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Meristic differences, habitat selectivity and diet separation of *Prosopium spilonotus* and *P. abyssicola*

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Three endemic species of *Prosopium* inhabit Bear Lake. These are the Bonneville cisco (*Prosopium gemmiferum*), Bonneville whitefish (*P. spilonotus*) and Bear Lake whitefish (*P. abyssicola*). Only *P. gemmiferum* can easily be distinguished from the other two by simple morphological characteristics. Until recently *P. abyssicola* and *P. spilonotus* could only be distinguished from each other because of the temporal differences in their spawning times or at total lengths greater than approximately 280 mm. Samples of the two whitefish were collected during their respective spawning seasons to verify the results of recent research which demonstrated that a combination of lateral line and above lateral line scale counts could be used to separate the species. Results indicated that *P. abyssicola* and *P. spilonotus* could be positively separated using scale counts, and we suggest a modification of the recently published method regarding counting scales to determine whitefish identity to species. In 1999–2001, samples of whitefish were collected from standardized gillnetting to determine if any differences in life histories and diets were apparent. Significant differences existed between the diets and depth preferences of the two species. *P. abyssicola* were found in greater abundance in depths greater than 30 m and fed mainly on ostracods while *P. spilonotus* preferred depths less than 35 m, were omnivorous in their diets, and became picivorous at total lengths of 350 mm and greater.

Introduction

Three endemic species of *Prosopium* are currently recognized from Bear Lake (McConnell *et al*. 1957, Sigler & Miller 1963, Sigler & Sigler 1987, Sigler 1997): the Bonneville cisco (*Prosopium gemmiferum*), the Bonneville whitefish (*P. spilonotus*), and the Bear Lake whitefish (*P. abyssicola*). The mountain whitefish (*P. williamsoni*) has also been collected from Bear Lake, albeit on rare occasions, and they have not established themselves in Bear Lake or its tributaries (McConnell *et al*. 1957, Sigler & Miller 1963; B. Nielson pers. comm.). Of the three species found in Bear Lake, the Bonneville cisco can be easily identified from the other two by simple morphological characteristics. Separation of the Bonneville and Bear Lake whitefish is, however, problematic.

Although recognized as two separate species, they have not been reliably separated based solely on morphological characteristics or genetics (Snyder 1919, Sigler & Miller 1963, White 1974, Sigler & Sigler 1987, Broughton 2000). Although the two whitefish occur sympatrically and could be readily separated due to their allochrony (differences in their times of spawning), no concise way existed to differentiate them morphologically or meristically during other periods of the year. This was particularly true for fish shorter than 275 mm in total length (TL). Bonneville whitefish longer than approximately 275 mm TL could be separated from Bear Lake whitefish since no mature Bear Lake whitefish have been observed larger than 264 mm TL (S. A. Tolentino unpubl. data). Since the inception of the Bear Lake Project in 1973 and for fisheries management purposes, the two species of whitefish have been combined and referred to as the Bear Lake whitefish complex. In addition there have been no recent investigations regarding the life history, diets, etc. of the two species.

In 1999, Tolentino and Nielson (1999) provided a comprehensive paper on the Bear Lake whitefish complex, however, they were unable to differentiate the whitefish to species. Historical publications have been very general in describing the endemic whitefish of Bear Lake (Snyder 1919, Locke 1929, Perry 1943, McConnell *et al.* 1957). Additionally, some limited research has been conducted on the genetics of the Bear Lake whitefishes by White (1974) and Ohlhorst (1985).

Researchers on other waters have corroborated the relatively high degree of plasticity and overlap of morphological and meristic characteristics (some caused by introgressive hybridization) among the various whitefish species (Smith 1964, Todd & Stedman 1989, Bodaly *et al.* 1992, Emlen *et al.* 1993). Smith and Todd (1992) reviewed many of the classic works on Coregonines of the genera *Coregonus*, *Prosopium*, and *Stenodus* by both European and American biologists and concluded that sympatric and allopatric forms of whitefish were connected by a "bewildering pattern of morphological similarities". They went on to analyze 50 characteristics of 26 different species or sub-species. Their study resulted in the question of species delineation being postponed, pending broader examination of the Coregonines based on more material.

