville whitefish were found within the fundamental thermal niche (14°C to 18°C) derived for *Coregonus* spp. in a laboratory setting (Magnuson et al. 1979; Christie and Regier 1988; Rudstam et al. 1994) and did not occupy the very shallowest depths with the warmest water temperatures (20°C). In contrast, Bear Lake whitefish occupied the coldest water in the lake during both seasons (4°C to 5°C). Temperature is one of the most important factors affecting a fish's growth, survival, and reproduction, so fish that occupy different thermal regimes likely differ in many other life history characteristics, other than distribution and diet, making them even more ecologically different.

Because Bonneville whitefish and Bear Lake whitefish have such large differences in distribution and diet, they likely have very diverse roles in the Bear Lake ecosystem. Benthic fish are important in the structure and function of lake ecosystems, yet most research in lakes has focused on the pelagic open water species. Recently, an effort has been made to reintegrate benthic processes back into our understanding of lakes (Vadeboncoeur et al. 2002). Fish that consume benthic invertebrates are important in this regard because they have

been shown to alter the distribution, composition, and abundance of many benthic invertebrate species (Luecke 1990; Carlise and Hawkins 1998). Also, many of these fish species are also prey for piscivores. Thus, they are important integrators of benthic and pelagic food webs (Vander Zanden and Vadeboncoeur 2002). The two whitefish in Bear Lake provide a unique example to this emerging field because of their unique upper and lower depth distributions and contrasting diets. The upper water habitat that Bonneville whitefish occupy in spring and summer is characterized by relatively higher amounts of food, more prey diversity, and higher densities of piscivorous fish (Wurtsbaugh and Hawkins 1990; Ruzycki and Wurtsbaugh 1999; Mazur and Beauchamp 2003). The high numbers of Bonneville whitefish found at these depths combined with diets of mostly Chironomidae and Pisidae, and a high susceptibility to pelagic piscivores make Bonneville whitefish central to the upper strata community as an integrator of benthic and pelagic food webs. In contrast, the deepest habitats found in Bear Lake are characterized by low amounts of food, less prey diversity, and fewer piscivores. The high numbers of Bear Lake whitefish found at these depths and diets dominated by Ostracoda indicate a strong predator prey relationship between Bear Lake whitefish and Ostracoda, and a lesser relationship with piscivores.

Although, ecological differences have been described for sympatric ecotypes of whitefish in both North America and Europe, these studies typically involved the genus *Coregonus* in recently glaciated lakes in very similar

ecoregions. We provide quantitative evidence of sympatric ecotypes of benthic whitefish of the genus *Prosopium* in a lake not recently glaciated and in a different ecoregion, thus increasing the generality of sympatric ecotypes in the subfamily Coregoninae. Fishes of the genus *Coregonus* have been the focus of many population divergence and speciation studies (Todd et al. 1981; Bernatchez et al. 1996; Lu and Bernatchez 1999). Populations of these fishes in recently glaciated lakes (~11,000 years old) in the Holarctic ecoregion of Northern North America and Northern Europe have been shown to be both morphologically and ecologically diverse, but genetically very similar. As mentioned previously, these populations are usually characterized by a larger benthic ecotype and a smaller limnetic ecotype (Lindsay 1963; Fenderson 1964; Bodaly 1979). There is evidence that sympatric ecotypes also occur in *Prosopium* species and may be the result of adaptive radiation, but they have been studied much less (McCart 1970; Benke 1972). Bear Lake, unlike many previously studied lakes, is in the arid Great Basin and is located south of other lakes containing sympatric ecotypes in North America by hundreds of kilometers. Additionally, Bear Lake is not recently glaciated. It has a long history (> 35,000 years) of lake level fluctuations and connections with other large and now extinct lakes in the Great Basin (Miller 1965). Changes in lake level and connectiveness were the result of climate associated with glaciation, earthquakes, and lava flows, but not glaciers directly. Furthermore, Bear Lake differs from many other lakes with sympatric pairs because unlike the usual one benthic-one limnetic ecotype,

it contains two benthic ecotypes in addition to the limnetic ecotype (Bonneville cisco). Bonneville whitefish represent a shallower benthic ecotype that forages on a variety of invertebrates and Bear Lake whitefish represents a deeper benthic ecotype that forages almost exclusively on Ostracoda. These data along with previously documented differences in genotype suggest that extending the generality of resource-based adaptive radiation in the subfamily Coregoninae to the *Prosopium* genus may be warranted. Additional studies on the evolutionary history of these species and examining if Bonneville whitefish can out-compete Bear Lake whitefish in shallower habitats and vice-versa for deeper depths would clarify these ideas further.

Conservation Implications

Bear Lake faces many potential threats including nutrient loading, invasion of non-native species and overstocking of piscivorous fishes. The distinct ecologies of each whitefish species in the Bear Lake indicates that these threats will likely have different effects on each species ultimately requiring complex conservation strategies. For example, increased nutrient loading could result in de-oxygenation of the profundal zone and may have severe consequences for profundal Bear Lake whitefish by causing death or immigration into shallower areas. Boats from many areas throughout Utah and Idaho are launched daily onto Bear Lake throughout the summer. This could lead to non-native benthic invertebrates becoming established thereby changing the prey base that these whitefish rely on (sensu Kolar and Lodge 2002). Additionally, piscivorous native

Bonneville cutthroat trout and non-native lake trout are stocked into the lake every year, which could directly reduce the population size of one or both whitefish species or cause a change in habitat use. A shift in either fish's distribution from any one of these threats may cause overlapping distributions and increased risk of competition and hybridization. Conservation of these fishes depends on conserving the diverse habitat that allows them have different distributions (Lu and Bernatchez 1999). Studies examining how each of the threats might impact Bear Lake whitefish are needed to improve conservation strategies for these endemic fishes.

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Table 2-1. – Description of five a priori models used in model selection process to estimate model-averaged number of whitefish caught per gill net night across depths (m) found in Bear Lake in spring and summer, 2000-2003.

Model Name	Hypothesis Description	Structure
Random	Random relationship between number caught and depth	B_0
Linear	Number caught changes with depth at a constant rate	$B_0 + B_1(\text{Depth})$
Pseudothreshold	Number caught changes with depth at a constant rate then approaches but does not reach an asymptote	$B_0 + B_1 \ln(\text{Depth})$
Flat then increasing or decreasing	Random relationship between number caught and depth then number caught changes with depth at a constant rate	$B_0 + B_1(\text{Depth}^2)$
Third order polynomial	Number caught reaches a maximal number at middle depths or number caught rapidly changes with depth	$B_0 + B_1(\text{Depth}) + B_2(\text{Depth}^2) + B_3(\text{Depth}^3)$

Table 2-2. – Ranking of a priori hypothesized models of whitefish distribution in Bear Lake in spring and summer, 2000-2003. Models were ranked by Akaike's information criterion values adjusted for small sample bias (AIC_c) and AIC_c weights (w_i). Low ΔAIC_c and high AIC_c weights indicate best approximating models. K is the number of parameters (including the intercept) plus the dispersion factor (a parameter to measure dispersion of catch per net night data). See Table 2-1 for model descriptions.

Species	Season	Model	K	N	AIC_c	ΔAIC_c	w_i
Bonneville Whitefish	Spring	Random-linear	3	84	-1229.10	0.00	0.56
		3rd polynomial	5	84	-1228.61	0.49	0.44
		Linear	3	84	-1220.11	8.99	0.01
		Pseudothreshold	3	84	-1208.56	20.54	0.00
		Random	2	84	-1192.78	36.32	0.00
	Summer	3rd polynomial	5	173	-5362.87	0.00	1.00
		Random-linear	3	173	-5351.60	11.27	0.00
		Linear	3	173	-5337.61	25.26	0.00
		Pseudothreshold	3	173	-5313.24	49.63	0.00
		Random	2	173	-5286.92	75.94	0.00
Bear Lake Whitefish	Spring	Random-linear	3	84	-199.91	0.00	0.76
		3rd polynomial	5	84	-196.24	3.67	0.12
		Linear	3	84	-196.22	3.69	0.12
		Pseudothreshold	3	84	-182.57	17.34	0.00
		Random	2	84	-146.58	53.33	0.00
	Summer	3rd polynomial	5	173	-1070.70	0.00	0.81
		Random-linear	3	173	-1067.70	3.00	0.18
		Linear	3	173	-1062.16	8.53	0.01
		Pseudothreshold	3	173	-1045.85	24.55	0.00
		Random	2	173	-943.54	127.16	0.00

Table 2-3. – Parameter estimates and 95% log likelihood profile confidence intervals from logistic regression analysis of factors influencing the consumption of four prey items by whitefish in Bear Lake. For the fish species parameter, positive values indicate a greater probability of food item being present in Bear Lake whitefish and negative values indicate a greater probability of the food item being present in Bonneville whitefish. For the season parameter, positive values indicated a greater probability of the food item being present in spring.

Prey Item	Parameter	df	Estimate	SE	95% CI	X²	P
Chironomidae	Intercept	1	2.626	1.201	0.334 to 5.076	4.78	0.029
	Fish Species	1	-2.568	0.459	-3.544 to -1.723	31.24	0.001
	Season	1	1.602	0.416	0.815 to 2.457	14.81	0.001
	Fish Length	1	-0.002	0.006	-0.013 to 0.009	0.14	0.710
Ostracoda	Intercept	1	1.65	0.92	-3.500 to 0.131	3.22	0.073
	Fish Species	1	3.967	0.561	2.979 to 5.229	49.97	0.001
	Season	1	0.701	0.379	-0.029 to 1.465	3.42	0.064
	Fish Length	1	0.003	0.004	-0.006 to 0.113	0.38	0.537
Pisidae	Intercept	1	-3.598	1.011	-5.688 to -1.703	12.67	0.001
	Fish Species	1	-2.537	0.51	-3.658 to -1.622	24.74	0.001
	Season	1	0.254	0.365	-0.459 to 0.980	0.48	0.487
	Fish Length	1	0.015	0.005	0.006 to 0.025	9.51	0.002
Terrestrial	Intercept	1	-3.339	1.033	-5.453 to -1.386	10.45	0.001
	Fish Species	1	-0.547	0.375	-1.304 to 0.174	2.13	0.145
	Season	1	-0.297	0.364	-1.020 to 0.413	0.67	0.415
	Fish Length	1	0.011	0.005	0.002 to 0.021	4.95	0.026

