Chapter 12

The Fishes of Lake Bonneville: Implications for Drainage History, Biogeography, and Lake Levels

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ABSTRACT

This chapter summarizes the paleontological and fish DNA evidence for the fishes that occupied the late Quaternary Bonneville basin and key biogeographic and hydrographic insights that emerge from analyses of those data. Fossils and mtDNA from modern fishes suggest nearly the entire assemblage of 21 species occurred in the region prior to the rise of Lake Bonneville. Ten sites have produced fish materials ($N > 16{,}100$ specimens) from the lake. The fauna was similar to that in modern Bear Lake, Utah–Idaho, and had two large salmonine top carnivores, three endemic whitefish zooplanktivores, three bottom or rocky shore dwelling sculpins, several minnows, a large lake sucker, a river sucker, and two mountain suckers. The collection from Homestead Cave, Utah, is the largest, and the richest late Quaternary fish assemblage from the basin. Fish bones from Stratum I of the cave provided $^{87}Sr/^{86}Sr$ values suggesting that they were derived from a low-elevation lake and change in fish size and taxonomic abundance suggest the fauna resulted from a series of die-offs resulting from increases in temperature and salinity. Radiocarbon dating suggests this occurred rapidly between 13.1 and 11.8 cal ka BP at the end of the regressive phase of Lake Bonneville. A recolonization of nearly the entire Lake Bonneville fish fauna occurred between 12.3 and 9.5 cal ka BP during the Gilbert episode, although the fauna is skewed to higher abundances of salinity- and temperature-tolerant taxa. No post-Gilbert early Holocene lake transgressions are suggested but peaks in *Gila atraria* frequencies in the upper strata may indicate Great Salt Lake reached highstands at ~3.6 and ~1.0 cal ka BP.

Keywords: Fishes, Lake Bonneville, Lake levels, Biogeography, Drainage history

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Developments in Earth Surface Processes, Vol. 20. http://dx.doi.org/10.1016/B978-0-444-63590-7.00012-3

12.1 INTRODUCTION

> *No inconsiderable part of the progress that has been made in elucidating the problems of the Great Basin has come from the joint consideration of biotic and physiographic data. Even greater advances should ensue, when the biological and geological approaches are more definitely integrated.*
>
> (Hubbs and Miller, 1948, p. 120)

In their landmark synthesis of fish biogeography in the Great Basin, Hubbs and Miller envisioned a future where further synergy of ichthyological and geological analyses would lead to deeper insights into past hydrography and climates. For their part, Hubbs and Miller embraced the notion that the native fishes of the Great Basin occur only in waters that they could have reached through surface water connections so that the dispersal of fishes is closely tied to regional aquatic systems history. This may be considered the first principle of fish biogeography and succinctly paraphrased: Fish colonize wherever they can swim, survive, and reproduce. It follows that climatic inferences can be derived by documenting previous hydrographic connections from the geographic distributions of fishes and deducing the levels of ancient lake systems that would have allowed for such connections. Hubbs and Miller also explicitly recognized that such reconstructions could be more readily achieved "if we had more than the present dribble of paleontological data on the fishes" (Hubbs and Miller, 1948, p. 25). A richer fossil fish record would thus enhance our understanding of historical fish biogeography and ultimately lead to a greater understanding of regional paleohydrography and climate change.

Hubbs and Miller did not elaborate specifically on the nature of more "definitely integrated" analyses of biological and geological data, but it is clear that inferences on the nature of past climates can be derived from fossil or subfossil fish assemblages in ways beyond the biogeographic arguments that were their focus. Fluctuations in the size and depth of a lake can, of course, have dramatic effects on water chemistry and temperature and, in turn, profoundly influence the nature of its fish populations. In addition to controlling whether a lake can support fish at all, water temperature and salinity, for example, play critical roles in determining the species composition, growth characteristics, and the age and size structure of fish populations. As a result, high-resolution fossil fish sequences from Lake Bonneville could provide fine-scale details on lake-level oscillations to test and refine hypotheses based on other geological sources. And since perhaps a no-more-sensitive measure exists of regional climate than the size of closed basin lakes, paleofish faunas can potentially provide one of the more direct proxies of climate change.

In this chapter, we synthesize the available paleontological and fish DNA evidence for the fishes that occupied Lake Bonneville and summarize key biogeographic and hydrographic inferences and insights that emerge from those data. Of these collections, the well-dated ichthyofauna from Homestead Cave represents the largest, and the richest late Quaternary fish assemblage from the entire Bonneville basin, and the only stratified well-dated, terminal Pleistocene fish fauna of the region. This fauna has provided an unprecedented opportunity to examine the dynamics of Lake Bonneville's fish populations as they fluctuated toward the end of the Pleistocene and sheds light on both the nature and timing of fine-scale, climate-driven, lake-level oscillations, and late Quaternary fish biogeography in the Bonneville basin. With now considerably more than a dribble, we have begun to pursue the greater advances that Hubbs and Miller had presaged nearly 70 years ago.

12.2 MATERIALS AND METHODS: LAKE BONNEVILLE ICHTHYOFAUNAS

The fish remains presented and discussed here have been recovered and analyzed from 10 primary localities in the Bonneville basin (Fig. 12.1; Table 12.1). The materials derive from a wide range of depositional contexts and reflect fish sampled from various aquatic environments in the Bonneville basin over that past ~60,000 years, although the vast majority of materials have come from late Pleistocene through early Holocene sediments. We describe here each of these localities, their location, the nature of the deposits, the depositional origin of fish remains, collection methods, and dating. These data are presented in chronological order from oldest to youngest. An annotated list of the Bonneville drainage fishes is provided in Table 12.2.

12.2.1 Deweyville

Utah, Box Elder Co., elevation 1310 m (Fig. 12.1, locality 3). Fossils of *Catostomus ardens* and *Oncorhynchus clarkii* were collected by Oviatt (1984) from alluvium or marsh sediments along a canal bank below Cutler Dam at an elevation of 1310 m in pre-Bonneville sediments near the Bear River at Deweyville, about 16 km above Brigham City. The Cutler Dam Alloformation was deposited during Marine Oxygen Isotope Stage 4, dated at about 60 ka BP (Oviatt et al., 1987; Kaufman et al., 2001). The bones were recovered from a small sand lens in the lacustrine facies in a coarsening-upward sequence indicative of a regressive phase of the saline lake. Oviatt et al. (1987) suggested that the fish had been washed in from their fresh water fluvial habitat, upstream. The sequence, here about 15 m thick, is bounded above by the Fielding Geosol, which is, in turn, overlaid by the Bonneville Alloformation, and is exposed above a covered base of Section 12.1 (Oviatt et al., 1987). The materials are curated at the Museum of Paleontology, University of Michigan.

12.2.2 Hot Springs

Utah, Salt Lake Co., elevation 1350 m (Fig. 12.1, locality 5). A diverse fossil fish fauna and site details for the Hot Springs locality are reported in Smith

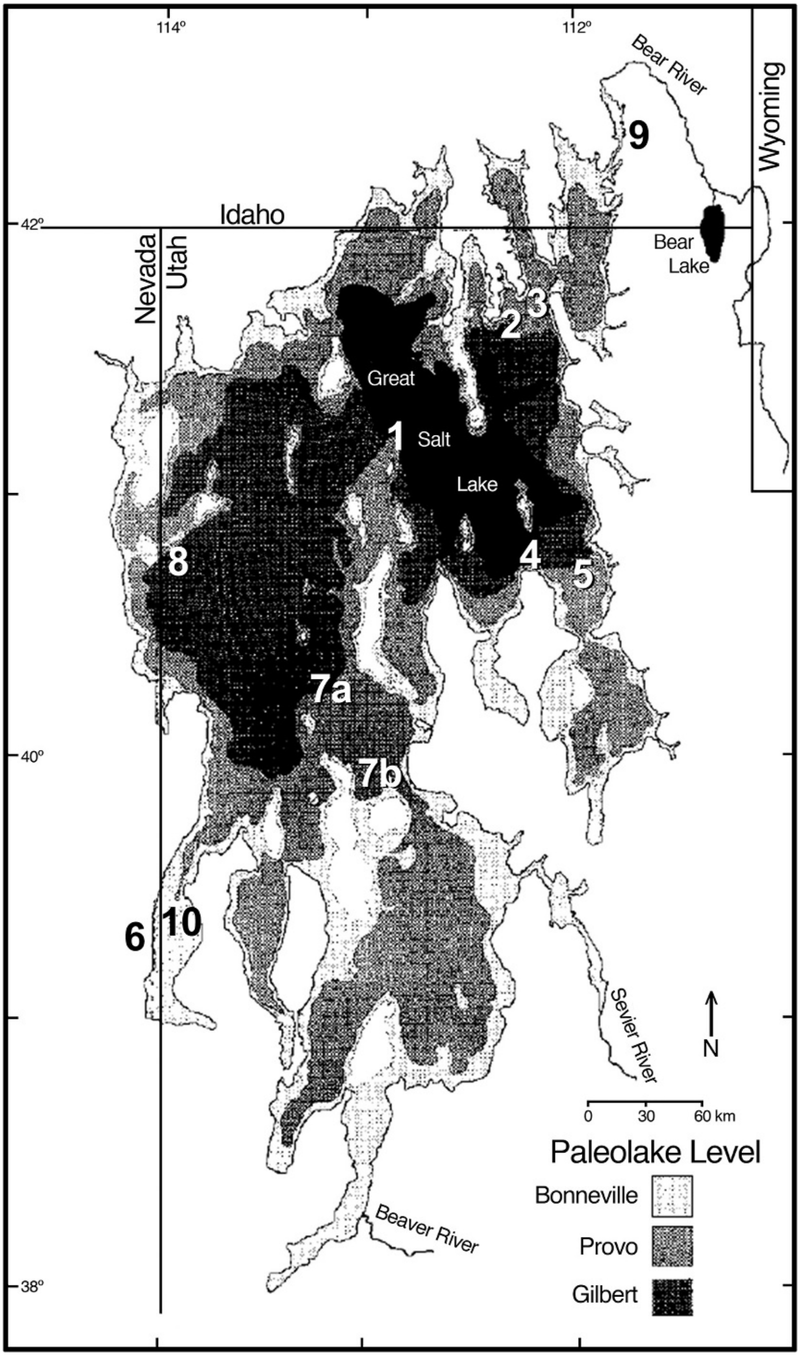

FIG. 12.1 Map of the Bonneville basin showing major paleolake levels and sites and locations discussed in the text. (1) Homestead Cave and Cathedral Cave, UT, (2) Public Shooting Grounds, (3) Deweyville, (4) Black Rock Canyon, (5) Hot Springs, (6) Smith Creek Cave and Cathedral Cave, NV, (7a and 7b) The Old River Bed, (8) Danger Cave, (9) Thatcher Basin, and (10) Crystal Ball Cave. *Adapted from Currey, D.R., 1990. Quaternary paleolakes in the evolution of semidesert basins, with emphasis on Lake Bonneville and the Great Basin, U.S.A. Palaeogeogr. Palaeoclimatol. Palaeoecol. 76, 189–214.*

TABLE 12.1 Numbers of Identified Fish Specimens per Taxon for Lake Bonneville Ichthyofaunas