It has been hypothesized (Miller 1965, Behnke 1972) that the Bear Lake whitefish complex evolved via sympatric speciation in geographical isolation during the Pleistocene Epoch, however Smith and Todd (1984) disagree. They believe that they evolved allopatrically involving several lake systems. Smith (1968) points out that Bear Lake endemic fish were at one time more widely distributed than at present. Other researchers (Brooke 1974, White 1974, Ohlhorst & Herron 1984, Ohlhorst 1985, Broughton 2000) have also presented evidence that both supports and disagrees with both the sympatric and allopatric evolutionary theories. It can be surmised that no one theory on the evolution of the Bear Lake whitefish complex is absolutely definitive.

To validate recent species identification techniques developed by a graduate student at Utah State University (Ward 2001) that could be used to separate Bear Lake and Bonneville whitefish raised in a laboratory environment, we undertook a study to "field test" these techniques. If Ward's (2001) technique worked then we hoped to identify any life history differences between the species. Ward's (2001) results suggested using scale counts in the lateral line and above lateral line on one side of the fish to separate the species. If lateral line scale counts were 75 or fewer and the scales above the lateral line were 8 or fewer, the fish was considered *P. abyssicola*. Any counts above these numbers and the fish was classified as *P. spilonotus*.

Finally, if we were able to validate the techniques of Ward (2001) in the field we would then examine the fish diets and catches of fish by depth to determine if any difference existed between the species.

Material and methods

Bear Lake is an ultra-oligotrophic lake located in the western United States and overlaps the state line between the states of Utah and Idaho (Fig. 1). It is approximately 32 km long and approximately 6–13 km wide. It is 1805 m above sea level and covers an area of 282 km^2 . It has a maximum depth of 63 m and a mean depth of 28 m. There are no major bays or coves. The lake was formed by tectonic faulting and is considered a tilted fault-block graben (Birdsey 1989). At the north shore, a pumping facility connects the lake with the Bear River; this allows the top 6.5 m to be manipulated and used as a storage reservoir for downstream irrigation and hydroelectric power generation. The lake is dimictic and the epilimnion rarely reaches temperatures exceeding 20 °C. The lake typically freezes in 4 of 5 years and ice formation can begin in December and last until early May.

The Utah Division of Wildlife Resources (UDWR) collected both Bear Lake and Bonneville whitefish in 1999 and 2000 using gill nets and angling during their respective spawning season. These fish were placed on ice and scale counts were made on fresh fish brought back to the laboratory or the fish were frozen whole so that scale counts could be made at a later date.

During the ice free periods (April–November) in 2000–2001, UDWR and Utah State University (USU) conducted gillnetting on Bear Lake. The UDWR gillnetting was part of the Bear Lake Project standardized contour gillnetting. The sampling consisted of setting monofilament, 5 panel, experimental, sinking 38.1-m long by 2-m tall gill nets along depth contours at 5, 10, 15, 20, 25 and 35 meters in depth at standardized locations (Nielson & Tolentino 1999). The mesh sizes of the gillnets were 12.7, 19.1, 25.5, 38.3 and 50.8 mm^2 and each panel was 7.6 m long. Two sites were sampled (Fig. 1; sites 1 and 2) and up to 10 randomly selected whitefish shorter than 250 mm TL were collected from each of the depths combining fish from both sites.

During the same time, USU sampled the lake using monofilament, experimental, sinking gill nets at similar depths, but added 40, 50 and 60 meter depths (Fig. 1; site 3). The gillnets used were 40.4 m long and consisted of nine different sized mesh panels each 4.6 m long. The mesh sizes were 12.7, 19.1, 25.5, 31.8, 38.3, 44.5, 50.8, 63.5, and 76.2 mm^2. All whitefish caught in these nets were analyzed.