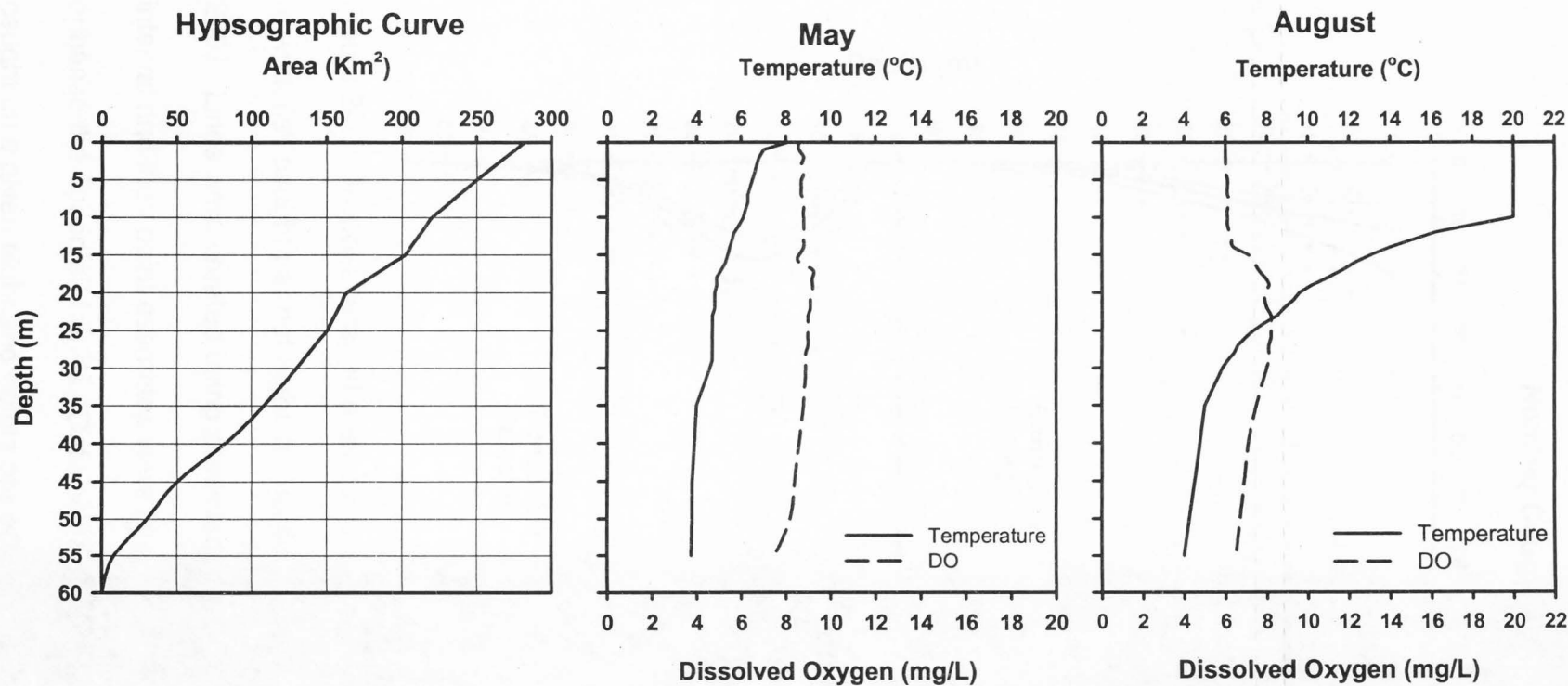


Figure 2-1. – Hypsographic curve, dissolved oxygen, and temperature profiles of Bear Lake. Hypsographic curve is derived from Wurtsbaugh and Hawkins (1990). Each rectangle represents 0.25 km³. Temperature measurements were taken in May and August 2003. Dissolved oxygen measurements were taken in May and August 2004.

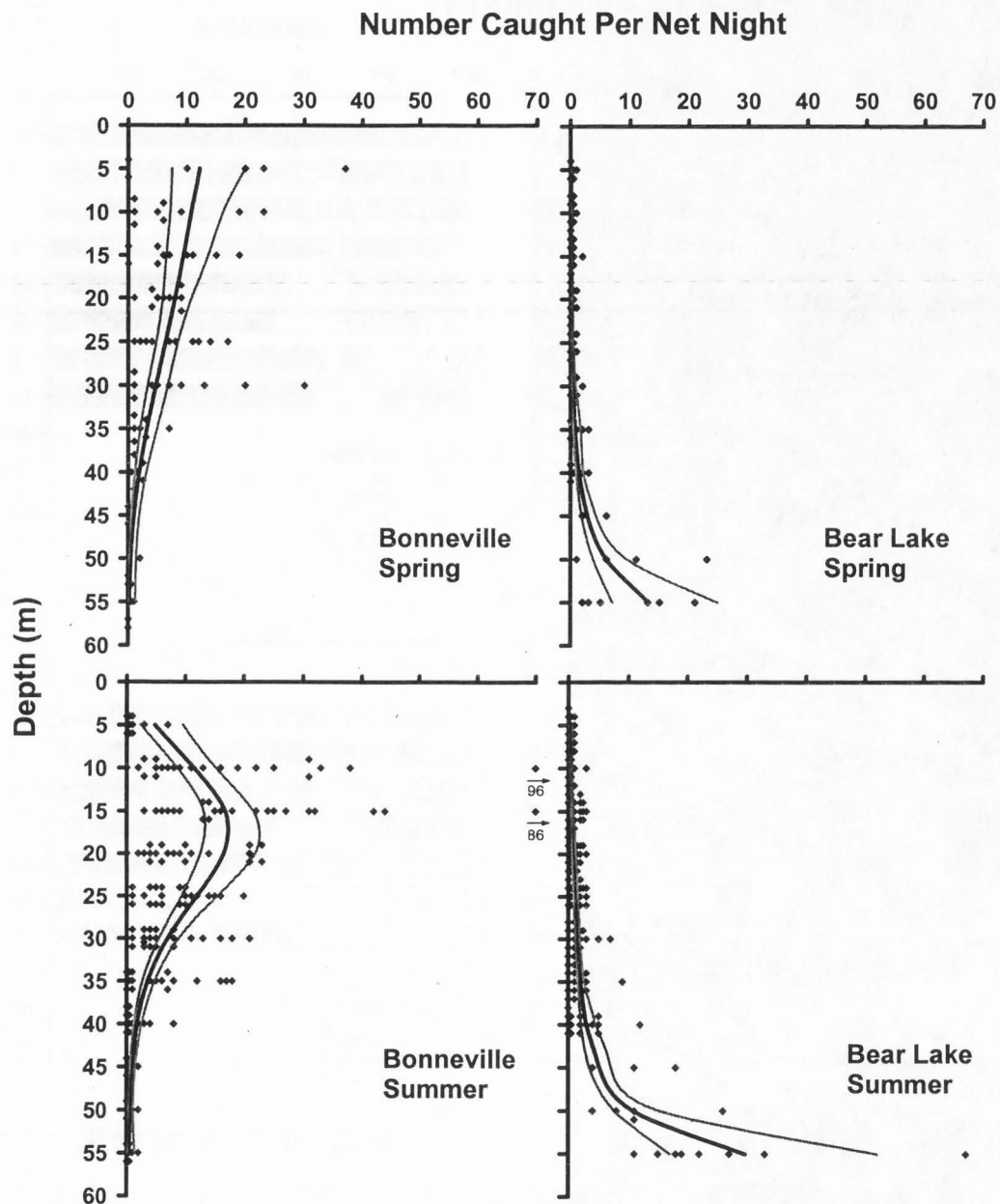


Figure 2-2. – Model-averaged mean and 95% confidence interval of the number of whitefish caught per net night across depth for spring and summer, 2000-2003. Lines were created using predicted CPUE estimates for each 5-m depth interval and then point estimates were connected to each other to visually enhance the observed trends. Data points indicate actual numbers of whitefish caught on a given night and points are offset for clarity.



Figure 2-3. — Average percents of dry weight biomass of five prey items in spring and summer diets of Bonneville and Bear Lake whitefish caught using gill nets at 5-m depth intervals in Bear Lake. At least 10 fish of each fish species were examined and averaged at each depth unless noted next to each bar. Terrestrial group consisted of mostly Homoptera and Hymenoptera. The “Other” group consisted of mostly Amphipoda and Annelida.

CHAPTER 3

DISTINCT SPATIAL DISTRIBUTIONS OF TWO ENDEMIC WHITEFISH
SPECIES RELATE TO CONDITIONS FOR GROWTH AND
PREDATION AVOIDENCE¹

Abstract. – Understanding processes that promote and maintain the existence of closely related species is a central question in ecology. Few studies have tested the idea that large-scale habitat differences in trade-offs between growth conditions and predation risk allow for the persistence of species separation. In Bear Lake, a large oligotrophic lake on the Idaho-Utah boarder, we examined how the shallow habitats used by benthic Bonneville whitefish (*Prosopium spilontus*) differed from deep habitats used by closely related and morphologically similar Bear Lake whitefish (*P. abyssicola*). Specifically, prey availability, water temperature, and predation risk in spring and summer were examined. Habitats occupied by Bonneville whitefish had higher prey availability and warmer more heterogeneous water temperatures, but had higher predation risks compared to habitats used by Bear Lake whitefish. Habitats avoided by both species had the disadvantages of low prey availabilities, cold water temperatures, and high predation risks. These results imply that individuals may maintain higher fitness at shallow or deep but not middle depths of Bear Lake due to better factors linked to survival and reproduction. Different growth

¹Coauthored by Benjamin M. Kennedy and Chris Luecke

schedules associated with different habitat use may have established the conditions allowing for different spawning times, thus resulting in their reproductive isolation.

Introduction

Environments containing closely related species pairs are model systems for studying the processes of speciation (Schluter 2000). Additionally, these systems are rare, requiring explicit conservation measures. Well known examples of closely related species pairs include the Galapagos finches (Geospizinae) and the cichlids of East African lakes (Cichlidae). Ongoing research on sticklebacks (*Gasterosteus* sp.) and whitefish (Coregonine) has produced important information on the processes of speciation.

Studies on sticklebacks and whitefish have focused on understanding adaptive radiation through studies on matching divergent phenotypes to different habitats and measuring the performance of specific traits in specific environments (Schluter 1996; Bernatchez et al. 1999). Most of these closely related pairs contain a benthic and a limnetic ecotype in lake environments. The limnetic form is a relatively small, slender zooplanktivore with a higher number of gill rakers that are longer in length than the larger benthic ecotype that eats benthic invertebrates (Schluter and McPhail 1993; Robinson and Wilson 1994). The phenotype of benthic ecotypes has been correlated with better foraging efficiency and growth in benthic habitats compared to limnetic ecotypes and

hybrids. The morphology of limnetic ecotypes has been correlated with better performance in open water habitats (Schluter 1995; Rogers et al. 2002). This divergent natural selection along with assortative mating are thought to give rise to the speciation of the ecotypes in the pair.