	Site										
Taxon	*Public Shoot. Grounds*	*Deweyville*	*Black Rock Canyon*	*Hot Springs*	*Homestead Cave*	*Smith Ck. Cave*	*Cathedral Cave*	*Old River Bed*	*Danger Cave*	*Thatcher Basin*	Total
Cypriniformes					2245			34			2279
Cyprinidae					120			8			128
Gila atraria	+[a]		2	12	958	4		11			987
Richardsonius balteatus					1						1
Catostomus sp.					1343						1343
Catostomus ardens		1		11	179			+			191
Pantosteus virescens.					5						5
Chasmistes sp.										+	0
Chasmistes cf. *liorus*			+								0
Salmoninae					1022					+	1022
cf. *Salvelinus confluentus*					1						1

Oncorhynchus cf. *clarkii*					60						60
Oncorhynchus clarkii		29	30		2	27		+	+		88
Prosopium sp.					7536			+			7536
Prosopium cf. *spilonotus*					84						84
P. spilonotus			2	1	41						44
P. spilonotus/ abyssicola					198						198
P. abyssicola					8						8
P. gemmifer			10	507	778						1295
Cottus sp.					259		539				798
Cottus cf. *bairdii*					1						1
Cottus bairdii			2	4	6		3				15
C. extensus/ echinatus					14		5				19
Cottus extensus			9	55	5						69
Total		30	55	590	14,866	31	547	53			16,172

[a] *+ indicates the presence of a taxon, but without enumeration of elements.*

TABLE 12.2 **Annotated List of Fishes of the Bonneville Drainage**

Family Catostomidae, Suckers	*Chasmistes liorus*, June Sucker. Endemic to Utah Lake; represented by fossils (Miller and Smith, 1981) and DNA analyses of recent populations (Krabbenhoft, unpublished data). Restricted to lakes except during spawning runs up tributaries
	Catostomus ardens, Utah Sucker. Endemic to the Bonneville and upper Snake River drainages; represented by fossils and DNA analyses of recent fishes. Inhabits rivers and lakes
	Pantosteus platyrhynchus, Mountain Sucker. Endemic to the Bonneville and Upper Snake drainages; represented by DNA analyses of recent fishes. Usually inhabits moving water (Smith et al., 2013; Unmack et al., 2014)
	Pantosteus virescens, Green Sucker. Endemic to the Bonneville and Upper Snake drainages; represented by fossils and DNA analyses of recent fishes (Unmack et al., 2014). Usually inhabits moving water, but wave-swept littoral habitat was possible (Broughton, 2000b,c; Smith et al., 2013; Unmack et al., 2014)
Family Cyprinidae, Minnows	*Gila atraria*, Utah Chub. Endemic to Lake Bonneville and tributaries. Represented by Lake Bonneville fossils and DNA analyses of recent fishes (see Johnson and Belk (1999) for DNA analysis). The Snake and Bear River populations attributed to this species are a different form—*Gila domninus* (Cope)
	Iotichthys phlegethontis, Least Chub. Endemic to the Bonneville basin; represented by DNA analyses of recent fishes. No known fossils
	Richardsonius balteatus, Redside Shiner. Native to the Bonneville, Snake, Columbia, and peripheral drainages; represented in the Bonneville basin by a single fossil specimen (Broughton, 2000b) and DNA analyses of recent fishes (Dowling and Markle, unpublished data.)
	Snyderichthys copei, Leatherside Chub. Endemic to the Bonneville and Upper Snake drainages; represented by DNA analyses and historical information. Sometimes interpreted as part of *Lepidomeda* from the Colorado River drainage, with two species in the Bonneville basin (Johnson et al., 2004) based on DNA evidence, but morphology and osteology refute the interpretation based on DNA markers, indicating past DNA transfer by introgression. No fossil record

TABLE 12.2 Annotated List of Fishes of the Bonneville Drainage—Cont'd

	Rhinichthys cataractae, Longnose Dace. Widespread across northern North America. Found in the northern Bonneville basin. No fossil record. Represented by DNA analyses of recent phylogeographic information (Dowling, unpublished data)
	Rhinichthys osculus, Speckled Dace. Widespread across western North America. Represented by DNA analyses of recent fishes and 10 million year old fossils in the Snake and Columbia drainages. DNA indicates ancient presence in the pre-Bonneville basin and divergent northern and southern Bonneville populations (Smith et al., 2016; Dowling, unpublished data)
Family Salmonidae, Subfamily Coregoninae	*Prosopium williamsoni*, Rocky Mountain Whitefish. Native to the Colorado, Great Basin (including the Bear lake drainage), Columbia, and north to the McKenzie and Hudson Bay drainages; represented by DNA analyses of recent fishes and possibly fossil scales from the Old River Bed of Lake Bonneville
	Prosopium abyssicola, Bear Lake Whitefish. Endemic to the Bonneville basin, recent only in Bear Lake; represented by DNA analyses of recent fishes and Lake Bonneville fossils (Smith and Todd, 1984; Broughton, 2000b,c)
	Prosopium spilonotus, Bonneville Whitefish. Endemic to the Bonneville basin, recent only in Bear Lake; represented by DNA analyses of recent fishes and Lake Bonneville fossils (Smith and Todd, 1984; Broughton, 2000b,c)
	Prosopium gemmifer, Bonneville Cisco. Endemic to the Bonneville basin, recent only in Bear Lake; represented by DNA analyses of recent fishes and Lake Bonneville fossils (Smith and Todd, 1984; Broughton, 2000b,c)
Family Salmonidae, Subfamily Thymallinae	*Thymallus arcticus*, Arctic Grayling. Grayling were collected in the Bear River and Green River in 1834 according to the account of Nuttall and Townsend (Townsend, 1978, pp. 84, 89). Nuttall and Townsend were familiar with trout, grayling, and char (see later) because of Nuttall's earlier work on the natural history of the Great Lakes region, where they encountered grayling and char (Smith et al., 2002, p. 218)

Continued

TABLE 12.2 Annotated List of Fishes of the Bonneville Drainage—Cont'd

Family Salmonidae, Subfamily Salmoninae	*Salvelinus confluentus*, Bull Trout. Native to the Intermountain West; represented by fossils, but not extant currently in the Bonneville basin. Townsend (1978, p. 89) wrote about a collection made from the Bear River, 12 mi above Soda Springs, Idaho, on 6 Jul. 1834: "Trout, grayling, and a kind of char are very abundant here—the first very large." The Nuttall/Townsend record is supported by the fossil from Homestead Cave (see later) (Smith et al., 2002)
	Oncorhynchus clarkii utah, Bonneville Cutthroat Trout. Endemic to the Bonneville drainage, including the Bear River, Bear Lake, and Snake Valley, Nevada. Represented by fossils from Lake Bonneville and pre-Bonneville clays along the Bear River (see later) and DNA analyses of recent fishes
Family Cottidae	*Cottus bairdii semiscaber*, Bonneville Mottled Sculpin. The Mottled Sculpin is widespread in North America, with distinctive subspecies in the West. Represented by Lake Bonneville fossils and DNA analyses of recent fishes (Smith et al., 1968; Broughton, 2000b,c)
	Cottus extensus, Bear Lake Sculpin. Endemic to the Bonneville basin. Represented by Lake Bonneville fossils and DNA analyses of recent fishes, but recent only in Bear Lake (Smith et al., 1968; Broughton, 2000b,c)
	Cottus echinatus, Utah Lake Sculpin. Endemic to the Bonneville basin. Extinct with no fossil or DNA record
	Cottus beldingi, Paiute Sculpin. Native to the Columbia and Snake rivers, Bear River, western Lahontan, and part of the upper Colorado drainage. Fossil records in the Lahontan basin (Taylor and Smith, 1981)

See text and Smith et al. (2002) for geographic, stratigraphic, and evolutionary context.

et al. (1968). The fossils were collected by surface picking and screen washing several hundred pounds of matrix by K.F. Horn in Jun. 1963, and subsequently by Horn and G.R. Smith, and finally by C. Barbour. The fossils were in 3–5 cm thick lenses of weakly cemented, well-sorted sand in strata between layers of moderately cemented gravel, exposed on a steep face by excavation for gravel and fill material. The deposits, in the lower Draper Formation (Morrison, 1965), are below the calcareous tufa of the well-defined Stansbury lake level (1375 m). Larger pebbles of the Stansbury level locally are coated with crusts of calcite on their upper surfaces, whereas limestone pebbles are eroded on their under surfaces, indicating hot water ascending through the lacustrine sediments. It is speculated that the fish were attracted to the offshore hot springs by thermal-based, high productivity and that the elevated temperatures contributed to the death assemblage. At the time of collection, the hot springs of Wasatch Park were 210 m south of the area (Stokes et al., 1964; Smith et al., 1968). The fossils are deposited in collections of the Natural History Museum, University of Kansas, and the Museum of Paleontology, University of Michigan.

12.2.3 Cathedral Cave

Utah, Box Elder Co., elevation 1383 m (Fig. 12.1, locality 1). Cathedral Cave is a large limestone cavern located on Homestead Knoll a northwestern spur of the Lakeside Mountains just west of Great Salt Lake, ~10 km SW of Lakeside, Utah. The cave overlooks the expansive playa of Great Salt Lake Desert but its mouth is completely covered by a talus cone of tufa/breccia. The top of the depositional sequence of the cave floor is 1383 m, between two Stansbury level beaches of ~1405 and 1363 m. Investigations in 1995 led by Madsen (2000) involved excavation of a $1 \times 0.5\ \mathrm{m}^2$ column sample with fill being passed in the field sequentially through 6.3 and 3.1 mm screens in addition to the collection of several bulk sediment samples. Eleven well-defined strata were evident in the column and two discrete sedimentary breaks divided the sequence into a lacustrine deposit (Zone 1) below and postlacustrine deposit (Zone 2) above. Fish remains, limited to several sculpin (*Cottus*) species, were confined to Stratum II, the first lacustrine deposit resting on limestone spall and bedrock (Stratum I) composed of laminated fine-grained lacustrine clays containing numerous ostracods and gastropods (Broughton, 2000a). The sculpin remains may owe their presence in these sediments to active burrowing or by settling out from natural mortality in the lake. A 15,310 ± 60 ^{14}C date was derived from pollen in an overlying stratum (Stratum IV). Fish remains and other fauna (see Madsen et al., 2001) are curated at the Natural History Museum of Utah.

12.2.4 Black Rock Canyon

Utah, Salt Lake Co., elevation 1423 m (Fig. 12.1, locality 4). J.H. Madsen, Jr., G.R. Smith, K.F. Horn, and A.D. Stock collected a diverse fish and gastropod fauna in November, 1964, from a fine- to medium-grained sand lens at an elevation of 1423 m. The site is below the Provo lake level, which is at an elevation of 1460 m in this area (Smith et al., 1968). Additional *Chasmistes* materials are reported in Miller and Smith (1981). Gastropod shells found with the fish were analyzed by M. Rubin, U.S.G.S. and yielded a radiocarbon age of 12,860 ± 400 ^{14}C years BP. This date and the elevation relative to the Provo terrace suggest assignment to the Upper Lacustrine Member of the Bonneville Formation of Morrison (1965). Associated gastropods, identified by Dwight Taylor, include *Fontelicella* sp., *Lithoglyphus hindsi*, *Lymnaea bonnevillensis*, *Physa* sp., and *Valvata humeralis*. The pelecypod, *Pisidium* sp. is also present. These materials are curated at the Natural History Museum of Utah and the Natural History Museum, University of Kansas.