In both UDWR and USU collections, the fish were placed in coolers on ice and transported back to the lab. In the laboratory, fish were measured (TL, mm) and weighed (g). Sex, state of maturity (immature, green, ripe, spent), and stomach contents were identified. Stomach

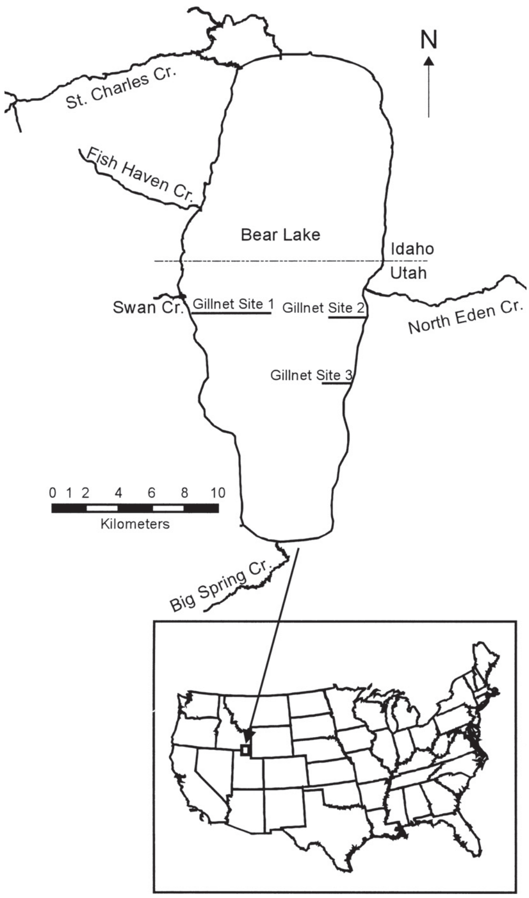

Fig. 1. Map of Bear Lake, Utah-Idaho, USA, showing gillnet sampling sites. Sites 1 and 2 were used exclusively by Utah Division of Wildlife Resources and the entire lake including Site 3 was used by Utah State University.

contents were visually classified into as many as 10 different categories, using a dissecting microscope when necessary, although most of the fish stomachs examined rarely contained more than three different items. The food categories used included: zooplankton, chironomids, terrestrial insects, ostracods, algae, clam shells, detritus, snails, fish and fish eggs. In UDWR samples, empty stomachs were counted, but all data presented were based on percent occurrence of a particular food item excluding empty stomachs. In USU samples, both percent occurrence and volumetric measurements were made of each food item found in the stomachs. Whitefish stomachs from both studies were either processed immediately after gillnetting, frozen whole, or stomachs removed and preserved in 95% ethanol.

Using the technique to separate *P. abyssicola* and *P. spilonotus* developed by Ward (2001), we counted scales in the lateral line and above lateral line on one side of the fish on known species of whitefish collected in 1999 to confirm his technique. In 2000–2001, fish scale counts were made using a slight modification of Ward's methods in which we counted the number of rows of scales above the lateral line on both sides of the fish. The number of scale rows above the lateral line was counted beginning one row above the lateral line at a point immediately ventral to the anterior insertion of the dorsal fin and then continuing dorsally and anteriorly to a point immediately on the crown of the back of the fish at the point of dorsal fin insertion; however, when the crown of the back of the fish was reached the scale count then continued on the opposite side of the fish by counting rows of scales posteriorly and ventrally to the row immediately above the opposite lateral line. Fish were confirmed as a Bear Lake whitefish when the number of rows of scales above the lateral line on one side of the fish was eight or fewer or when the number of rows of scales on both sides of the fish was 17 or fewer and the number of scales in the lateral line was 75 or less. If the counts exceeded this number in either above lateral line or within lateral line scales, the fish was confirmed as a Bonneville whitefish.