Despite this extensive research on littoral versus open water ecotypes, few studies have examined other important environmental differences. In addition to horizontal resource gradients (benthic to open water), lakes vary enormously along vertical gradients (shallow to deep). Differences in water temperature, light, prey diversity, prey abundance, and predator distribution can have major affects on the growth, survival, and reproduction of fish. These influences likely relate to phenotypic diversity and can drive reproductive isolation as species adapt to these different environments by changing life histories and behaviors.

Bear Lake, Utah-Idaho contains a closely related endemic whitefish complex with three species that are genetically and morphologically similar, reproductively isolated, and differ in distribution and diet. These species are the Bear Lake whitefish (*Prosopium abyssicola*), Bonneville whitefish (*P. spilontus*), and Bonneville cisco (*P. gemmifer*). They are closely related, but they are considered separate species (Bernatchez et al 1991; Vuorinen et al. 1998; Toline et al. 1999). Available genetic evidence from Bonneville whitefish and Bonneville cisco indicates they are very similar, diverging relatively recently (< 35,000 years ago) and that gene flow does not occur presently. Additionally, these species are

more related to *P. williamsoni* than other members of the genus. Additional phylogenetic studies with the inclusion of Bear Lake whitefish would be useful. In addition to genetic differences, these species are reproductively isolated, with Bonneville whitefish spawning in early December, Bonneville cisco spawning in early January, and Bear Lake whitefish spawning from mid-February to mid-March (White 1974).

Bonneville cisco is a limnetic ecotype and Bonneville whitefish and Bear Lake whitefish are benthic ecotypes. Bonneville cisco occupy the pelagic zone of the lake and eat zooplankton and like other systems with a limnetic ecotypes, they have more gill rakers that are longer than the benthic species' (White 1974; Luecke and Wurtsbaugh 1993). Bear Lake and Bonneville whitefish are morphologically very similar and difficult to identify. Unlike many closely related whitefish populations these two species have gill rakers of similar number and length. Bonneville whitefish are found in relatively shallow benthic habitats and Bear Lake whitefish are found in deepest areas of the lake (Fig. 3-1; Chapter 1). Both species avoid the middle depths of the lake. Associated with differences in distribution, Bonneville whitefish and Bear Lake whitefish have different diets. Bonneville whitefish forage on a variety of invertebrates including Chironomidae, Pisidae, Ostracoda, and terrestrial insects but Chironomidae are the dominant prey item (Chapter 1). Bear Lake whitefish eat almost exclusively Ostracoda. These diet differences exist even at depths where the two species overlap in low numbers (Chapter 1).

Many environmental factors are associated with the distribution of a species, and researchers can gain a more complete understanding of these factors by integrating data on environmental growth conditions and predation risk together instead of treating these topics independently (Godin 1997). Growth conditions are important to an individual because in general, higher growth is associated with higher survival and reproduction. A habitat with growth conditions that result in high growth rates should have a high amount of food available, and a water temperature that allows for maximal growth. Predation is important to an individual because it can affect survival directly through mortality or indirectly through a change in habitat use. If predation risk is constant or non-existent across habitats, individuals may be distributed in relation to growth conditions only. If growth conditions are similar across habitats, individuals may be distributed in relation to predation risk only. Most often, growth conditions and predation risk will vary creating a complex set of trade-offs. Theory suggests that organisms should minimize the ratio of mortality to growth in order to maximize fitness from which individuals should use habitats with the best growth conditions and lowest predation risk (Werner and Gilliam 1984). The best way to assess these trade-offs is to examine these factors concurrently.

The goal of this study was to examine how distributions of Bonneville whitefish and Bear Lake whitefish were associated with differences in growth and predation risk conditions. Specifically, our objectives were to examine how food availability, water temperature, and predation risk varied with depth and season

for both species. Typically, in large lakes that stratify like Bear Lake, the shallower depths will have the most food, the warmest temperatures, and the most predators. We assessed the degree to which both species associated with growth and predation loss by comparing the depth distribution of each whitefish species to distribution of temperature, food availability, and predation risk.

Materials and Methods

Study Area

Bear Lake is an oligotrophic lake located at 42°N, 111°20'W and straddles the northeast Utah-Idaho boarder (Lamarra et al. 1986; Wurtsbaugh and Hawkins 1990). At full pool, the lake covers 282 km² at an elevation of 1,805 m above sea level. Bear Lake has a maximum depth of 62 m and a mean depth of 28 m. In approximately three of every 4 years the lake will ice over. The watershed geology consists mostly of limestone and other soft sedimentary rocks, causing the lake to be alkaline with calcite precipitation that strips phosphorus from the water. The substrate is dominated by fine marl sediments with limited areas of rock, sand, and snail shells from an extinct species of gastropod. Bear Lake is dimictic, cold, and dissolved oxygen is greater than 5 mg/L throughout the water column during spring and summer (Fig. 3-2). Epilimnetic mid-summer chlorophyll- α concentrations range from 0.5 – 1.2 $\mu\text{g/L}$ and zooplankton communities are dominated by the copepod *Epischura nevadensis* and *Bosmina lacustris*, with *Daphnia pulex* and *Daphnia galeata*

occasionally present. Benthic invertebrate biomass ($0.34 \text{ g dry wt/m}^2$) is among the lowest recorded for mid-latitude lakes (Wurtsbaugh and Hawkins 1990). The Bear Lake fish assemblage contains 13 fish species including nine that are native, four of which are endemic. The dominant piscivores in the system are native Bonneville cutthroat trout (*Oncorhynchus clarki utah*) and non-native lake trout (*Salvelinus namaycush*), both of which are maintained primarily by stocking. Currently the top 6.5 m of water in Bear Lake is managed as a storage reservoir where water is diverted into the lake during spring and pumped out throughout the summer and fall.

Temperature and Light

Spatial and temporal differences in the thermal structure and oxygen concentration of Bear Lake were sampled throughout the water column of the lake during each sampling season with a YSI Model 58 temperature probe (YSI Inc., Yellow Springs, Ohio, USA).

Ambient light level lux (lx) was measured at depths from 0 m to 30 m at 1 m depth intervals on 13 May 2003 and 15 August 2003. These data were used to calculate an extinction coefficient (K_t). Ambient light levels were then calculated for each depth at 1 m depth intervals from 1 m to 55 m for each date using the equation:

$$(1) \quad L_{z,t} = L_{0,t} * \exp(-K_t * Z),$$

where ambient light is an exponential decay of incident light level $L_{0,t}$ during season t and Z was depth. L_0 was measured as the ambient light level at the

surface at noon on 13 May 2003 and 15 August 2003. The skies were clear during each of these sample dates.

Food Availability

To examine how prey availability varied both spatially and temporally, benthic macroinvertebrates were collected with a Ponar dredge (0.0529 m²) in summer 2002 (24 July to 21 August) and spring 2003 (6 May to 14 May) along four transects at eight depths starting at a randomly selected point along each shore (north, south, east, west) and ending at a randomly selected point at a depth of 55 m. Three separate samples were collected in the vicinity of the transect line at depths of 1 m, 4 m, 8 m, 15 m, 25 m, 35 m, 45 m, and 55 m. These locations encompassed the epilimnetic, metalimnetic, and hypolimnetic zones of the lake and covered most of the spatial variation in light, temperature, and oxygen. Samples were not collected from the East transect at 1 m because large rocks prevented the Ponar dredge from operating properly. The soft sediments sampled effectively with the ponar dredge accounted for greater than 99% of the benthic substrate. From each sample a sub-sample was taken for Ostracoda analysis, and the rest of the sample was sieved through a 0.5 mm screen and preserved in 75% ethanol. In the laboratory, Ostracoda were counted from the sub-samples and Chironomidae, Pisidae, and terrestrial invertebrates (mainly Hymenoptera and Homoptera) were counted from the remaining sample. Length was converted to dry weight using relationships from Wurtsbaugh and Hawkins (1990). Differences in biomass across depth and

season were analyzed using two-way analysis of variance (ANOVA) on log-transformed data using PROC GLM (SAS 2001). Results were considered significant at $\alpha < 0.05$. After statistical analysis, Ostracoda data were converted into a relative index of biomass across depth due to unusually high absolute biomasses. The highest amount of Ostracoda sampled at a depth was weighted to 100 and the percentage of biomass relative to the highest biomass was calculated for each depth.

Predation Risk

To assess how predation risk varied across depth and season, we created a mechanistic model incorporating individual predator search volume and predator distribution to estimate the volume of water searched by predators at a given depth during a typical day in May and a day in August. We modeled the relative search volume by predators ($RSV_{z,t}$) at depth z and season t as the product of the number of predators ($P_{z,t}$) at depth z and season t and an individual predator's search volume ($SV_{z,t}$) at depth z and season t divided by the total volume of water search by predators at all depths:

$$(2) \quad RSV_{z,t} = [P_{z,t} * SV_{z,t} / \sum (P_{z,t} * SV_{z,t})] * 100$$

The number of predators at depth z and season t was measured as the number of predators caught in gill nets set overnight at a given depth. During May and August 2002, four gill nets were set at randomly selected locations at depths of 15 m, 20 m, 25 m, 30 m, 35 m, and 40 m. Two gill nets were set at

randomly selected locations around the lake at 50 m and again at 55 m, the number of predators caught at 50 m and 55 m was multiplied by two because only two nets instead of four were set at these depths. During May and August 2003 four gills nets were placed randomly around the lake at 5 m and again at 10 m. Linear interpolation was used to estimate predator distribution at 1 m depth intervals that fell in between sampling depths. An individual predator's search volume was measured as the volume of water scanned by a predatory fish for the duration of a second. We modeled search volume as a cylinder where the fish's reaction distance ($RD_{z,t}$) (maximum distance at which a predatory fish can see a potential prey) was the radius of the cylinder and the distance swam in one second ($DS_{z,t}$) was the height:

$$(3) \quad SV_{z,t} = \pi RD_{z,t}^2 * DS_{z,t}.$$

The distance swam by a predatory fish during one second was calculated individually from swimming speeds for lake trout and cutthroat trout. Swimming speeds for lake trout were estimated from laboratory data collected by Mazur and Beauchamp (2003). Swimming speeds for cutthroat trout were estimated from field data collected by Baldwin et al. (2002). We calculated the reaction distance as a function of ambient light level ($L_{z,t}$) for each species using models developed by Mazur and Beauchamp (2003), where the reaction distance for a lake trout at depth z and season t was:

$$RD_{z,t} = RD_{\max} = 96.680 \text{ cm for } L_{z,t} \geq 18.000 \text{ lx}$$

and for cutthroat trout:

$$(5) \quad RD_{z,t} = 33.70 * L_{z,t}^{0.194} \text{ for } L_{z,t} < 17.00 \text{ lx}$$

$$RD_{z,t} = RD_{\max} = 58.38 \text{ cm for } L_{z,t} \geq 17.00 \text{ lx.}$$

In addition to the model, predation risk was assessed experimentally across depth and season using tethered fish. In August 2002 (18 July to 22 August), May 2003 (20 May to 28 May) and August 2003 (11 August to 21 August) ten fish at each depth were individually tethered and set for 24 hours at depths of 5 m, 15 m, 25 m, 35 m, 45 m, and 55 m along three of the four previously described transects (north, south, west). Hatchery rainbow trout *Oncorhynchus mykiss* of similar size and shape to adult whitefish (150-200 mm total length) were used as surrogates for whitefish because of logistical constraints of collecting a sufficient number of live whitefish. An individual tether consisted of a fish with a 1 m long tether of 14 kg test fishing line threaded through the jaw and opercle and the tether was attached 1.5 m off the bottom to a vertical piece of bailing twine that ran from the surface of the lake to the bottom. Individual tethers were set 150 m apart. Data were recorded as the number of fish eaten per 10 fish trial. Differences in the number of fish eaten in a trial were analyzed across depth and date (e.g. August 2002) using two-way

ANOVA on square root transformed data using PROC GLM (SAS 2001). Results were considered significant at P -value < 0.05 .

Results

Temperature and Light

The thermal structure of Bear Lake changed dramatically with both depth and season (Fig. 3-2). In general, warmer and more heterogeneous water temperatures were found in the Bonneville whitefish dominated zone whereas colder more homogeneous water temperatures were found in the Bear Lake dominated zones. During spring, the lake was nearly isothermic with water temperatures being the highest at the shallowest depths (7°C at 1 m). Then temperature decreased gradually with depth and reached its lowest value at the deepest part of the lake (4°C at 55 m). In summer, Bear Lake was strongly stratified. Epilimnion temperatures exceeded 20°C , a thermocline developed at 10 m creating a zone of rapidly changing temperatures from 19°C to 7°C at a depth of 25 m. In the hypolimnion, temperatures decreased gradually from 7°C to 4°C at 55 m.

Light varied with both depth and season (Fig 3-2). During midday of both seasons light was high throughout most depths. Light levels were lowest at the deepest depths of the lake. In spring, the light extinction coefficient was higher (0.208) than in summer (0.187) causing light levels to be higher in summer at a given depth than in spring at a given time of day.

Food Availability

In both spring and summer, the highest amounts of prey were found at depths occupied by Bonneville whitefish and the lowest amounts of prey were found at depths used by Bear Lake whitefish. The two-way ANOVA of the invertebrate biomass data (excluding Ostracoda) showed significant effects of depth, season, and a significant interaction of depth and season (Table 1), indicating that the effect of depth depended on season. In spring, Chironomidae, Pisidae, and terrestrial insect biomasses were highest at the shallowest depths of the Bonneville whitefish zone (5 m) and biomass decreased steadily with increasing depth (35 m) where biomass leveled off and was similar across depths in the Bear Lake whitefish zone (Fig. 2). In summer, Chironomidae, Pisidae, and terrestrial biomasses were moderate at the depths sampled above the Bonneville dominated zone (5 m) and highest at depths of 10 m and 15 m in the Bonneville zone (Fig. 3-2). Biomass then decreased from the deeper part of the Bonneville zone to the avoidance zone (15 m to 35 m) where prey amounts again leveled off. ANOVA analysis of the Ostracoda data showed significant effects of depth and season (Table 3-1). In both spring and summer, Ostracoda biomass index indicated that biomass increased with depth through the Bonneville whitefish zone to a maximum biomass at 25 m then decreased with increasing depth (Fig. 3-3). Unlike the other food items, Ostracoda biomass continued to decrease after the avoidance zone (35 m) so that prey amounts

were lowest in the deepest part of the Bear Lake whitefish dominated zone (55 m).

Predation Risk

The number of predators caught in gill nets varied with both depth and season (Fig. 3-5). In spring, the number of predators caught across depth was bimodal with peaks at 25 m and 50 m. At depths near 25 m both cutthroat trout and lake trout were caught. At 50 m only cutthroat trout were caught. Very few predators were caught at 5 m and 10 m. In summer, the highest number of predators caught were at 15 m and 20 m. The number of predators caught then decreased with depth. At 15 m and 20 m the majority of predators caught were cutthroat trout, however, at 25 m and 30 m the majority of predators caught were lake trout. Like spring very few predators were caught at 10 m and 55 m.

Individual reaction distances of predators in Bear Lake also varied with depth and season (Fig. 3-6). In spring, individual reaction distances of predators were maximized from 1 m to 41 m because of high light levels. Reaction distances then decreased with depth as light became limiting. In summer, maximum reaction distance extended from 1 m to 46 m. Individual reaction distance then decreased with light. The additional depths where predators had maximum sight was associated with higher levels at these depths associated with a smaller light extinction coefficient. Lake trout had a longer reaction distance than cutthroat trout at all depths and both seasons, but this difference was largest under unlimited light.

The predator foraging model predicted that the relative volume of water searched and subsequent predation risk in spring and summer should be highest at depths occupied by Bonneville whitefish and the lowest risk was predicted to occur in the Bear Lake whitefish zone (Fig. 3-7). In spring, the model predicted that relative volume searched should be low at the shallower depths of the Bonneville whitefish (5 m and 10 m) dominated zone and increase through this zone to a maximum level at the deeper depths of this zone (25 m). Volume of water searched was then estimated to decrease to a depth of 40 m then increase somewhat to the start of the Bear Lake whitefish zone (45 m) and then decrease to a low level at the deepest depth of the Bear Lake whitefish zone (55 m). Cutthroat trout search volume had two smaller peaks and lake trout had one large peak in volume of water searched. In summer, the estimated search volume was again highest at depths occupied by Bonneville whitefish. However, in this season, the peak was wider. In summer, most of the volume searched in the upper depths was by cutthroat trout and most of the volume searched at deeper depths was from lake trout. The model estimated that 69% of the volume of water searched at depths 11 m to 20 m was by cutthroat trout whereas 79% of the volume of water searched at depths 21 m to 30 m was by lake trout. Most of the variation in the model at depths shallower than 40 m was due to predator density as light was unlimited at these depth permitting maximum reaction distances (Figs. 3-5 and 3-6). Also, the maximum reaction distance for lake trout was much higher than that of cutthroat trout so that one lake trout had more of an

impact on the relative amount of water volume searched. Below 40 m light became limiting and had a major impact on the model. For example, in spring, eight predators were caught at 50 m which was similar to the number caught at 25 m and 30 m yet the relative amount of predation at depths near 50 m was less than half that of depths around 25 m to 30 m.

In the fish tethering experiment, there was no consistent relationship in spring between the number of fish eaten per trial and depth, but in summer there was a relationship similar to what the foraging model predicted with the highest number of fish eaten occurring at shallow and middle depths and the lowest number of fish being eaten at the deepest depths found in the lake. The two-way ANOVA showed a significant interaction between depth and season (Table 3-2). In summer, the highest numbers of fish eaten were at depths occupied by Bonneville whitefish and at depths avoided both species (15 m, 25 m, and 35 m). The lowest numbers of fish eaten were at depths occupied by the highest numbers of Bear Lake whitefish (45 m and 55 m). Although the number of fish eaten was low at these depths there was still some predation.

Discussion

Our data support the idea that Bonneville whitefish and Bear Lake whitefish occupy habitats with different conditions associated with growth and predation risk in both spring and summer. Habitats occupied by high numbers of Bonneville whitefish had relatively high food availabilities and warmer water

temperatures. These habitats were also associated with high levels of predation risk. In contrast, habitats occupied by Bear Lake whitefish had low food availabilities and only cold water temperatures but the advantage of lower predation risks. Areas avoided by both species had the disadvantages of low to moderate food availabilities, cold water temperatures, and a moderate to high predation risk and no advantages. Our data for invertebrates other than Ostracoda were similar to previous studies on Bear Lake both in absolute biomasses and trend with depth. Our relative index of Ostracoda biomass provided similar patterns in the depth distribution of these food items compared to a previous study conducted by Wurtsbaugh and Hawkins (1990). Our high absolute counts likely included dead individuals. Our relative biomass index of Ostracoda allowed us to compare ostracod distribution to the distribution of fish.

A fish's growth rate is dependent on the amount of energy consumed minus the energy used for maintenance. Prey availability and water temperature are important environmental conditions affecting growth. Moderate or warmer water temperatures and high prey availability found in habitats occupied by Bonneville whitefish should allow for higher growth rates compared to growth rates habitats occupied by Bear Lake whitefish.

Bear Lake is an oligotrophic system so food is probably limiting and as a result, water temperatures below the optimum reported under unlimited food could provide maximum growth (Rudstam et al. 1994). This interaction between temperature and food availability may be the reason why Bonneville whitefish

were distributed between 10 m and 25 m where water temperatures ranged from 19°C to 7°C. These ideas are supported by a previous study that found that Bonneville whitefish have a faster growth rate and grow to a larger size than Bear Lake whitefish (Thompson 2003). Our results indicate that this higher growth rate is likely due to the use of habitats with higher temperature and increased food availability.

In contrast to Bonneville whitefish, Bear Lake whitefish occupied habitats with the lowest biomass of invertebrates and cold water temperatures year around. At these temperatures maintenance costs were very low so only a small amount of energy is required to grow. However, the maximum growth attainable at these temperatures is also very low. These factors suggest that either Bear Lake whitefish are more limited by water temperature and do not gain much by foraging a little shallower in an area of more food, or increased predation keeps them from foraging in that area. Likely a combination of the two plays a role. Previous research on larval Bear Lake sculpin (*Cottus extensus*) occupying waters with similar water temperatures to Bear Lake whitefish found that this species of fish was limited in growth more by water temperature than by prey availability adding more evidence that Bear Lake whitefish may be more limited in growth by temperature (Wurtsbaugh and Neverman 1988). At depths occupied by low numbers of both species, growth conditions are better than Bear Lake whitefish habitats because of more prey availability; however, these

habitats appear worse than habitats occupied by Bonneville whitefish because of constant cold water temperatures.