12.2.5 Smith Creek Cave

Nevada, White Pine Co., elevation 1950 m (Fig. 12.1, locality 6). Smith Creek Cave is located in Smith Creek Canyon in the Snake Range on the Utah–Nevada border on the west shore of Lake Bonneville. Lake Bonneville reached an elevation of 1580 m, 4 km from the entrance of Smith Creek Canyon in Snake Valley (Mead et al., 1982). Although Smith Creek Cave has a long history of excavation and analysis, a small sample of fossil fish bones from three species was recovered from a single sedimentary layer, the Reddish-brown Silt Zone described by Bryan (1979). Bryan obtained a ^{14}C date of ~28 ka, but that may be inaccurate (Mead et al., 1982). The reddish-brown unit has abundant bird and mammal remains that could be the same age as fossils in Cathedral Cave, across the canyon from Smith Creek Cave. The reddish silt in the unit is interpreted to be either an eolian deposition or derived from erosion from water issuing from a nearby ceiling conduit: the abundant fossil material, including the fish bones, in the stratum are believed to have resulted from raptor activity (Mead et al., 1982). The chronology of the Reddish-brown silt unit is not well constrained, but a radiocarbon date of 12,600 ± 170 ^{14}C BP from an adjacent unit stratigraphically above is suggested to represent a minimum age for the deposit. Mead et al. (1982) reported *O. clarkii* and *Gila atraria* from the collection; recent work revealed specimens of *C. ardens*. The fish bones were collected in 1977 and 1978 by J. Mead, R.S. Thompson, and T.R. Van Devender (Mead et al., 1982). These specimens are curated at the Museum of Northern Arizona, Flagstaff.

12.2.6 Homestead Cave

Utah, Box Elder Co., elevation 1406 m (Fig. 12.1, locality 1). Homestead Cave (22BO763) is a wave-constructed cavern located in the Lakeside Mountains just west of Great Salt Lake, 10 km SW of Lakeside, Utah, in the northern Bonneville basin. The site is located on Homestead Knoll just ~850 m SW of Cathedral Cave. In 1993 and 1994, a 1 × 1 m^2 sample column was excavated to a depth of 3 m in the rear cave-floor sediments. The well-defined deposits contained 18 separate strata. Materials removed from the column were passed through a series of 6.4 and 3.2 mm screens in the lab. The deposits consisted primarily of degrading owl pellets, rich in small vertebrate remains, with little evidence of contamination by human foragers. A total of 93 radiocarbon dates spanning from 13.1 to 0.7 cal ka BP[1] have been obtained from a range of organic materials, including vertebrate bone (Madsen, 2000; Broughton et al., 2008; Smith and Betancourt, 2013; Terry and Novak, 2015). Overall, the chrono-stratigraphic coherency of the ^{14}C results suggests that the deposits were laid down sequentially over the past ~13.1 ka years, although a recently derived series of 56 dates from *Dipodomys* spp. (kangaroo rat) bone collagen expand both the temporal range and overlap of several strata in the deposit (Terry and Novak, 2015). Still, the relationship between stratum depth and mean calibrated age is highly significant ($r_s = 0.995$, $P < 0.0005$). A large and diverse fish fauna was concentrated in the lowest strata of the deposit (Strata I and II) with dates ranging from 13.1 to 9.5 cal ka BP. This period of time encompasses the very end of the regressive phase of Lake Bonneville, a postregressive lake near Great Salt Lake elevations, the Gilbert episode, and the first two early Holocene millennia of the hypersaline Great Salt Lake. A few late Holocene-aged strata also contain abundant fish remains. We follow Broughton (2000b) and report in the descriptive summary later the fish remains, by element, from 6.4 and 3.2 mm fractions of Stratum I and five noteworthy specimens present in higher strata of the cave. However, we present and draw on the entire sequence in our analyses of lake-level fluctuations. Analyses of the fish are described in Broughton (2000b,c) and Broughton et al. (2000, 2006); the Homestead Cave vertebrate fauna is housed at the Natural History Museum of Utah.

12.2.7 The Old River Bed

Utah, Juab, Toole, and Utah counties, elevation 1300 m (Fig. 12.1, localities 7a and 7b). In the regressive phase of Lake Bonneville when the lake fell below the threshold that separated the Sevier basin from the Great Salt Lake basin, a shallow lake in the Sevier basin overflowed at its north end, creating a river that carved a narrow, meandering valley on the floor of the basin—the Old River Bed. The lacustrine and fluvial geomorphology of this valley and the surrounding region have been recently investigated through geological assessments, including analyses of stratigraphy and dating of materials collected from backhoe pits and trenches (Oviatt et al., 2003; Madsen et al., 2015). Utah Chub (*G. atraria*) remains, (identified by JMB) dating between 12.9 and 9.9 cal ka BP, were present in several riverine "sand-channel" deposits derived from these trenches (42TO1161, 42TO1000, 42TO1182) and were reported briefly in Oviatt et al. (2003). We describe these materials (as Old River Bed I, locality 7a, Fig. 12.1), in more detail later. Earlier work in the region, that we designate here as Old River Bed II (locality 7b, Fig. 12.1), reported *C. ardens* bones from shut-off spit gravel deposits in a major

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[1] Notes: All dates within the radiocarbon time scale are provided in calibrated ka BP following CALIB 7.1 (Reimer et al., 2013; Stuiver et al., 2013) unless otherwise noted.

transgressive sequence at the Shutoff (Oviatt, 1984). *O. clarkii* bones and bones and scales of *Prosopium* sp. were recovered from nearby deep-water phase, white marl deposits of Lake Bonneville (Oviatt, 1984). The specimens from Old River Bed II are curated at the University of Michigan Museum of Paleontology; Old River Bed I materials are housed at the Department of Anthropology, University of Utah.

Several other localities have produced fish materials apparently derived from Lake Bonneville but refined identifications could not be made for them owing to the nondiagnostic elements represented (eg, vertebrae) or their state of preservation, or species level identifications are provided but elements are not enumerated. These include *O. clarkii* elements (identified by GRS) from basal deposits of Danger Cave, Tooele Co., Utah; small teleost vertebrae from Crystal Ball Cave, Utah, Millard Co., (Heaton, 1985), and Cathedral Cave, White Pine Co., Nevada (Jass, 2007); *G. atraria* materials from the Public Shooting Grounds, Box Elder Co., Utah (Murchison, 1989a); and *Chasmistes* sp. and salmonine fossils from late Pleistocene beds in the Thatcher Basin, Franklin Co., Idaho (Bright, 1963, 1967; Miller and Smith, 1981). We do not include these materials in Section 12.3 that provides the numbers of elements per taxon, but indicate their presence at these sites in Table 12.1 and draw on them in our biogeographic discussions.

12.3 RESULTS: SYSTEMATICS AND OSTEOLOGY

In this section, we describe the universe of fish materials that have been identified and quantified from the Lake Bonneville-aged deposits described earlier and discuss pertinent aspects of the distribution and habitat of the represented species and the biogeographic implications that follow from their occurrence at these localities. Our discussion of the taxa present and element representation is focused on species-level identifications but quantitative data on order, family and genus-level identifications are presented by site in Table 12.1. With few exceptions (noted later), the detailed osteological criteria used to make these identifications are provided in Smith et al. (1968), Miller and Smith (1981), and Broughton (2000b,c). Selected diagnostic fish elements from Hot Springs, Black Rock Canyon, and Homestead Cave are illustrated in Figs. 12.2–12.7.

Order Cypriniformes
Cyprinidae—Minnows
Gila atraria (Girard, 1856)
Utah Chub

Material—Homestead Cave: Frontal (40), ethmoid (4), infraorbital (2), vomer (6), parietal (29), pterotic (30), basioccipital (29), parasphenoid (2), articular (9), dentary (43), premaxilla (1), maxilla (11), posttemporal (7), quadrate (25), epihyal (14), ceratohyal (23), urohyal (8), pharyngeal (154), hyomandibular (34), opercle (49), preopercle (26), cleithrum (45), supracleithrum (3), pectoral fin spine (9), basipterygium (9), scapula (5), coracoid (3),

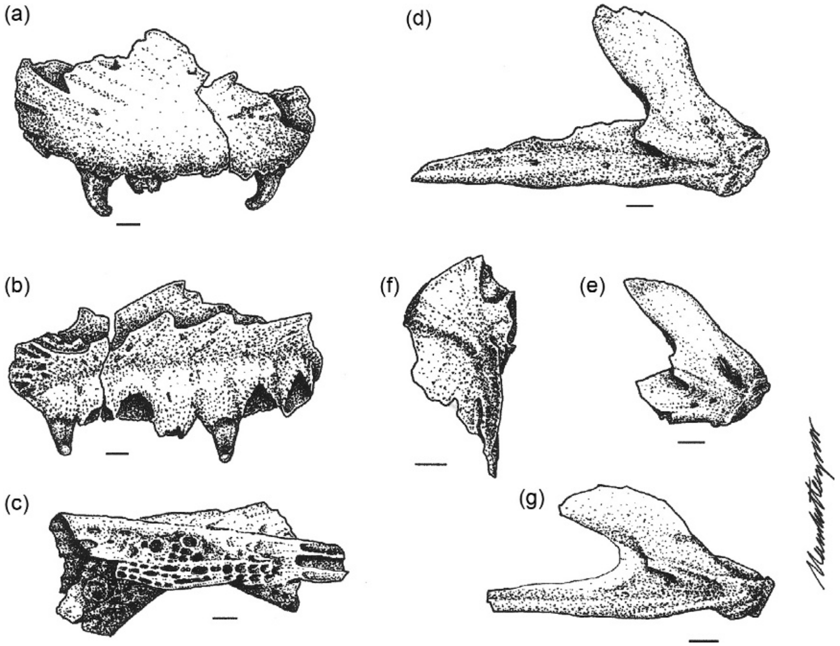

FIG. 12.2 Selected diagnostic salmonid elements from Homestead Cave. (a) Lateral view of right premaxilla of cf. *Salvelinus confluentus*; (b) mesial view of right premaxilla of cf. *S. confluentus* (same specimen as (a)); (c) basibranchial of *Oncorhynchus clarkii* (dorsal view); (d) left dentary of *Prosopium spilonotus*; (e) left dentary of *Prosopium abyssicola* (the ventral ramus is broken off); (f) left hyomandibular of *Prosopium gemmifer* (the posterolateral ridge is on the lower, right margin of the bone), and (g) left dentary of *P. gemmifer*. Scale: Bar length = 1 mm. *From Broughton, J.M., 2000b. Terminal Pleistocene fish remains from Homestead Cave, Utah, and implications for fish biogeography in the Bonneville basin. Copeia 2000, 645–656.*

supraorbital (1), supraoccipital (1), 1st vertebra (8), 2nd vertebra (16), 3rd vertebra (4), 4th vertebra (2), Weberian apparatus (8). Hot Springs: Pharyngeal (10), hyomandibular (1), opercle (1). Black Rock Canyon: Pharyngeal (1), Weberian suspensorium (1). Smith Creek Cave: Basioccipital (1), vertebra (3). Old River Bed I: Pharyngeal (10), dentary (1).