Results

Length/weight relationships

We captured a total of 333 Bear Lake and 1200 Bonneville whitefish during the 2000–2001 sample period. The resulting length/weight relationships for both species were very similar with slopes near 3.0 (Fig. 2).

Identification

In order to validate Ward's (2001) suggestion of using scale counts to separate the species of whitefish we counted scales on a total of 163 whitefish (36 Bear Lake whitefish and 127 Bonneville whitefish) that were collected during their respective spawning seasons. We confirmed that of the 36 Bear Lake whitefish, only 4% had more than 75 scales in the lateral line. When above lateral line scale counts were made using one side of the fish, 53% (N = 8) of the Bear Lake whitefish had more than 8 rows of scales. When the above lateral line scale counts were made using both sides of the fish, 10% (N = 2) of the Bear Lake whitefish had more than 17 rows of scales. However, when both scale counts (lateral line and above lateral line) were used together to determine a positive identification, we were able to classify 100% of the whitefish to species correctly.

Of the 127 Bonneville whitefish that we made scale counts for, less than 1% (N = 1) had less than 76 scales in the lateral line. When above lateral line scale counts were made using one side of the fish, 100% of the Bonneville whitefish had more than 8 rows of scales. When the above lateral line scale counts were made using both sides of the fish, less than 1% (N = 1) of the Bonneville whitefish had less than 18 rows of scales. Again we observed 100% correct identification when both scale counts (lateral line and above lateral line) were used together to determine a positive identification.

Diet and depth preferences

Examination of stomach contents revealed distinctive differences in the feeding ecology of the two whitefish species. We examined 805 Bonneville whitefish stomachs and 231 Bear Lake whitefish stomachs from 2000–2001. The occurrence of food items, excluding empty stomachs, revealed that chironomids were the preferred food item of Bonneville whitefish of total length classes 100–300 mm (Fig. 3). The diet of Bonneville whitefish longer than 351 mm TL consisted of mainly Bear Lake sculpin (*Cottus extensus*) (98 %), terrestrial insects (1%) and ostracods (< 1%) (Fig. 3).

Smaller size classes of Bonneville whitefish (100–150 mm TL and 151–200 mm TL) primarily utilized ostracods and chironomids. Once Bonneville whitefish exceeded a total length of