Although Bonneville whitefish occupy the best habitats in Bear Lake for maximizing growth, Bear Lake whitefish occupy depths with the lowest predation risk. The simulation model estimated that habitats deeper than 50 m received a low percentage of the total volume of water searched by predators in Bear Lake, although risk was higher in spring than summer. Our tethering experiments also showed that predation risk was lower at these depths in the summer but not spring. The discrepancy in spring at shallower depths may have been due to our model underestimating the density of cutthroat trout at deeper depths or overestimating the density of lake trout at deeper depths. Low light levels at deeper depths may provide a refuge for Bear Lake whitefish by decreasing the volume of water a predator can scan and reducing a predator's capture efficiency (Mazur and Beauchamp 2002). Our model predicted that habitats occupied by Bonneville whitefish and low numbers of both species were characterized by high predation risk. This high risk was mainly due to increased light levels and higher numbers of predators. Volume searched by cutthroat and lake trout and fish caught on tethers (Kennedy and Luecke unpublished data) indicated that predation risk was not equally caused by both predators. Instead it varied with depth and was due to species specific differences foraging ability and habitat preference.

Bonneville whitefish and Bear Lake whitefish occupy distinct habitats in Bear Lake both of which are better than habitats occupied by low numbers of both species, and this knowledge has important implications for how closely related species maintain isolation. One hypothesis on the evolution of reproductive isolation is that it evolves from the same forces that cause phenotypic change (Mayr 1942). If this is true then the same forces that maintain phenotypic change may maintain reproductive isolation. Most studies of this type link habitat differences in terms of prey type to phenotypic changes in morphology (body size, shape, and feeding apparatus) and habitat use (benthic vs pelagic) where individuals at extreme phenotypes have a higher fitness than intermediate phenotypes (Schluter 1993, 1995). Reproductive isolation occurs through mate selection based on morphological differences (Schluter and Nagel 1995).

Our study in Bear Lake provides evidence that habitat differences in growth conditions and predation risk are likely associated with phenotypic differences beyond morphology, where individuals using shallow and deep depths can have a higher fitness through better trade-offs in growth and mortality than individuals using middle depths. Additionally, traits that allow Bonneville whitefish and Bear Lake whitefish to outperform each other in their primary habitat have not been tested but could include swimming ability, foraging differences under different light conditions, predator avoidance strategies, and growth differences in different water temperature given equal food amounts.

Reproductive isolation could be a by-product of different growth schedules associated with habitat use. One plausible hypothesis is that each species spawns right after the end of the growing period for their given habitat. In habitats occupied by Bonneville whitefish these conditions are likely to occur in late fall early winter as water temperatures cool and prey becomes less available and is consistent with the timing of Bonneville whitefish spawning. In habitats occupied Bear Lake whitefish, cold water temperatures could delay growth and the maturation of reproductive organs by a couple of months. Ultimately, conservation will depend on maintaining conditions that allow for these trade-offs to persist.

Lastly, in relation to other studies of habitat use, this study demonstrates the value of looking at both growth conditions and predation risk over a whole lake scale. If we had looked at only growth conditions or predation risk or only looked at shallow or deep depths our conclusions would be very different. If we had only looked at growth conditions it would have been hard to explain why Bear Lake whitefish did not occupy middle depths. Conversely, if we had only looked at predation risk, it would have been hard to explain why Bonneville whitefish occupied the habitats they were found in. By looking at both growth conditions and predation risk across the whole lake we were able see significant tradeoffs and a more complete picture of the costs and benefits associated with different habitats.

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Table 3-1. – Analysis of variance (ANOVA) of the effect of depth and season on prey availability from 186 Ponar grabs across eight depths during summer 2002 and spring 2003. Data were log-transformed to meet assumptions of ANOVA.

Group	Factor	df	<i>F</i>	<i>P</i>
Invertebrates (no ostracoda)	Depth	7	56.8	<0.001
	Season	1	6.6	0.01
	Depth X Season	7	3.2	0.003
	Error	170		
Ostracoda	Depth	7	48.64	<0.001
	Season	1	4	0.03
	Depth X Season	7	0.71	0.59
	Error	169		

Table 3-2. – Analysis of variance (ANOVA) of the effect of depth and season on the number of fish eaten per tethering trial. Sixty-two trials were performed across seven depths during summer 2002, spring 2003, and summer 2003. Data were square-root transformed to meet assumptions of ANOVA.

Factor	df	<i>F</i>	<i>P</i>
Depth	5	7.97	<0.001
Date	2	11.95	<0.001
Depth X Date	10	3.41	0.003
Error	35		

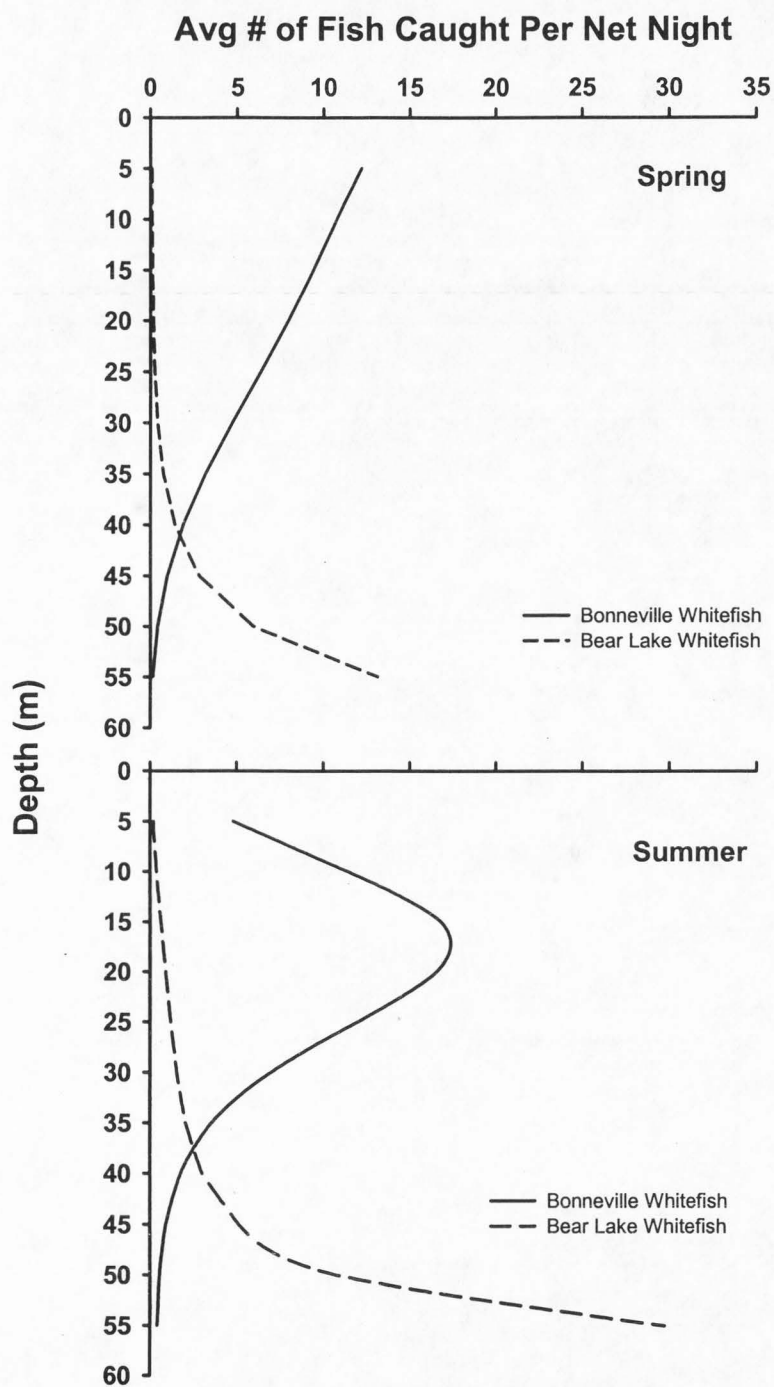


Figure 3-1. – Diagram showing benthic depths of Bear Lake occupied by high numbers of Bonneville whitefish, high numbers of Bear Lake whitefish, and low numbers of both species during spring and summer seasons.