Richardsonius balteatus (Richardson, 1836)
Redside Shiner

Material—Homestead Cave: Pharyngeal (1).

Remarks—Six cyprinid species are native to the Bonneville basin: *G. atraria*, *Snyderichthys copei*, *Iotichthys phlegethontis*, *Rhinichthys cataractae*, *Rhinichthys osculus*, and *R. balteatus* (Table 12.2). With the exception of *G. atraria*, these fishes rarely attain total lengths over 150 mm. *G. atraria*, however, can reach lengths up to 559 mm but typically range from 127 to 305 mm (Sigler and Sigler, 1996). *Gila domninus* Cope, a close relative of *G. atraria*, lives in the Bear River, the Snake River above Shoshone Falls,

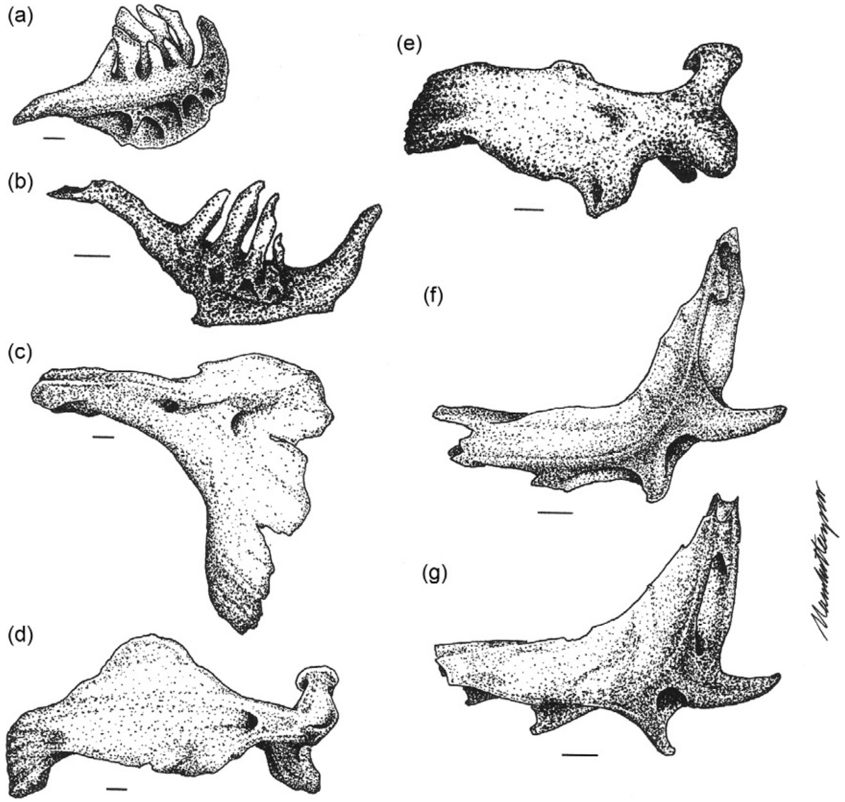

FIG. 12.3 Selected diagnostic cyprinid, catostomid, and cottid elements from Homestead Cave. (a) Left pharyngeal tooth of *Gila atraria*; (b) right pharyngeal tooth of *Richardsonius balteatus*; (c) left dentary of *Catostomus ardens*; (d) right maxilla of *C. ardens*; (e) right maxilla of *Pantosteus virescens*; (f) left preopercle of *Cottus bairdii*; and (g) left preopercle of *Cottus extensus*. Scale: Bar length = 1 mm. *From Broughton, J.M., 2000b. Terminal Pleistocene fish remains from Homestead Cave, Utah, and implications for fish biogeography in the Bonneville basin. Copeia 2000, 645–656.*

and the lower Wood River system, Idaho (Table 12.2). *G. atraria* has been reported from six of the Lake Bonneville-era ichthyofaunas and was apparently widespread in the lake at various levels.

G. atraria was identified from sand-channel deposits of the Old River Bed (I) dating from ~12.9 to 9.9 cal ka. The consistent presence of chubs in these contexts suggests that water flowed more-or-less continuously over this period (Oviatt et al., 2003). As we discuss later, changes in abundance of *G. atraria* across the Holocene sequence of deposits at Homestead Cave may reflect lake level variation of Great Salt Lake.

R. balteatus is widely distributed in northwestern North America (Lee et al., 1980) but the Homestead Cave specimen represents the only record of this species for Lake Bonneville. The presence of only a single pharyngeal

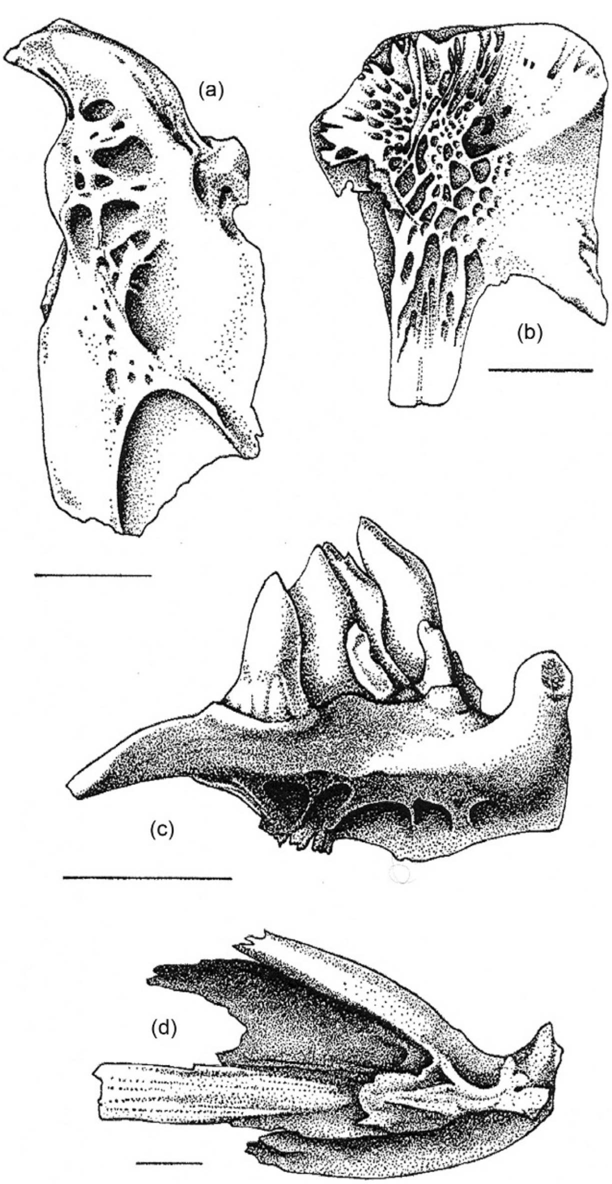

FIG. 12.4 Selected catostomid, cyprinid, and salmonine elements from Hot Springs and Black Rock Canyon. (a) Right hyomandibular of *Catostomus ardens* from the Hot Springs locality; (b) left hyomandibular of *Oncorhynchus clarkii*; (c) left pharyngeal arch of *Gila atraria*; and (d) right articular–angular of *O. clarkii* from the Black Rock Canyon locality. Scales for (a) and (c) = 5 mm; those for (b) and (d) = 10 mm. *From Smith, G.R., Stokes, W.L., Horn, K.F., 1968. Some late Pleistocene fishes of Lake Bonneville. Copeia 1968, 807–816.*

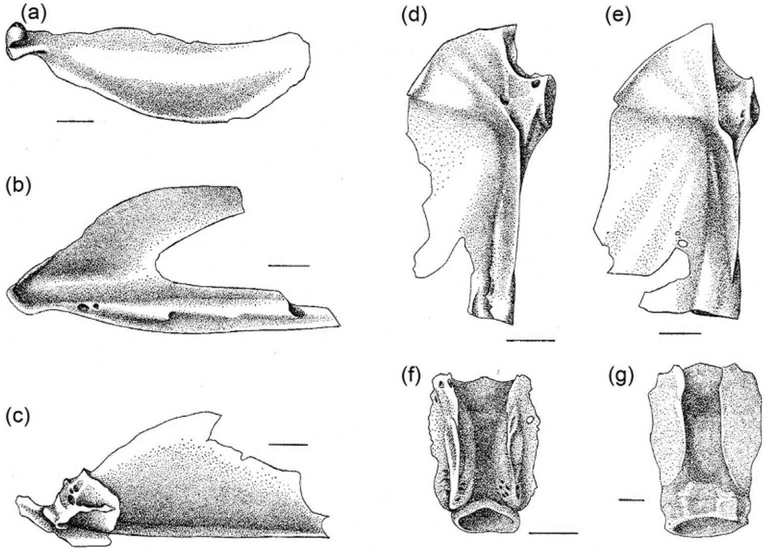

FIG. 12.5 Selected *Prosopium* elements from Hot Springs, Black Rock Canyon and modern Bear Lake. (a) Right maxilla, (b) left dentary, (c) left articular–angular, (d) left hyomandibular of fossil *Prosopium gemmifer* from the Hot Springs locality; (e) left hyomandibular of modern *P. gemmifer* from Bear Lake, Utah (KU 11748); ventral views of basioccipitals of (f) *P. gemmifer*, and (g) *P. spilonotus*, from the Black Rock Canyon locality. Scale = 1 mm. *From Smith, G.R., Stokes, W.L., Horn, K.F., 1968. Some late Pleistocene fishes of Lake Bonneville. Copeia 1968, 807–816.*

of the small *R. balteatus* may, in part, be function of recovery bias. Analysis of the as yet unexamined 1.6 mm fraction of the Homestead Cave fish materials may also document the presence of *S. copei*, *R. osculus* and *I. phlegethontis*, other widespread diminutive minnows of the Bonneville basin. Because *R. balteatus* specimens were previously unknown from Lake Bonneville faunas but were present in Pliocene Lake Idaho has led to the suggestion that this species entered the Bonneville basin from the Snake system as recently as about 14.0 cal ka (Sigler and Sigler, 1996, p. 24), but DNA evidence indicates that *Richardsonius* colonized the Bonneville basin from the Snake River drainage approximately 0.5 Ma (Houston, 2009).

Catostomidae—Suckers
Catostomus ardens (Jordan and Gilbert, 1881)
Utah Sucker

Material—Homestead Cave: Dentary (73), maxilla (74), premaxilla (16). Hot Springs: Ceratohyal (1), quadrate (2), hyomandibular (1), parietal (2), opercle (2), subopercle (1), maxilla (1), dentary (1). Deweyville: 2nd vertebra of Weberian apparatus (1). Smith Creek Cave: Cleithrum (1).