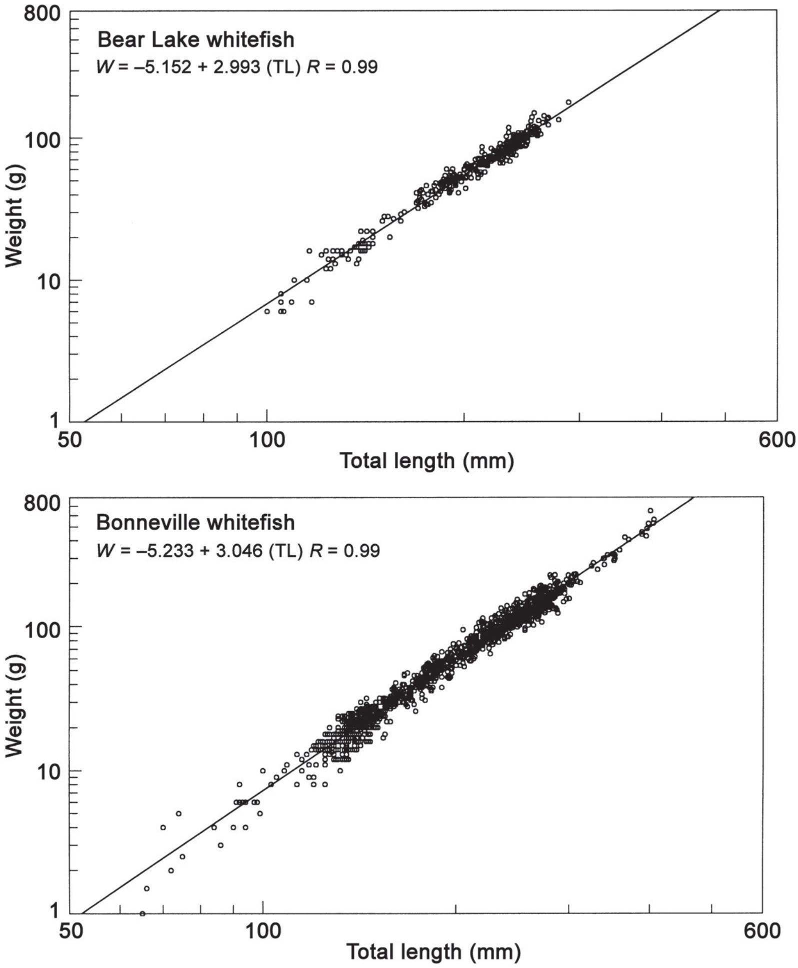

Fig. 2. Total length/weight relationships of Bear Lake whitefish (top) and Bonneville whitefish (bottom) collected from Bear Lake using gillnets in 2000–2001.

200 mm TL they fed more heavily on terrestrial insects and spharid clams, although chironomids comprised a major portion of the diet. The diet analysis also revealed that once Bonneville whitefish reached a size of > 300 mm TL they fed almost exclusively on Bear Lake sculpin, most of which were age 0 (Fig. 3).

Bear Lake whitefish exhibited a more homogeneous diet throughout all size classes than did Bonneville whitefish (Fig. 4). Individuals in the 100–150 mm TL size class exhibited the highest degree of generalism in their diets. They consumed ostracods, chironomids, zooplankton, terrestrial insects, and fish eggs. The diet of Bear Lake whitefish greater than 150 mm TL was dominated by ostracods. They continued this selectivity throughout their life history and did not exhibit any prey switching at sizes greater than 150 mm TL. Size classes 151–200 mm TL, 201–250 mm TL, and greater than 250 mm TL contained 83%, 90% and 99% ostracods within their stomachs, respectively (Fig. 4).

Stomach samples from the 2001 sampling period were also examined to determine if lower lake levels (Bear Lake was 1.5 m lower than the previous year) had any effect on the diets of the whitefish. Following the examination of 50 stomachs of each species it was determined that food selectivity closely resembled that which was observed in 2000.

Bear Lake whitefish diets were similar throughout the year regardless of the size class, however, Thompson (2003) found large masses of oligochate worms in larger Bear Lake whitefish. He also found that Bear Lake and Bonneville whitefish consumed more terrestrial insects