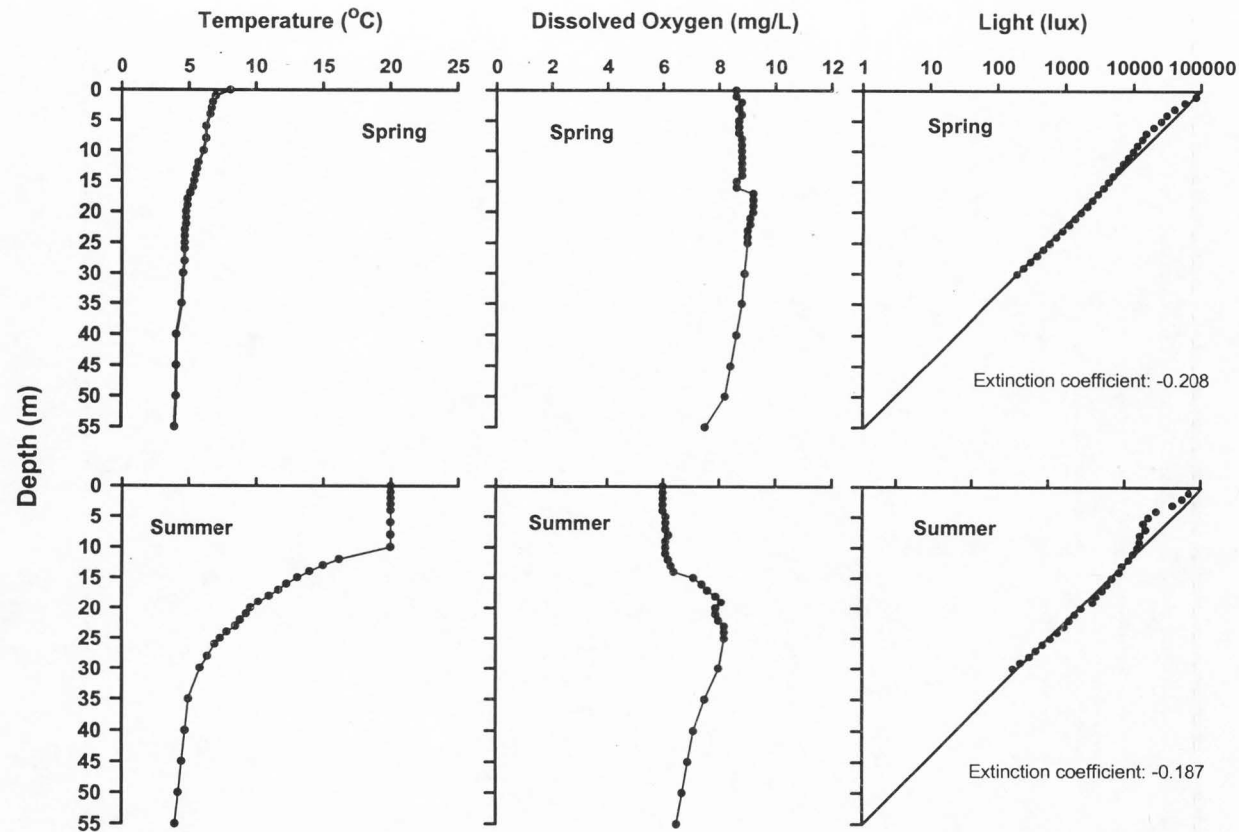


Figure 3-2. – Temperature, dissolved oxygen, and light profiles of Bear Lake during spring and summer seasons. Temperature measurements were collected on 14 May 2003, 22 August 2002. Dissolved oxygen measurements were collected on 12 May 2004 and 9 August 2004. Light measurements were collected on 14 May 2003 and 13 August 2003. Light levels below 30 m were calculated using a light extinction coefficient.

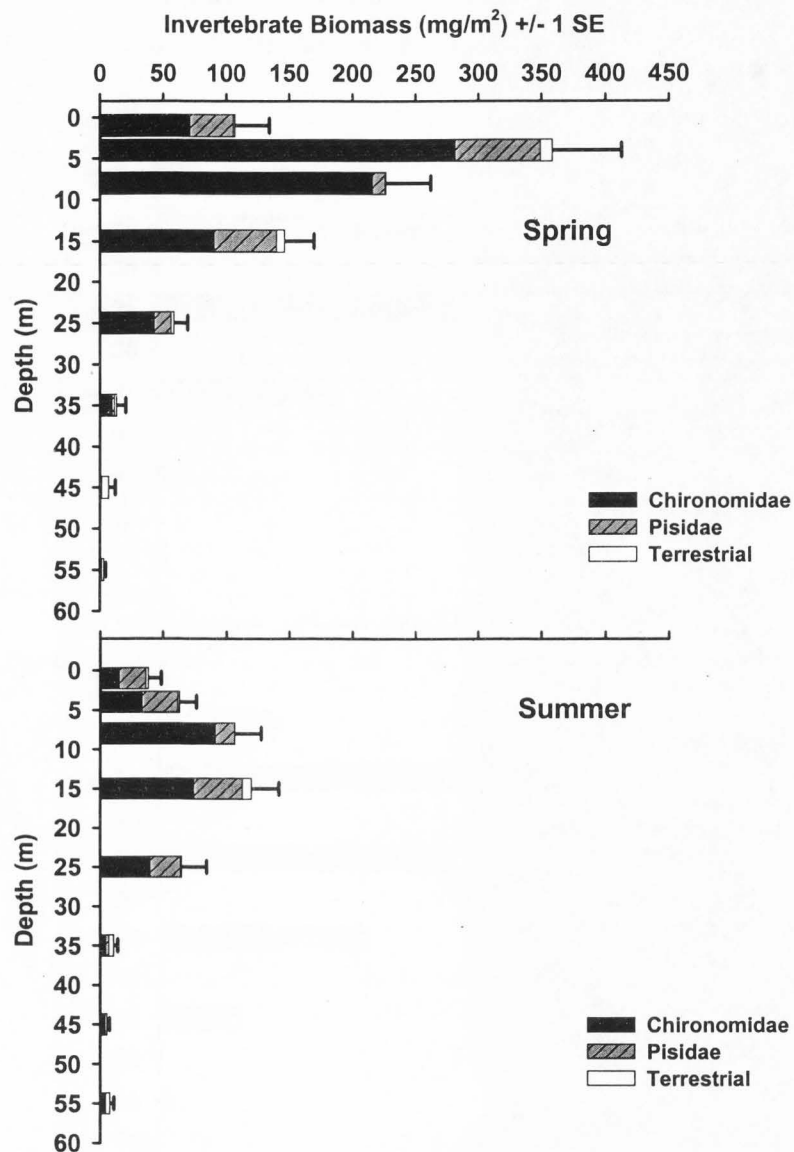


Figure 3-3. – Biomass (mg/m²) of Chironomidae, Pisidae, and terrestrial insects across depth in Bear Lake during summer 2002 (24 July to 21 August) and spring 2003 (6 May to 14 May). Samples were collected with a Ponar dredge (0.0529 m²) along four transects at eight depths. Three separate samples were collected in the vicinity of the transect line at depths of 1 m, 4 m, 8 m, 15 m, 25 m, 35 m, 45 m, and 55 m. Error bars represent one standard error.

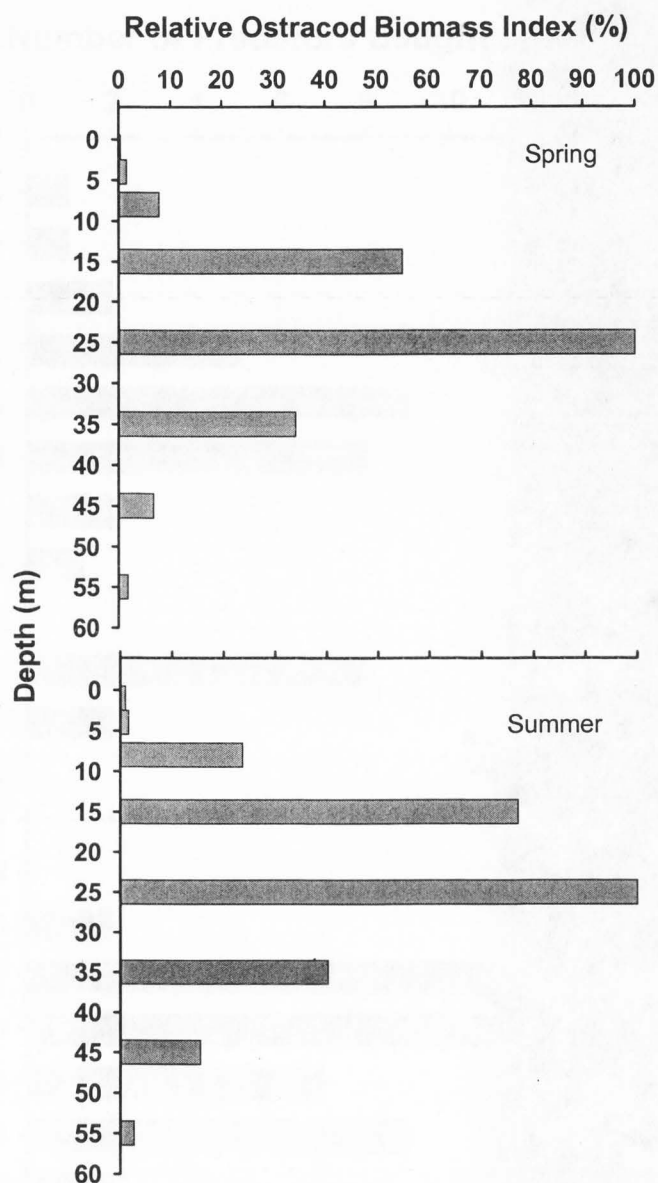


Figure 3-4. – Relative Ostracoda biomass across depth in Bear Lake during summer 2002 (24 July to 21 August) and spring 2003 (6 May to 14 May).

Samples were collected with a Ponar dredge (0.0529 m²) along four transects at eight depths. Final estimates for each season were calculated by dividing the average biomass at each depth by the largest average biomass found.

The largest average biomass was found at 25 m for both seasons.

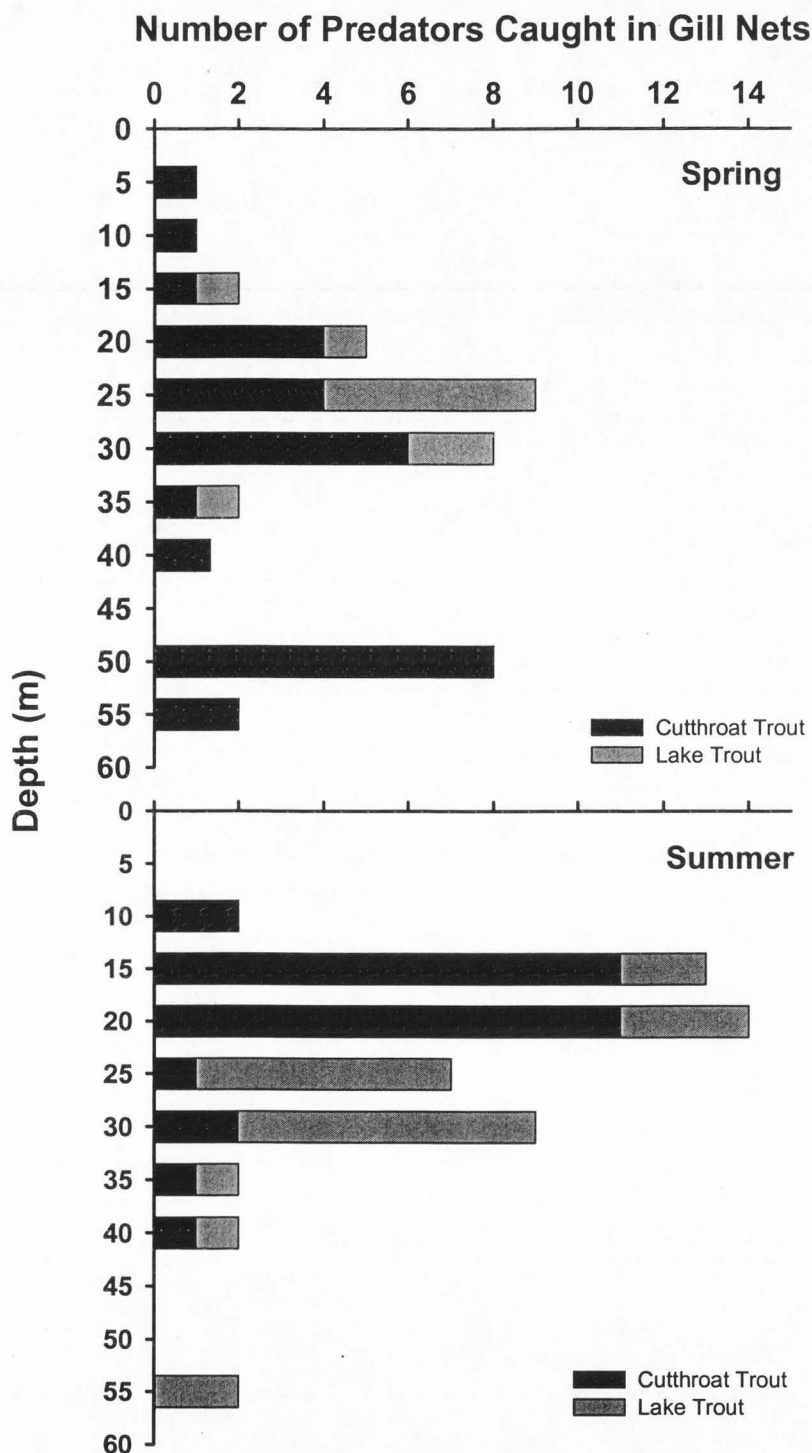


Figure 3-5. – Total number of cutthroat trout and lake trout caught in gill nets during spring and summer across depths found in Bear Lake.