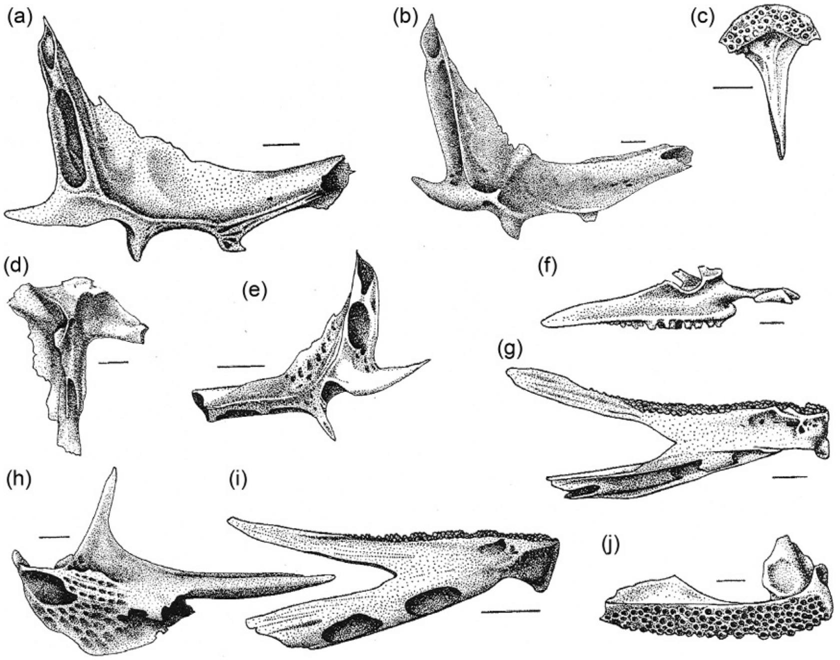

FIG. 12.6 Fossil *Cottus* from Black Rock Canyon and Hot Springs. (a, b, and i) are from the Black Rock Canyon locality. (b) is a specimen of *C. bairdii* (KU 16085); (a) and (i) represent *C. extensus* (KU 16089); the remainder of the specimens are from the Hot Springs locality and represent *C. extensus* (KU 16088) (a) and (b), right preopercles, old individuals; (c), prevomer; (d), left hyomandibular; (e), left preopercle, young individual; (f), right palatine; (g), right dentary, old individual; (h), right articular–angular; (i), right dentary, young individual; and (j), left premaxilla. Scale = 1 mm. *From Smith, G.R., Stokes, W.L., Horn, K.F., 1968. Some late Pleistocene fishes of Lake Bonneville. Copeia 1968, 807–816.*

Pantosteus virescens (Cope, 1872)
Green Sucker

Material—Homestead Cave: Dentary (1), Stratum VI; maxilla (3), Stratum IX; dentary (1), Stratum X.

Chasmistes cf. *liorus*
June Sucker

Material—Black Rock Canyon: Coracoid (1), dentary (1).

Remarks—Four catostomid species are native to the Bonneville basin: *Chasmistes liorus*, *C. ardens*, *Pantosteus virescens*, and *P. platyrhynchus* and all but the latter have now been securely identified from Lake Bonneville deposits. Both *C. liorus* and *C. ardens* can reach substantial sizes (>600 mm TL), whereas *P. virescens* and *P. platyrhynchus* reach maximum lengths of 457 and 305 mm, respectively (Sigler and Sigler, 1996). To judge from site occurrences and relative abundance, *C. ardens* was the most widespread and

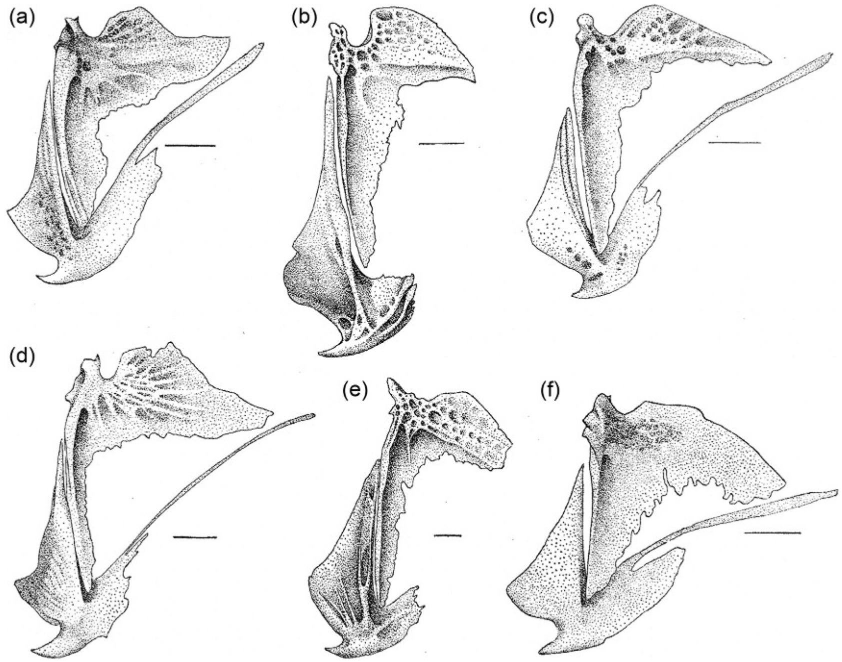

FIG. 12.7 Left opercles and subopercles of Great Basin sculpins. (a) *Cottus echinatus* (UMMZ 156794), Utah Lake, Utah; (b) *C. extensus* (opercle, KU 16089, Black Rock Canyon; subopercle, KU 16088, Hot Springs); (c) *C. extensus* (KU 11934), contemporary Bear Lake, Utah; (d) *C. bairdii* (KU 11940) contemporary Heiners Canyon, Utah; (e) *C. extensus* (KU 16086), Hot Springs locality; and (f) *C. beldingi* (KU 11933), contemporary Heiners Canyon, Utah. Scale = 1 mm. *From Smith, G.R., Stokes, W.L., Horn, K.F., 1968. Some late Pleistocene fishes of Lake Bonneville. Copeia 1968, 807–816.*

abundant sucker in the lake. It is also abundant in many late Holocene archaeological contexts in the basin (eg, Janetski and Smith, 2007).

Homestead Cave has provided the only record of *P. virescens* in Lake Bonneville and the only fossil record of the genus in the Great Basin. Today, two disjunct populations occur in swift and cool, mountain streams of the Bonneville basin: one in the upper Weber River drainage and one in the Bear River drainage. This present-distribution pattern led Smith (1966, p. 121) to suggest that the Weber River population must have colonized that system before the Bear and Weber Rivers were isolated by the desiccation of Lake Bonneville at the end of the Pleistocene. *P. virescens* probably occupied the Bonneville drainage prior to Late Pleistocene Lake Bonneville (Unmack et al., 2014), and was at least a transient along the stretch of shoreline between the Bear River and Weber Rivers, but evidence of their presence in the lake was lacking before the Homestead Cave record. The presence of *C. virescens* at Homestead Cave indicates not only that they occurred in Lake Bonneville but also that they ranged widely across the lake. Since *P. virescens* is a stream-adapted species, their presence also implies that populations of these fish had adapted to some aspect of the lacustrine environments of Lake Bonneville or suitable fluvial environments occurred near Homestead Cave in the past.

The distribution patterns of stream fishes in the Great Lakes region provide insight into how *P. virescens* may have adapted to lacustrine environments of Lake Bonneville. High-energy wave action along the shorelines of the Great Lakes creates substrate types and associated benthic algal and diatom communities that are analogous to those found in riffle sections of stream environments. As a result, some fish species that are primarily restricted to swift streams or rivers with rock or gravel substrates, also occur in certain high-energy shoreline settings of the Great Lakes (Hubbs and Lagler, 1958). Wave-swept shorelines clearly characterized Lake Bonneville and may have provided suitable habitat for *P. virescens* in those settings.

It is also possible that stream habitats may have existed near Homestead Cave in late Pleistocene times even though they do not occur there today. In this context, we note that riparian vegetation and avian taxa associated with such vegetation have been reported for the basal deposits of Homestead Cave and may reflect the presence of local fluvial habitats in the past (Madsen et al., 2001; Wolfe and Broughton, 2016). We also note that an ancient stream channel that would have drained much of the western margin of the Lakeside Mountains is located ~0.5 km from the mouth of the cave (Madsen, 2000).

C. liorus is a large, planktivorous lake sucker that is endemic to the shallow eutrophic waters of Utah Lake today, although it substantially introgressed with *C. ardens* in that setting (Miller and Smith, 1981). This sucker is rare in Lake Bonneville deposits. Miller and Smith (1981, p. 33) report a fragmentary coracoid and dentary referable to *Chasmistes* cf. *liorus* from the Black Rock Canyon locality. Hyomandibulae assigned to *Chasmistes* sp. were reported by Bright (1967) from Late Pleistocene sediments in the Thatcher Basin (Miller and Smith, 1981, p. 33). It is absent in the Homestead ichthyofauna that provided a substantial catostomid collection. The paucity of *C. liorus* is thus intriguing and may reflect a restricted spatial distribution of these fish in late Pleistocene Lake Bonneville. Perhaps they were restricted to warmer, shallower bays of the lake near major input rivers. *C. liorus* has been identified from late Holocene contexts adjacent to Utah Lake (Heaton and Smith, 2016).

Order Salmoniformes
Salmonidae—Trouts and Whitefish
cf. *Salvelinus confluentus* (Suckley, 1858)
Bull Trout

Material—Homestead Cave: Premaxilla (1 fragment).

Oncorhynchus cf. *clarkii* (Richardson, 1836)
Cutthroat Trout

Material—Homestead Cave: Vomer (15), basioccipital (2), maxilla (2), premaxilla (31), ceratohyal (1), glossohyal (9).

Oncorhynchus clarkii (Richardson, 1836)
Cutthroat Trout

Material—Deweyville: Vertebra (1), ceratohyal (1), prootic (1), pterotic (2), epiotic (2), cranial fragments (21), frontal (1). Homestead Cave: Basibranchial (2). Black Rock Canyon: Hyomandibular (1), supraethmoid (1), vomer (1), parasphenoid (1), articular–angular (2), quadrate (3), maxilla (1), preopercle (1), opercle (1), subopercle (1), ceratohyal (1), urohyal (1), cleithrum (1), and vertebra (13). Smith Creek Cave: Articular–angular (1), dentary (1), vertebra (25).

Remarks—Cutthroat Trout are present in a number of Lake Bonneville deposits and would have represented the dominant piscivore of the Lake Bonneville ecosystem, ecologically parallel to Lake Trout (*Salvelinus namaycush*) in the Great Lakes of eastern North America. Indeed, we observe that many of the salmonine elements from Homestead Cave (most likely representing *O. clarkii*) were very large and clearly represented very large individual fish. For example, many vertebrae exceeded 9.0 mm in maximum diameter, which based on vertebral measurements from known-sized reference specimens, would have represented live weights over 2.6 kg; some exceed 11.0 mm, suggesting weights over 6.2 kg (see Follett, 1980, p. 15; Follett, 1982; Fig. 12.3).