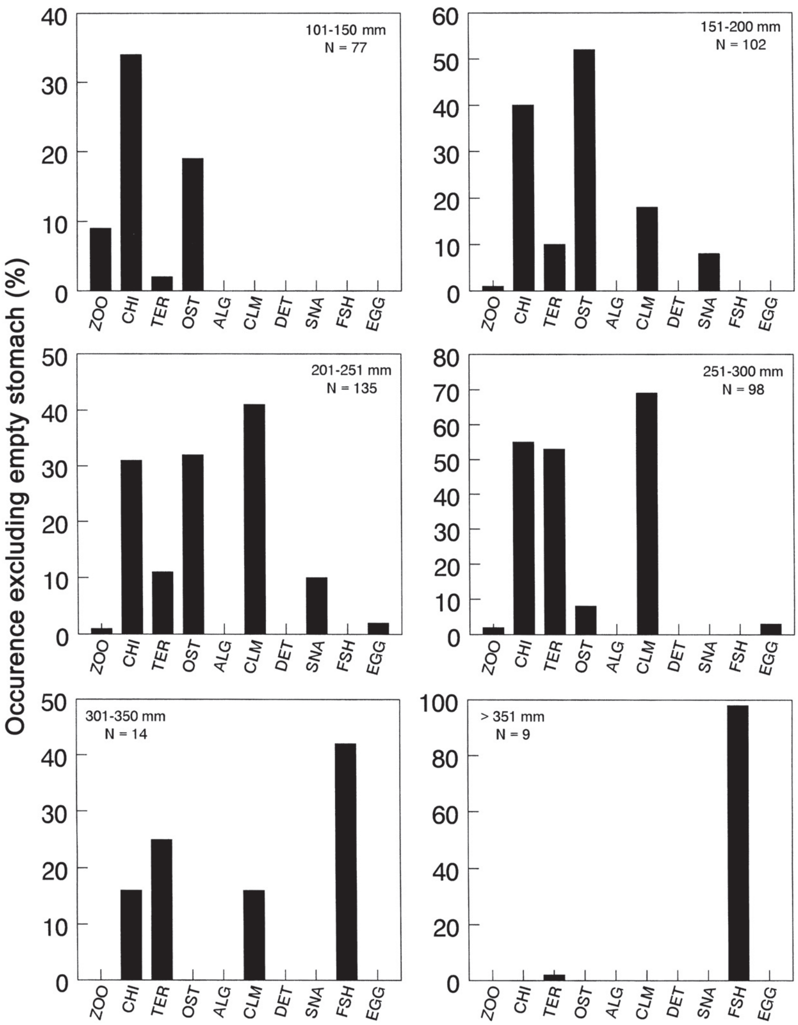

Fig. 3. Diet of Bonneville whitefish collected from Bear Lake using gillnets in 2000–2001 by total length (TL) groups. ZOO = zooplankton; CHI = chironomids; TER = terrestrial insects; OST = ostracods; ALG = algae; CLM = clams; DET = detritus; SNA = snails; FSH = fish; EGG = fish eggs.

during the spring than at other times of the year. Most of these terrestrials were made up of Coleopterans that likely flew over the lake and were not able to sustain their flight; they drowned, sank and were likely eaten as part of benthic foraging by both species.

Whitefish catches by depth were also analyzed (Fig. 5). Bonneville whitefish were more abundant in shallower depths during both years and all the sampling periods. Pooled data over both years revealed that 96% were caught in depths of 5–35 meters while only 4% were caught in depths of 40–60 meters. Bear Lake whitefish were more abundant in the deeper depths. Ninety-two percent were caught in depths ranging from 40–60 meters while only 8% were found at depths of 5–35 meters (Fig. 5).

Discussion

We were able to positively identify all of the whitefish to species using both lateral line and above lateral line scale counts. Ward's (2001) method suggested whitefish with less than 75 lateral line and 8 rows or fewer above lateral line scales be classified as Bear Lake whitefish. We observed 4% of the Bear Lake whitefish with more than 75 scales in the lateral line and 53% with more than 8 rows of scales above the lateral line. Therefore, we suggest counting the