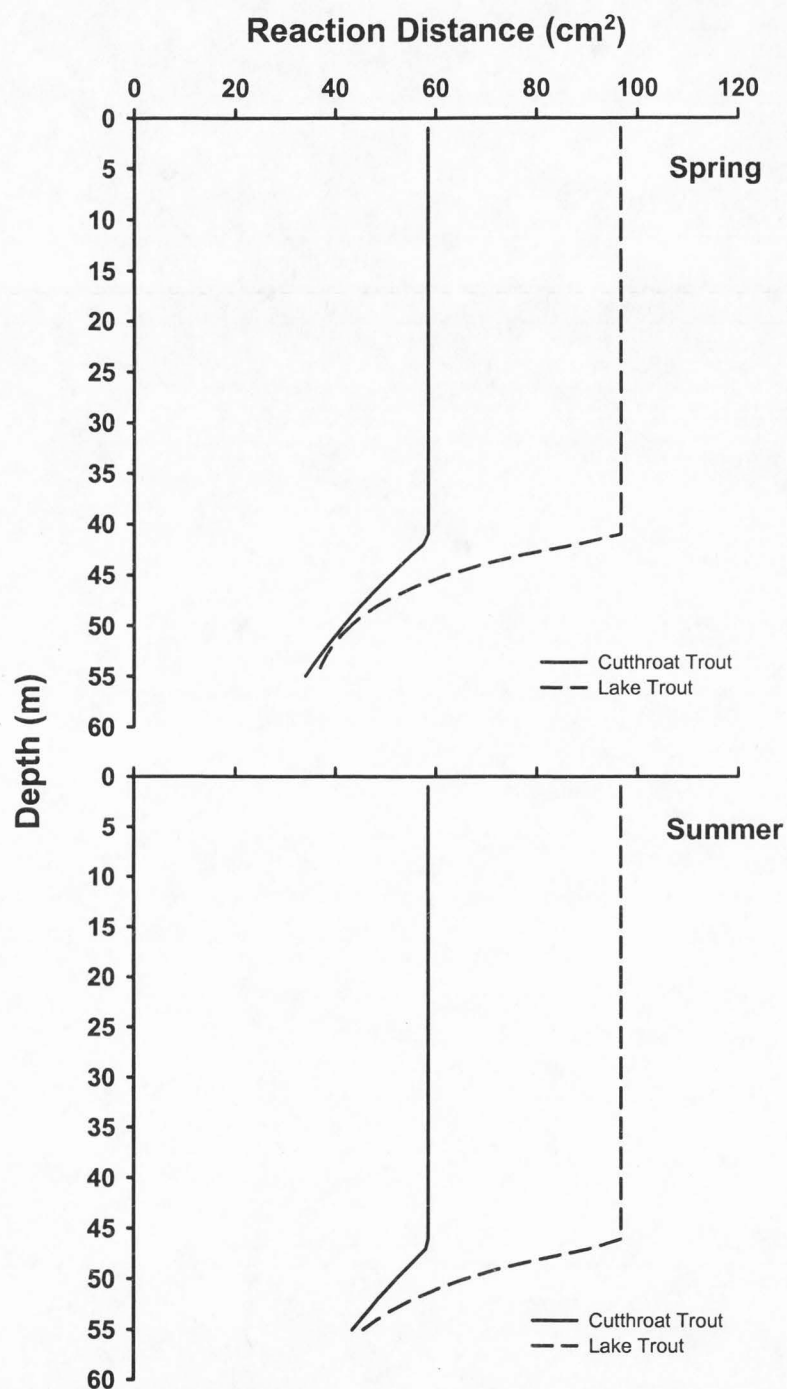


Figure 3-6. – Reaction distances of cutthroat trout and lake trout at depths throughout Bear Lake. Distances were calculated by entering depth and season specific light levels into a model developed by Mazur and Beauchamp (2002).

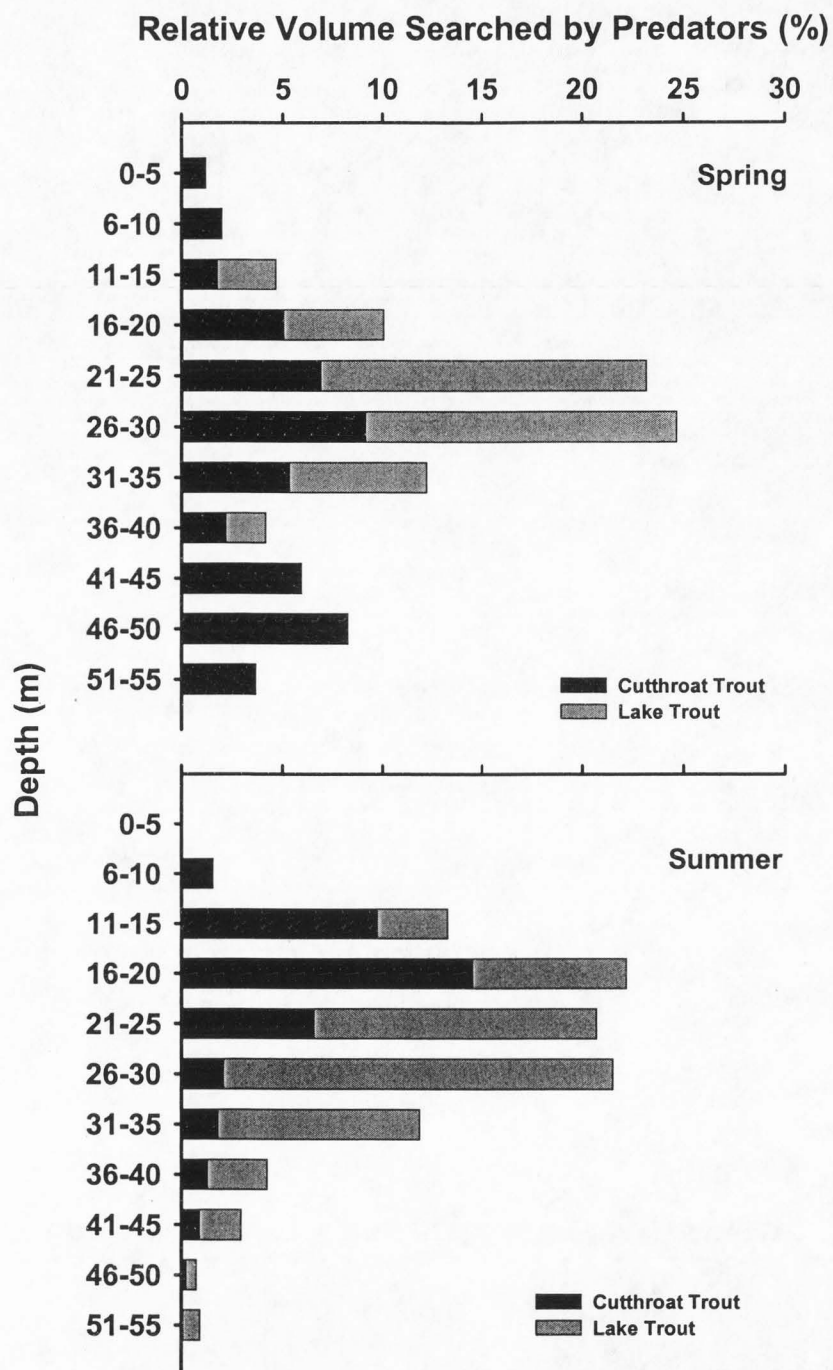


Figure 3-7. – Relative search volume at different depths by cutthroat trout and lake trout in Bear Lake for a representative day in spring and summer.