One the most surprising aspects of our recent work with Lake Bonneville fish faunas is the probable presence of Bull Trout (*S. confluentus*) in this system. A single premaxilla distinct from *O. clarkii* but exhibiting *Salvelinus* features was discovered in the Homestead Cave material and was examined by JMB and GRS (as well as K. Gobalet)—all concurred on the identification of *S. confluentus*. This specimen represents the first specimen record for the genus *Salvelinus* in the Great Basin during Quaternary times. A single historic account of char in the Bonneville basin was, however, provided in the early 19th century by Townsend (1978) whose account has also been considered "dubious" (Hass and McPhail, 1991, p. 2204). The Bonneville system may have been colonized by *S. confluentus* from the Snake River system when Lake Bonneville overflowed into the Snake approximately 18.0 cal ka BP. Alternatively, *S. confluentus* could have reached the Bonneville system sometime after approximately 50.0 cal ka BP when Lake Thatcher of southern Idaho, filled by the Bear River, began to spill southward into the Bonneville basin (Bouchard, 1997; Bouchard et al., 1998; but see also Bright, 1963, 1967). For a species as large as *S. confluentus*, the presence of only a single specimen at Homestead Cave suggests that even by ~13.1 cal ka BP they were uncommon in the Bonneville basin, or at least in Lake Bonneville. If *S. confluentus* was ever abundant in the Bonneville system, their decline appears to have begun before the Pleistocene–Holocene transition. The suggestion that *S. confluentus* was once a native species to cold waters of the Bonneville basin may have implications for the modern management of this species.

Prosopium spilonotus or *abyssicola* (Snyder, 1919)
Bonneville or Bear Lake Whitefish

Material—Homestead Cave: Opercle (80), prootic (45), exoccipital (29), dentary (17), quadrate (7), ceratohyal (4).

Prosopium cf. *spilonotus* (Snyder, 1919)
Bonneville Whitefish

Material—Homestead Cave: Dermethmoid (1), frontal (1), parietal (3), prootic (1), epiotic (2), maxilla (3), infraorbital (2), basioccipital (1), articular (5), quadrate (1), epihyal (3) ceratohyal (3), hyomandibular (11), preopercle (3), subopercle (3), supracleithrum (5), basipterygium (1), vertebra (40).

Prosopium spilonotus (Snyder, 1919)
Bonneville Whitefish

Material—Homestead Cave: Prootic (1), ceratohyal (6), opercle (4), dentary (23), quadrate (4). Hot Springs: Opercle (1). Black Rock: Basioccipital (1).

Prosopium abyssicola (Snyder, 1919)
Bear Lake Whitefish

Material—Homestead Cave: Dentary (8).

Prosopium gemmifer (Snyder, 1919)
Bonneville Cisco

Material—Homestead Cave: Articular (29), basioccipital (23), ceratohyal (10), dentary (302), maxilla (42), opercle (286), prootic (9), hyomandibular (58), parasphenoid (2). Hot Springs: Maxilla (63), dentary (54), articular-angular (63), quadrate (15), hyomandibular (62), preopercle (3), opercle (49), urohyal (40), posttemporal (18), frontal (13), supraoccipital (4), exoccipital (15), basioccipital (72), parasphenoid (10), prootic (17), hypural (9). Black Rock Canyon: Opercle (3), parietal (2), hyomandibular (1), articular-angular (2), maxilla (1), parasphenoid (1).

Remarks—Three of the four whitefish that occur today in the Bonneville drainage—*P. abyssicola*, *P. spilonotus*, and *P. gemmifer* (Fig. 12.8)—have been identified from Lake Bonneville ichthyofaunas. All three, now endemic to Bear Lake, apparently evolved from a *Prosopium williamsoni* ancestor, the more widespread and morphologically least-derived, western whitefish species (Smith and Todd, 1993). When and where the endemic Bonneville basin whitefish speciated remains uncertain, as we discuss later, although the documentation that they all lived in Lake Bonneville indicates that they have existed since the late Pleistocene.

Smith et al. (1968) identified differences in the shape of the hyomandibular between *P. gemmifer* from Lake Bonneville and those from modern Bear Lake. The fossil hyomandibulae of *P. gemmifer* from the Hot Springs locality

FIG. 12.8 Bonneville Cisco (*Prosopium gemmifer*) from Bear Lake, Utah–Idaho. A planktivorous whitefish, cisco were the most abundant fish species in Lake Bonneville.

differed from modern specimens in having a more perpendicular posterolateral ridge and a narrower gap between the dorsal and opercular condyles. The latter difference was evident in the ratio of the distance between the two condyles and the length of the dorsal condyle, which was substantially lower in the fossil form than in the sample of modern specimens from Bear Lake. Those differences were interpreted as evidence for the further specialization (ie, elongation) of the jaw structure in *P. gemmifer* over the last approximately 11.0 ka and were substantial enough to suggest that the Pleistocene and modern forms may even represent separate species (Smith et al., 1968; Smith, 1981). Table 12.3 provides the hyomandibular condylar ratios for the fossil and modern *P. gemmifer* materials provided by Smith et al. (1968) as well as those from the Homestead Cave and an additional modern sample from Bear Lake. The ratios are also provided for the sample of *P.* cf. *spilonotus* hyomandibulae recovered from Homestead Cave, as well as a modern sample of *P. spilonotus* from Bear Lake. These data show that the hyomandibular morphology of the two Lake Bonneville samples of *P. gemmifer*, Hot Springs and Homestead Cave, are similar, with ratios of 0.45 ± 0.017 and 0.49 ± 0.015, respectively. The ratios from the two modern samples of this species are nearly identical and are substantially higher (sample $A = 0.57 \pm 0.015$, sample $B = 0.56 \pm 0.010$) than the Pleistocene samples. The increase in this ratio documented between the fossil and modern samples of *P. gemmifer* is toward *P. spilonotus*. The sample of *P. gemmifer* from Homestead Cave is different from modern *P. gemmifer* and both *P. spilonotus* from Homestead Cave and modern *P. spilonotus* (Table 12.4). However, modern *P. gemmifer* does not differ from either the Homestead Cave sample of *P. spilonotus* or the modern sample of the latter. There is also no difference between the Homestead Cave and modern samples of *P. spilonotus* (Table 12.4). Insofar as these differences are reflecting

TABLE 12.3 **Hyomandibular Condylar Ratios for Lake Bonneville and Modern *P. gemmifer* and *P. spilonotus***

Species	*N*	Mean	Range	SD	SE
P. gemmifer (Homestead Cave)	17	0.49	0.35–0.15	0.064	0.015
P. gemmifer (Hot Springs)	27	0.45	0.38–0.54	–	0.017
P. gemmifer (Modern A)[a]	22	0.57	0.51–0.65	–	0.015
P. gemmifer (Modern B)	23	0.56	0.48–0.65	0.047	0.01
P. cf. *spilonotus* (Homestead Cave)	11	0.53	0.46–0.61	0.05	0.015
P. spilonotus (Modern)	25	0.55	0.44–0.67	0.068	0.014

[a] *From Smith et al. (1968).*

TABLE 12.4 **Test Statistics for Comparisons of Hyomandibular Condylar Ratios for the Lake Bonneville and Modern *Prosopium gemmifer* and *P. spilonotus***

Species (Sample) Comparison	*t* Statistic	*P*-Value
P. gemmifer (HC)/*P. gemmifer* (Modern sample B)	−4.13	<0.001
P. gemmifer (HC)/*P. spilonotus* (HC)	−1.96	=0.06
P. gemmifer (HC)/*P. spilonotus* (Modern)	−3.25	<0.01
P. gemmifer (Modern B)/*P. spilonotus* (HC)	−1.57	>0.10
P. gemmifer (Modern B)/*P. spilonotus* (Modern)	0.25	>0.50
P. spilonotus (Modern)/*P. spilonotus* (HC)	−1.01	>0.30

approximately 11,000 years of time, *P. gemmifer* has come to be phenotypically more similar to *P. spilonotus* over this interval; *P. spilonotus*, however, has not changed. Although the evolutionary mechanisms and significance of this are not clear, it is possible that introgression of morphological characters from *P. spilonotus* to *P. gemmifer* has occurred during their Holocene occupation of Bear Lake. Indeed, many examples of hybridization are known among coregonin populations including *Prosopium* populations from Bear Lake. Sigler and Miller (1963) reported three fish from Bear Lake they believed to be *P. gemmifer* × *P. spilonotus* hybrids. White (1974) also reported

"*P. gemmiferum*-like" fish from Bear Lake, suggesting they resulted from combinations of *P. gemmifer* and either *P. spilonotus* or *P. abyssicola*.

Order Scorpaeniformes
Cottidae—Sculpins
Cottus cf. *bairdii* (Girard, 1850)
Mottled Sculpin

Material—Homestead Cave: Preopercle (1).

Cottus bairdii (Girard, 1850)
Mottled Sculpin

Material—Homestead Cave: Preopercle (6). Hot Springs: Preopercle (3), subopercle (1). Black Rock Canyon: Preopercle (1), hyomandibular (1). Cathedral Cave: Preopercle (3).

Cottus extensus or *echinatus* (Bailey and Bond, 1963)
Bear Lake or Utah Lake Sculpin

Material—Homestead Cave: Preopercle (12). Cathedral Cave: Preopercle (5).

Cottus extensus (Bailey and Bond, 1963)
Bear Lake Sculpin

Material—Homestead Cave: Preopercle (5). Hot Springs: two partially complete, disarticulated individuals, including most of the skull bones and other bony elements, and assorted disarticulated bones including preopercle (7), hyomandibular (4), subopercle (4), opercle (2), palatine (5), articular–angular (12), dentary (8), premaxillae (11). Black Rock Canyon: Preopercle (4), opercle (1), articular–angular (1), dentary (3).

Remarks—Four species of sculpin are known from the Bonneville basin: *Cottus beldingi*, *C. bairdii*, *C. extensus*, and *C. echinatus*, a Utah Lake endemic that is now extinct. Of the four, *C. bairdii* and *C. extensus* have both been identified in several Lake Bonneville ichthyofaunas including Homestead Cave, Cathedral Cave (UT), Black Rock Canyon, and Hot Springs. The fact that *C. echinatus* has not yet been identified from Lake Bonneville deposits is noteworthy. Smith et al. (1968) suggested that *C. extensus* occurred in Lake Bonneville and Bear Lake during the late Pleistocene and underwent little evolution in the relatively cold and stable environment of Bear Lake during the Holocene. In contrast, they argued that in Utah Lake—the shallow, unstable low-elevation remnant of Lake Bonneville—*C. echinatus* diverged from a relictual *C. extensus* population over the last approximately 11,000 years. This suggestion was based on the historical distributions of these fishes as well as the fact that *C. extensus* was known from the fossil record of Lake Bonneville, but *C. echinatus*, as of the late 1960s, was not. This scenario is thus supported by the current pattern where both *C. echinatus* and *C. bairdii* are demonstrably present in the Lake Bonneville ichthyofauna but *C. echinatus* is not.