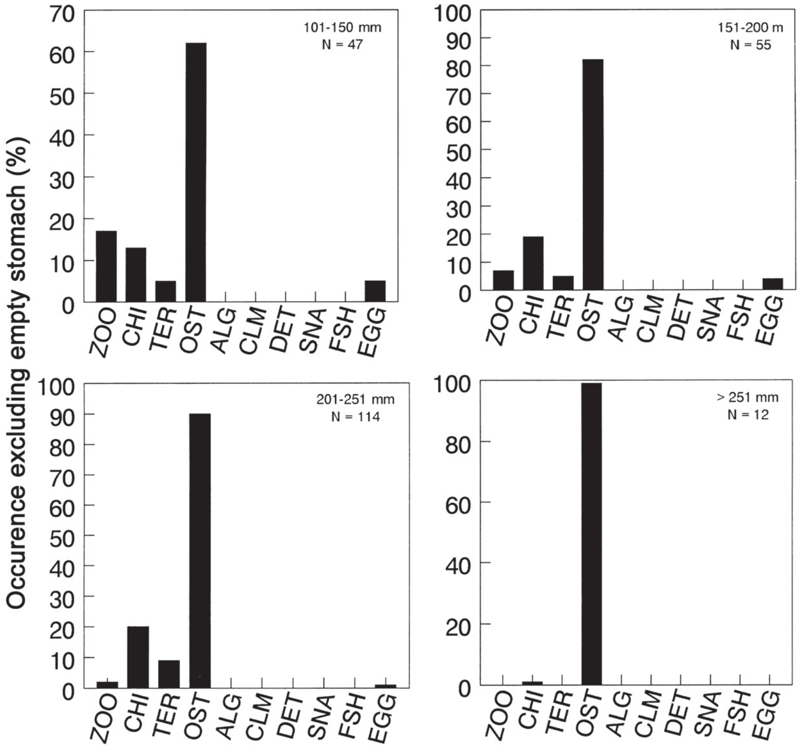

Fig. 4. Diet of Bear Lake whitefish collected from Bear Lake using gillnets in 2000–2001 by total length (TL) groups. ZOO = zooplankton; CHI = chironomids; TER = terrestrial insects; OST = ostracods; ALG = algae; CLM = clams; DET = detritus; SNA = snails; FSH = fish; EGG = fish eggs.

total row of scales above the lateral line on both sides of the fish and when the number of rows of scales were 16 or less it was classified as a Bear Lake whitefish. Even with this count we still observed 33% of the Bear Lake whitefish having more than 16 rows of scales but never more than 17 rows. However, when both scale counts (lateral line and above lateral line) were used together we observed 100% correct species identification.

Only 1% of Bonneville whitefish had less than 17 rows of scales above the lateral line on both sides of the fish. Additionally, less than 1% of the Bonneville whitefish had less than 76 scales in the lateral line. When both counts were used together we observed 100% correct species identification.

McConnell *et al.* (1957) were the first to examine the diets of whitefish from Bear Lake, however, they did not report how they differentiated between the two species, the location(s) at which the collections were made, the time of year the samples were collected, or the size of the fish they sampled. They did report that all Bear Lake whitefish were taken from gill nets set in water "exceeding 75 feet in depth". A total of 65 Bonneville whitefish stomachs were sampled. Of those, 52% contained aquatic insects,

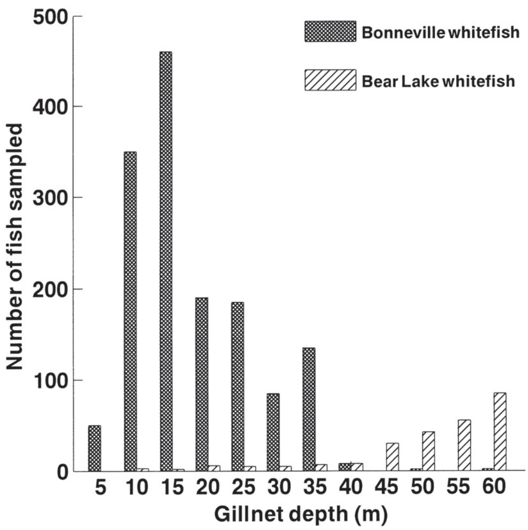

Fig. 5. Pooled, sub-sampled, gillnet catch of Bear Lake and Bonneville whitefish from three sites and three sample periods by depth from Bear Lake in 2000–2001.