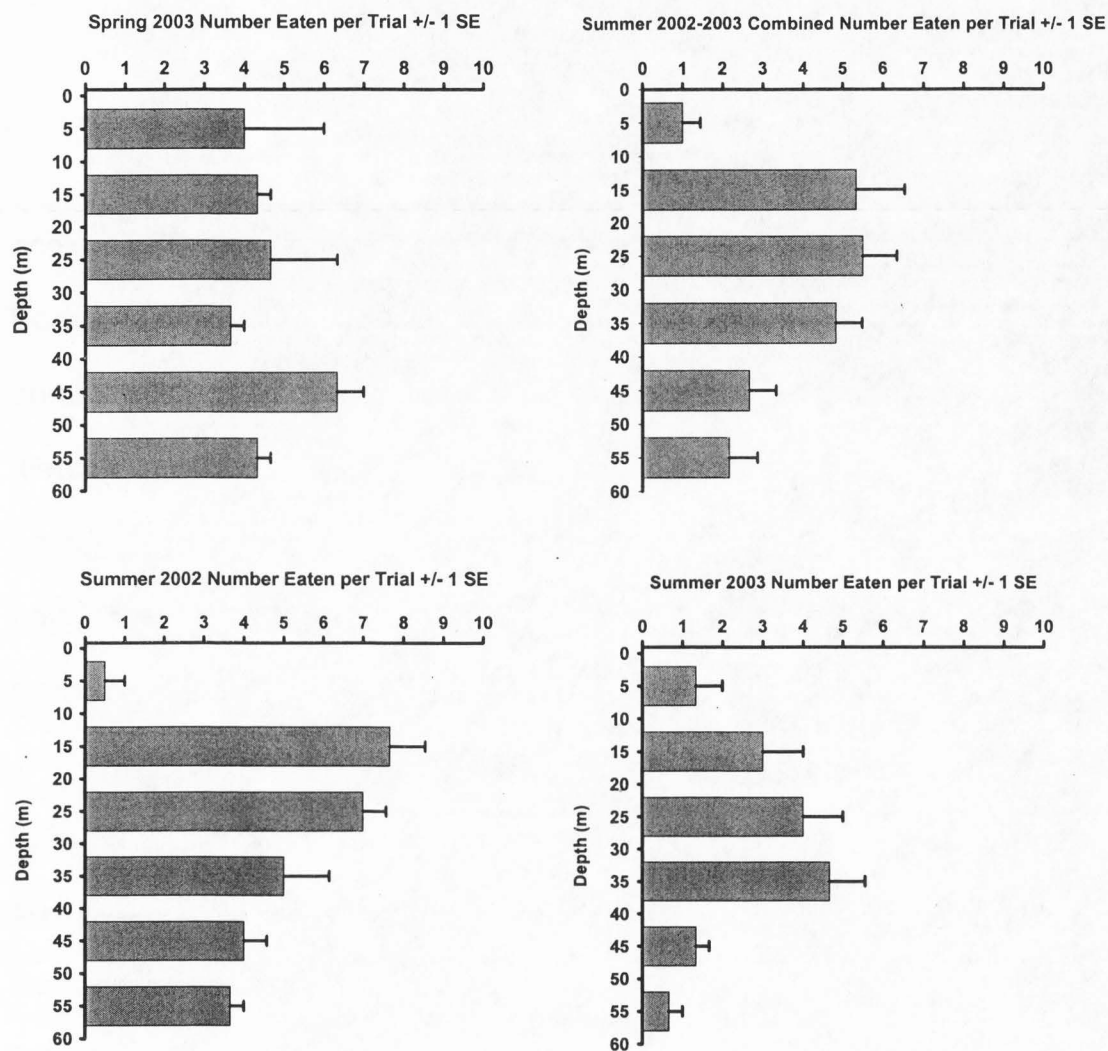


Figure 3-8. – Mean number of fish eaten from a set of 10 fish tethered during summer 2002 (18 July to 22 August), spring 2003 (20 May to 28 May), and summer 2003 (11 August to 21 August). Ten fish were individually tethered and set for 24 hours at depths of 5 m, 15 m, 25 m, 35 m, 45 m, and 55 m along three transects (north, south, west).

CHAPTER 4

CONCLUSIONS

My results support the idea that the two benthic whitefish in Bear Lake are ecologically very different. First, these species inhabited different depths, with Bonneville whitefish dominating the upper strata and Bear Lake whitefish dominating the deep profundal zone. Second, these species had very different diets even at depths where the species overlapped, with Bonneville whitefish eating a variety of benthic invertebrates, but mostly Chironomidae, and Bear Lake whitefish eating mostly Ostracoda. These patterns were evident in both spring and summer seasons.

Additionally my data support the idea that Bonneville whitefish and Bear Lake whitefish occupy habitats with different conditions associated with growth and predation risk in both spring and summer. Habitats occupied by high numbers of Bonneville whitefish had relatively high food availabilities and warmer water temperatures. These habitats were also associated with high levels of predation risk. In contrast, habitats occupied by Bear Lake whitefish had low food availabilities and only cold water temperatures but the advantage of lower predation risks. Areas avoided by both species had the disadvantages of low to moderate food availabilities, cold water temperatures, and a moderate to high predation risk and no advantages.

Given these distributions, Bonneville whitefish occupy a much larger benthic area than Bear Lake whitefish. Assuming Bonneville whitefish actively

occupy depths of 5 m to 30 m in spring and 10 m to 30 m in summer they would inhabit an area of 120 km² and 90 km² respectively when the lake is at full pool (282 km²). If Bear Lake whitefish actively occupy depths of 45 m to 55 m, they would inhabit an area of only 50 km². At 5 m shallower than full pool, which can occur during drought conditions, Bonneville would occupy an area of 110 km² in spring and 90 km² in summer and Bear Lake whitefish would occupy an area of only 30 km² in both seasons. This would be one third less area than they occupy when the lake is at full pool.

Although, ecological differences have been described for sympatric ecotypes of whitefish in both North America and Europe, these studies typically involved the genus *Coregonus* in recently glaciated lakes in very similar ecoregions. We provide quantitative evidence of sympatric ecotypes of benthic whitefish of the genus *Prosopium* in a lake not recently glaciated and in a different ecoregion, thus increasing the generality of sympatric ecotypes in the subfamily Coregoninae. Fishes of the genus *Coregonus* have been the focus of many population divergence and speciation studies. Populations of these fishes in recently glaciated lakes (~11,000 years old) in the Holarctic ecoregion of Northern North America and Northern Europe have been shown to be both morphologically and ecologically diverse, but genetically very similar. As mentioned previously, these populations are usually characterized by a larger benthic ecotype and a smaller limnetic ecotype. There is evidence that sympatric ecotypes also occur in *Prosopium* species and may be the result of adaptive

radiation, but they have been studied much less. Bear Lake, unlike many previously studied lakes, is in the arid Great Basin and is located south of other lakes containing sympatric ecotypes in North America by hundreds of kilometers. Additionally, Bear Lake is not recently glaciated. It has a long history (> 35,000 years) of lake level fluctuations and connections with other large and now extinct lakes in the Great Basin. Changes in lake level and connectiveness were the result of climate associated with glaciation, earthquakes, and lava flows, but not glaciers directly. Furthermore, Bear Lake differs from many other lakes with sympatric pairs because unlike the usual one benthic-one limnetic ecotype, it contains two benthic ecotypes in addition to the limnetic ecotype (Bonneville cisco). Bonneville whitefish represent a shallower benthic ecotype that forages on a variety of invertebrates and Bear Lake whitefish represents a deeper benthic ecotype that forages almost exclusively on Ostracoda. These data along with previously documented differences in genotype and head morphology suggest that extending the generality of resource-based adaptive radiation in the subfamily Coregoninae to the *Prosopium* genus may be warranted. Additional studies on the evolutionary history of these species would clarify these ideas further.

Bear Lake faces many potential threats including nutrient loading, invasion of non-native species and overstocking of piscivorous fishes. The distinct ecologies of each whitefish species in the Bear Lake indicates that these threats will likely have different effects on each species ultimately requiring complex

conservation strategies. For example, increased nutrient loading could result in de-oxygenation of the profundal zone and may have severe consequences for profundal Bear Lake whitefish by causing death or immigration into shallower areas. Boats from many areas throughout Utah and Idaho are launched daily onto Bear Lake throughout the summer. This could lead to non-native benthic invertebrates becoming established thereby changing the prey base that these whitefish rely on. Additionally, piscivorous native Bonneville cutthroat trout and non-native lake trout are stocked into the lake every year, which could directly reduce the population size of one or both whitefish species or cause a change in habitat use. A shift in either fish's distribution from any one of these threats may cause overlapping distributions and increased risk of competition and hybridization. Conservation of these fishes depends on conserving the diverse habitat that allows them have different distributions. Studies examining how each of the threats might impact Bear Lake whitefish are needed to improve conservation strategies for these endemic fishes.

APPENDIX

Table A-1. – Model-averaged estimates of catch per net night of Bonneville and Bear Lake whitefish across depth in spring and summer, 2000-2003.

Season	Depth	n	Bonneville		Bear Lake	
			Mean	95% CI	Mean	95% CI
Spring	5	6	12	8-20	0	0-0
	10	10	11	7-16	0	0-0
	15	10	9	7-14	0	0-0
	20	10	8	6-11	0	0-0
	25	10	6	5-9	0	0-1
	30	10	5	3-7	0	0-1
	35	8	3	2-5	1	1-1
	40	7	2	1-3	1	1-2
	45	2	1	1-2	3	2-4
	50	4	0	0-1	6	4-9
	55	6	0	0-1	13	7-25
Summer	5	11	5	2-9	0	0-1
	10	22	11	9-15	0	0-1
	15	22	17	13-22	1	1-1
	20	22	17	13-22	1	1-1
	25	22	12	9-15	1	1-2
	30	22	7	6-9	2	1-2
	35	19	4	3-5	2	2-3
	40	16	2	1-3	3	2-4
	45	3	1	1-1	5	4-8
	50	5	1	0-1	11	8-15
	55	8	0	0-1	30	17-52

Table A-2. – Spring and summer diet composition of Bonneville whitefish and Bear Lake whitefish caught in gill nets during May and August 2002 and 2003 sampling. Data are the number of stomachs within a dry weight percentage group for a given food item. Terrestrial group consisted of mostly Homoptera and Hymenoptera.

Season	%	Bonneville whitefish					Bear Lake whitefish				
		Chironomidae	Ostracoda	Pisidae	Terrestrial	Other	Chironomidae	Ostracoda	Pisidae	Terrestrial	Other
Spring	absent	2	37	43	54	46	9	3	39	38	27
	1 – 10	7	19	2	6	14	17	1	1	3	14
	11 – 20	3	4	3	2	3	3	1	0	0	1
	21 – 30	3	2	0	2	1	4	0	0	1	0
	31 – 40	3	1	2	1	2	2	0	1	0	0
	41 – 50	2	2	3	0	0	2	1	0	0	0
	51 – 60	5	1	1	0	0	1	3	0	0	0
	61 – 70	5	0	2	0	1	0	2	0	0	0
	71 – 80	9	0	1	1	0	1	5	0	0	0
	81 – 90	5	1	4	0	0	1	8	0	0	0
	91 – 100	23	0	6	1	0	2	18	1	0	0
Summer	absent	5	44	36	44	43	32	1	51	43	31
	1 – 10	3	6	0	5	9	2	2	0	3	15
	11 – 20	9	2	2	1	1	5	3	1	1	5
	21 – 30	3	0	1	3	1	3	2	0	0	1
	31 – 40	1	0	2	0	0	2	4	0	1	0
	41 – 50	2	1	1	0	1	2	3	0	2	1
	51 – 60	2	0	2	0	0	2	4	0	0	0
	61 – 70	2	0	0	0	0	2	1	0	0	0
	71 – 80	2	0	3	0	0	1	3	0	0	0
	81 – 90	5	2	6	1	0	2	7	0	1	0
	91 – 100	22	1	3	2	1	0	23	1	2	0