It is also noteworthy that the Cathedral Cave (UT) fish fauna is represented exclusively by sculpin and this appears to relate to the unique sampling mechanism involved in forming that deposit. Indeed, ostracod data, marl sediments, and a radiocarbon date of 15,310 ± 60 from an overlying stratum suggest that the material represents a deep-water phase deposit from the Bonneville or Provo level deposit that accumulated under 100–200 m of water (Oviatt, 2000). The presence of *C. extensus* is consistent with this suggestion, since these are the most abundant fish that occur in the greater depths of Bear Lake. These fish are also known to actively burrow into the soft marl sediments in the bottom of the lake (McConnell et al., 1957; Dalton et al., 1965; Sigler and Sigler, 1996). Although *C. bairdii* is a bottom dwelling, cold-water stream fish over most of its range (Sigler and Sigler, 1996), lake populations are also known for a form of this species in all of the Great Lakes of eastern North America (Keleher, 1952; Trautman, 1981, pp. 708–710).

12.4 THE LAKE BONNEVILLE ICHTHYOFAUNA

The fish fauna of Lake Bonneville can be understood from a combination of fossils and inference from the differentiation of recent fish DNA data. Assuming that the nearby tributary species were transients in estuaries and along the shore, the fauna comprised at least 21 species (Table 12.2) including two, large salmonine, top carnivores known from fossils; three endemic whitefish zooplanktivores, three known from fossils; three bottom or rocky shore dwelling sculpins, two known from fossils; several minnows, one abundantly represented by fossils; a large lake sucker known from fossils; a river sucker, abundantly represented by fossils; and two mountain suckers, one represented by fossils. Four small minnows and a small sculpin are inferred from their DNA diversity inside vs outside the basin to have been present in the drainage probably before the lake, but were too small to have left an easily detectable fossil record. The fauna of Bear Lake, a cold, high elevation, deep lake on the Utah–Idaho border, has 8 of the 21 species, and probably had two others, based on DNA, morphology, and historical accounts. All of the native species represented in Bear Lake are now known to also have occurred in Lake Bonneville. The small minnow, *R. osculus* surely occurred in all parts of the basin, probably since the Pliocene, based on ancient and diverged endemic DNA in all parts of the Bonneville basin, including Snake Valley in the west and Thousand Springs in northeast Nevada (Oakey et al., 2004). Patterns of relative abundance appear to be similar as well. The zooplanktivorous *P. gemmifer* (Fig. 12.8), for instance, was the most abundant fish in both Lake Bonneville and Bear Lake, along with Utah Chubs and Utah Suckers, whereas the large piscivorous cutthroat trout was as abundant as expected of the top carnivore in both settings.

On a broader continental scale, the Lake Bonneville fish assemblage also resembled the ecological composition of modern Lake Michigan. Although the two lakes are separated by over 13,000 years of time and ~2000 km of distance, they were similar in size, depth, regional air temperatures (Smith et al., 1968) and their short-lived histories. The Lake Michigan fauna is considerably richer however, reflecting the great diversity of its source fauna in the Mississippi, Missouri, Arctic, and eastern drainages (Bailey and Smith, 1981). The comparison of these two faunas is instructive relative to the importance of sources for colonization, ecological time, and evolutionary time. The Lake Michigan fauna has eight times the number of fish species as the Bonneville fish fauna, yet the lake has been in existence for less than 14,000 years (Hubbs and Lagler, 2004). Paleontological evidence (Shoshani and Smith, 1996) indicates that warm-water catfish and sunfish colonized the Great Lakes through warm, headwater-stream captures, prior to 11,000 BP, while cold-water fishes were colonizing through the cold, glacial outlet channels (Smith, 1985). The comparison shows that 10^3–10^4 years is enough ecological time to build up a fauna of scores of species if the source fauna is near. On the other hand, few species of fishes in Lake Michigan (coregonins) and few species in Lake Bonneville (coregonins and sculpins) have been suspected of having evolved in such a short time, and those examples may be questioned (Smith et al., 2010).

12.5 FISH INFERENCES REGARDING BONNEVILLE BASIN DRAINAGE HISTORY

Hydrographic drainages, if isolated as in the Great Basin, always have distinctive fish faunas. For example, only 4 of the 10 or 12 fish species in the Lahontan drainage occur among the 21 species in the Bonneville system. Differences between major geographic provinces are even greater: only 5 of the 21 species in the Bonneville drainage are native among the 35 species in the Colorado drainage. Therefore, species presence or absence in drainages is a useful source of information—most importantly, shared occupancy by the same species of fish in adjacent drainages is informative about past aquatic connections. On the basis of restriction of fishes to water (and lack of evidence for dispersal of fish eggs on birds' feet along flyways) past connections are assumed to be through lake spillovers, stream captures, and shared headwaters in upland meadows such as Two-Ocean Pass in the Tetons (Evermann, 1895) and Isa Lake in Yellowstone National Park.

Fish fossils and recent fish DNA both provide information concerning paleohydrology of the Great Basin. These data may be studied in the same way that stream-pebble petrology and source can be studied for provenance. Fish differ from stream pebbles in an important way, however—fish migrate long distances upstream just as frequently as they migrate downstream. Provided that the fish fossils are accurately identified and their host sediments are accurately dated by radiogenic or biostratigraphic ages, fish fossils provide information about where and when the species lived and died. Mitochondrial DNA differences between related fish can be used to estimate the date of the splitting event that created two populations if we can calibrate the genetic distances with fossil fish, their associated apomorphies, and their stratigraphic data (Smith et al., 2013).

Fossil fishes and DNA of recent fishes provide information about the timing and size of past outlets and tributaries to Lake Bonneville. Fish distributions help document precursor lakes, potential water balance, possible sources of sediment and salinity, and hydrographic connections that contributed to accumulation of its aquatic fauna. DNA of living fishes in the Great Basin, Snake River, and Colorado River is particularly useful in this regard because each member of the Bonneville fish fauna carries a record of its connection to relatives in or outside the basin and the timing of evolutionary separation from those relatives. This method depends on the principal that when a panmictic population is divided by a barrier, the daughter populations begin to accumulate DNA sequence differences at a quasi-constant rate (the molecular clock) that can be precisely measured (Broham and Penny, 2003).

12.5.1 Snake River to Great Basin Connections

Minnows (chubs, shiners, and dace) are the most common fishes in the Columbia-Snake and Bonneville drainages. Some of their mtDNA genes have been analyzed to determine evolutionary relationships within species and the genetic distances are rather small between drainages, but not as small as predicted if it is assumed that the Bonneville overflow at Red Rock Pass is the first connection. MtDNA sequence divergences between dace and chubs in the Bonneville and Snake Basins is greater than 1%, indicating that the two drainages were connected at times between 3.8 and 1.6 Ma assuming that the rate of substitution in these genes is about 1% per million years (Johnson and Belk, 1999; Dowling unpublished data).

Prior to that, the Salt Lake Formation was broadly connected to the western Snake River Plain, as indicated by shared fish lineages in the late Miocene Cache Valley Member and the Chalk Hills Formation in the Western Snake River Plain. Nine genera in four families of fishes are known from the Junction Hills local fauna of the Cache Valley member (McClellan and Smith, 2016): minnows (Cyprinidae) include pikeminnow (*Ptychocheilus*), chiselmouth chub (*Acrocheilus*), a snail crusher (*Mylocheilus* cf. *M. whitei*), hitch (*Lavinia*), and chub (*Gila*). Suckers (Catostomidae) include a relative of the Utah Sucker (*C. ardens*) and a lake sucker (*Chasmistes*). A bullhead catfish (*Ameiurus*) and a sunfish (*Archoplites*) complete the fish list. All of these except the *Catostomus*, a possible northern Utah endemic, have their closest relatives on the Western Snake River Plain (but species of *Catostomus* also occur in the MioPliocene of the Western Snake River Plain). This aquatic connection is important because it somehow circumvents the hypothetical hot spot bulge of the Twin Falls volcanic field (10.5–8.6) between the eastern and western Snake River Plains. None of these species and only three of the genera are in the Lahontan basin, casting doubt on the hypothesis that the upper Snake River flowed into the Humboldt (Beranek et al, 2006; Houston, 2009). The chiselmouth chub, *Gila* chub, *Catostomus*, and *Chasmistes*, persisted into the Pleistocene Bonneville basin, although the chiselmouth chub went extinct before the Holocene.

The Bonneville basin was also connected to the Virgin, Kanab, and Meadow Valley Wash drainages about 1.1 Ma according to evidence of morphological introgression and genetic distance measurements in dace (*Rhinichthys*) and mountain suckers (*Pantosteus*) from these drainages (Smith et al., 2002; Smith and Dowling, 2008; Unmack et al., 2014; Smith et al., 2016). The Speckled Dace (*R. osculus*) of the Sevier drainage is derived from the Virgin River, not the northern Bonneville basin, and populations of Speckled Dace and mountain suckers in Shoal Creek (Park Canyon Creek) tributary to the Sevier Drainage near Enterprise, Utah, show evidence of introgression with their counterparts in the nearby Meadow Valley Wash Drainage of eastern Nevada, possibly through the region near Modena. The modern irrigation diversions cited by Hubbs and Miller (1948, pp. 29–31) as possible sources of fish transfer across divides mentioned earlier were not responsible for the much older connections indicated by the mtDNA distances. Our DNA methods are not sensitive enough to detect differences evolved in 100–200 years.

Fishes in Snake Valley, at the western edge of the Bonneville basin between the Snake Range and the Deep Creek range, are the expected Bonneville species (Hubbs and Miller, 1948, p. 29) and include an additional form of *Rhinichthys*, formerly thought to be a distinct species (Miller, 1984; Smith et al., 2002). Observers have long struggled, however, to resolve the unusual morphological diversity among populations in Snake Valley. This puzzle was solved when Tom Dowling sequenced the cytochrome *b* gene, of the mitochondrial DNA of several populations and discovered two haplotypes one related to *Rhinichthys* of the Sevier and Virgin rivers and the other related to dace in the Lahontan Basin, but more than a million years older than other populations in that basin. The two mtDNA haplotypes were found in one population that showed evidence of having been mixed with other populations of dace in Snake Valley. The presence of the older dace haplotype as well as the presence of mountain suckers associated with this drainage (Smith, 1966) suggest a connection between the pre-Bonneville and Lahontan drainages as much as 3.3 Ma (Dowling unpublished data).

Dace in the ~1000 km^2 Thousand Springs drainage in northeast Nevada attest to an ancient and long-existent connection between the Bonneville and Snake River drainages. Dace from Rock Springs in the Thousand Springs drainage are part of one of the oldest lineages in the Snake River, according to mtDNA. The Rock Springs dace are morphologically similar to northern Bonneville dace, and Thousand Spring Creek can be traced to below the higher Bonneville shorelines (Hubbs and Miller, 1948, p. 29).

These connections offer insights into the antiquity of the Bonneville and pre-Bonneville fish fauna. Hubbs and Miller (1948) were tempted to explain many of the Bonneville fish species as arrivals through the outlet through Red Rock Pass. DNA data suggest that the entire fish fauna predates Lake Bonneville, but is not as old as the Cache Valley Member of the Salt Lake Formation.

The separation of Bonneville fishes into northern and southern drainage groups was first pointed out by Johnson et al. (2004) on the basis of differentiation in the Leatherside Chub, *S. copei*. Similarly, Smith and Dowling (2008) noted major DNA differences between northern and southern basin *R. osculus*. Unmack et al. (2014) followed with evidence in *P. platyrhynchus* suggestive of over 3 million years of differentiation that is consistent with evidence for water in the basin as early as 3 Ma (Oviatt, 1994).