34% contained detritus/shells, 21% contained zooplankton/eggs/copepods and 10% contained terrestrial insects. It is uncertain whether empty stomachs were included or excluded from the analysis. This is somewhat similar to what we observed for Bonneville whitefish. In size category, 251–300 mm TL, we observed similar percentages of insects and zooplankton in the guts of Bonneville whitefish (Fig. 3). It is important to note that no fish were found in the Bonneville whitefish stomachs examined by McConnell *et al*., whereas fish made up the majority of the diet in Bonneville whitefish > 300 mm TL in 2000–2001. Since McConnell *et al*. (1957) did not report the sizes of the fish they used in their diet analyses, they may not have included any whitefish in their sample which were large enough to consume other fish. We were also unable to ascertain whether the portion of diet identified as "detritus/shells" included ostracods in their study. Since ostracods are small, they may have been lumped into this category, however, McConnell *et al*. did classify ostracods as a separate food item for Bear Lake whitefish. During 2000–2001 we observed ostracods in 7%–53% of the stomachs that we examined from Bonneville whitefish from 100–300 mm TL.

McConnell *et al*. (1957) also examined a total of 33 Bear Lake whitefish stomachs. They reported that ostracods were present in greater than 80% of the stomachs and aquatic insects in 48% of the stomachs. Other food items including fish, copepods and other insects were found "in the occasional" Bear Lake whitefish stomach although these items were considered "unimportant". Their observations were remarkably similar to what we observed in 2000–2001 where we found that ostracods were found in 63%–99% of all Bear Lake whitefish stomachs that we examined.

We agree with McConnell *et al*. (1957) that the Bonneville whitefish were far-ranging opportunistic feeders, whereas the diets of the Bear Lake whitefish suggest a dependence on the soft marl bottom in deep water as a source of food which is the habitat of the ostracods.

Between 1995 and 1997, Tolentino and Nielson (1999) reported the diet of the Bear Lake whitefish complex consisted mainly of zooplankton. No differences in diets were noted in their study between sample sites or the three times of the years they collected fish. In the fall 1995 sample, zooplankton were found in nearly 100% of the whitefish stomachs that contained food and they were found in at least some of the whitefish stomachs sampled from both of their sites and at almost all depths during all sampling periods. Aquatic insects and ostracods were also important components of the whitefish complex diet. When Tolentino and Nielson (1999) examined whitefish diets by length of the fish they found that ostracods were consumed primarily by whitefish less than 250 mm TL, whereas, whitefish that averaged greater than 300 mm TL fed mainly on Bear Lake sculpin.

Other fish, including Bonneville cisco, Bear Lake sculpin, Utah sucker (*Catostomus ardens*), and Utah chub (*Gila atraria*), prey on the eggs and larval forms of both Bonneville and Bear Lake whitefish at certain times of the year. However, no attempt has been made to quantify predation by those species and it is not likely to impact the whitefish since these species have co-evolved for thousands of years (Tolentino & Nielson 1999).

Bear Lake whitefish comprised only 17% of the total catch of whitefish between UDWR and USU sampling over the two year period 2000–2001, which covered all possible depths and habitat substrates. At first one may think this is a surprisingly low percentage, but this species preferred depths greater than 30 meters and the highest catches were observed from depths of 50–60 meters. This habitat selectivity limits them to a small portion of Bear Lake which contains these depths. The catch per unit effort (Department of Aquatic, Watershed, and Earth Resources, Utah State University, Logan, Utah, U.S.A unpubl. data) of these species was nearly equal to that observed for Bonneville whitefish in the 15–25 meter depths where they were most concentrated. Although significantly less Bear Lake whitefish were captured overall, these data suggest there is no evidence that would indicate a declining or threatened population.

The UDWR has annually monitored the relative abundance of the Bear Lake whitefish complex and in 1999 began monitoring the relative abundance of the individual species. Using the annual gillnetting index coupled with restricted harvest, regular angler creel surveys, and no commercial fishery we feel the possibility of over fishing would be highly unlikely. Furthermore, Bear Lake whitefish are rarely harvested due to their diminutive size.

Since species identification has proven possible using the techniques described above, we suggest that research be continued that better defines the life history and age structure of both the Bear Lake and Bonneville whitefish. We hope to investigate the life histories of both of these unique, endemic species and will continue to monitor their population dynamics.

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