12.5.2 Evolution of Prosopium Species in Lake Bonneville and Bear Lake

The six North American species of *Prosopium* exhibit profound morphological and geographic diversity. The Round Whitefish (*P. cylindraceum*) occurs from the Great Lakes and across most of Canada to Alaska, the Pygmy Whitefish (*P. coulterii*) occurs in the Rocky Mountains from Montana and Washington to Alaska and the deep waters of Lake Superior. The Rocky Mountain Whitefish (*P. williamsoni*) occurs in the Intermountain West, including the Bear River drainage, north to the Yukon Territory; the other three species occur in Bear Lake, Utah and Idaho, and existed in Lake Bonneville. This is a cold-water group with a special evolutionary history.

As the diversity of *Prosopium* at Hot Springs and Homestead Cave became known, including apparent Holocene morphological change in *P. gemmifer* as described earlier, the question of Lake Bonneville's contribution to the evolution of the Bear Lake species became important (Broughton, 2000b,c). It is tempting to assume that the larger Pleistocene lake was the original place of origin of at least some of the diversity. But Bear Lake is one of the oldest continuous lakes on the North American continent (Kaufman et al., 2009). Bear Lake also has the most direct connection to the long-lived, Pliocene Glenns Ferry Lake on the Western Snake River Plain. This Pliocene lake had one large and one small species of *Prosopium* for up to 2 million years (Stearley and Smith, 2016). Therefore, when the Bear River was tributary to the upper Snake River, it was in the same drainage as the Glenns Ferry Lake. Although the connection was hydrographic, the genetic communication among the fishes was not contemporaneous. Genes of lacustrine *Prosopium* were probably sequestered in fluvial *Prosopium*.

The inference that the Snake River drainage was an important site of *Prosopium* evolution, with six species in the Pliocene and Pleistocene, is a starting point for considering the role of Lake Bonneville, which was also an important part of the Snake River drainage at times. This investigation benefits from the Global Lakes Drilling program, which extracted long cores from the Great Salt Lake sediments (Dean et al., 2002) as well as Bear Lake (Kaufman et al., 2009). The question we ask of the comparison of these cores is: (1) What were the comparative histories of cold *Prosopium* habitat in the two basins? (2) What do these histories tell us about possible times of origin and times of extinction of the Bear Lake *Prosopium* species flock? (Smith and Todd, 1984).

All of the fossil and recent species, except the Round Whitefish, have a significant presence in the Snake-Columbia River drainage. The earliest two, *Prosopium prolixus* and *P.* sp., in the Pliocene, are in no ways "primitive," but are as advanced as any of the modern species. This implies that the group had a much longer history, probably in the Snake-Columbia river drainage. A corollary is that the morphologically divergent Bear Lake Whitefishes are possibly older than Pleistocene.

Bear Lake and Lake Bonneville were exposed to the same regional climatic and precipitation changes, with secondary features governed by local geomorphic and fluvial processes (Reheis et al., 2009). Lake-level fluctuations were actually greater in the Bonneville basin because of its confinement. Bear Lake did not dry out during the last 220,000 years (Kaufman et al., 2009), but the Bonneville basin accumulated salts and saline marsh sediments during dry episodes (Oviatt et al., 1999; Balch et al., 2005). Dry episodes in the Bear Lake basin, by contrast, interrupted the connections between Bear Lake and the Bear River (Kaufman et al., 2009). These two processes provide the most important controls on population dynamics and population genetics of *Prosopium* in the two connected systems. Optimal lake habitat was approximately continuous in Bear Lake, but not in Lake Bonneville, and opportunities for immigration between the lakes were best when both were fresh.

Balch et al. (2005) found four periods of marsh deposits when the Bonneville core site was above lake level and two periods under a deep lake. Deep water was indicated at ~170, 60, 45–35, and 25–15 ka. The Great Salt Lake core records low water levels at 215, 130, 105, and 45 ka. The Bear Lake core records low water levels in response to aridity at the first three of these dry intervals, but records a continuous lake, with a high stand at 47–39 ka, which delivered increased output of sediment to Lake Bonneville (Balch et al., 2005). These multi-millennial cycles surely selected for lacustrine adaptations, but with more serious extinctions and population bottlenecks in Lake Bonneville. Lake Bonneville was possibly a repeated dead end for *Prosopium* and other lacustrine fish evolution.

12.6 BONNEVILLE BASIN FISHES AND LATE QUATERNARY LAKE LEVELS

Although we have learned a great deal about the timing and size of past outlets and tributaries to Lake Bonneville from the collective sample of fish fossils and DNA of recent fishes, analysis of the large, well-dated fossil fish sequence from Homestead Cave provides an opportunity to understand the chronology and nature of change in the fauna as lake levels fluctuated over the last ~13,000 years. Most notably, this sequence provides a singular record on when fish were first eliminated from the lake toward the end of the Pleistocene and the timing and nature of several apparent recolonization events that occurred during the Holocene. We address these issues through analyses of: (1) the chronology of fish bone deposition in relation to reconstructions of lake level history; (2) strontium isotopes derived from the fish remains; (3) change in fish size; and (4) change in taxonomic composition in connection with taxon-specific temperature and salinity tolerances.

Recent geological research suggests that Lake Bonneville declined to elevations approaching those of modern Great Salt Lake by about 13.0 cal ka BP and remained at low altitudes for the next 1400 years. At about 11.6 cal ka BP, the lake transgressed again to a maximum altitude of 1295–1297 m, but regressed about 15 m to altitudes comparable to modern Great Salt Lake a very short time later (Oviatt, 2014, 2015a; Oviatt et al., 2015; Fig. 12.9). Analysis of sediments from the latter transgression, referred to as the Gilbert episode, suggest that the lake was not hypersaline at this time and did not contain brine

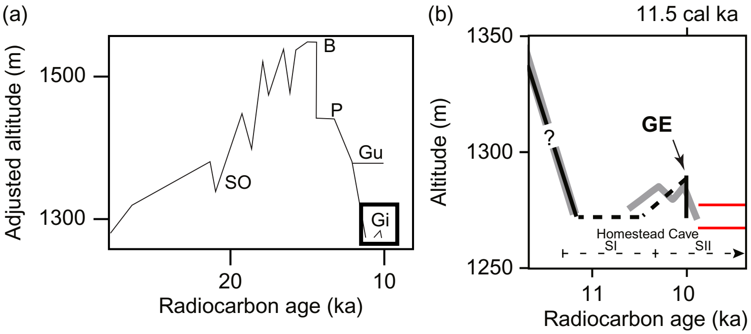

FIG. 12.9 Late Quaternary shoreline history of the Bonneville basin. (a) Generalized hydrograph for Lake Bonneville. *SO* = Stansbury oscillation; *B* = Bonneville shoreline; *P* = Provo shoreline; *Gu* = Gunnison shoreline; *Gi* = Gilbert shoreline; *T* = transgressive phase; *O* = overflowing phase; *R* = regressive phase. The *dark rectangle* shows the area enlarged in (b). (b) Enlargement of the part of (a) that shows the Gilbert episode. The *gray line* represents the interpretation of Oviatt et al. (2005); the *solid black line* is the reconstruction provided in Oviatt (2014); the *thick dashed line* reflects uncertainty in lake level chronology during the pre-Gilbert interval; and the two horizontal *red lines* younger than the Gilbert episode show the upper and lower altitude limits of Holocene Great Salt Lake fluctuations. The *thin dashed line* represents the period of deposition of the Homestead Cave fishes from Stratum I (SI) and Stratum II (SII). *GE* = Gilbert episode. *From Oviatt, C.G., 2014. The Gilbert episode in the Great Salt Lake Basin, Utah. Miscellaneous Publication 14-3, Utah Geological Survey. Panel (a): Modified after Oviatt, C.G., Miller, D.M., McGeehin, J.P., Zachary, C., Mahan, S., 2005. The Younger Dryas phase of Great Salt Lake, Utah, USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 219, 263–284; Reheis, M.C., Adams, K.D., Oviatt, C.G., Bacon, S.N., 2015. Pluvial lakes in the Western United States—a view from the outcrop. Quatern. Sci. Rev. 97, 33–57.*

shrimp (*Artemia franciscana*) and may have instead been brackish (Oviatt, 2014). Although previous work had suggested that the rich Stratum I fish fauna from Homestead Cave represented fish derived from the Gilbert episode lake (Broughton, 2000a,b; Broughton et al., 2000; Madsen et al., 2001), we propose an alternative interpretation here that is consistent with the current understanding of lake history and refinements in the Homestead Cave chronology.

12.6.1 The Homestead Cave Fish Sequence

Fish remains were heavily concentrated in Stratum I of the cave, although Stratum II and several higher units contain substantial numbers of fish as well (Fig. 12.10). Stratum I consists primarily of degraded organic material, including vast quantities of small vertebrate bone (Grayson, 1998; Madsen, 2000). Stratum I was removed as a single layer because the numerous microlaminae evident in the unit could not be confidently separated. However, the laminated nature of the Stratum I sediments, together with a difference in more than a 1000 years in radiocarbon ages from the top to the bottom of the stratum (Table 12.5) suggest it is actually composed of multiple depositional events. To increase the stratigraphic resolution within Stratum I, sediment samples of the upper and lower halves of the stratum were collected from the profile and samples were also taken from the upper and lower 10 cm of Stratum I where it was thickest. Stratum Ia is the arbitrarily defined lower half of Stratum I, whereas Stratum Ib is the arbitrarily defined upper half. Five radiocarbon assays on individual *Neotoma* (woodrat) fecal pellets collected from the lowest 5 cm of Stratum Ia, directly overlying bedrock, are statistically indistinguishable and range from 13.1 to 13.0 cal ka BP. Three dates, also from fecal pellets, taken directly from the upper 5 cm of Stratum Ib

FIG. 12.10 View of the mouth Homestead Cave.

TABLE 12.5 Radiocarbon Dates from Homestead Cave (Age Estimates Are Listed Chronologically Within Stratigraphic Units)

Stratum	^{14}C Age (yr BP)	Cal Age (yr BP)[a]	Median Cal Age	Lab. No.	Material
XVII[b]	1020 ± 40	820–1050	940	Beta101877	30 g artiodactyl pellets
XVI[b]	1200 ± 50	990–1260	1130	Beta66940	Charcoal
XV[c]	767 ± 41	690–760	700	AA72777	Bone collagen
XV[d]	980 ± 40	800–960	870	CAMS70099	1 artiodactyl pellet
XV[d]	1790 ± 40	1610–1820	1760	CAMS70100	1 artiodactyl pellet
XV[c]	1890 ± 45	1720–1930	1830	AA72779	Bone collagen
XV[c]	2221 ± 46	2130–2340	2230	AA72784	Bone collagen
XV[e]	2025 ± 775	520–3860	2090	–	*Neotoma* fec. pellet(s)
XV[c]	2073 ± 44	1930–2150	2040	AA72774	Bone collagen
XV[c]	2216 ± 45	2130–2340	2230	AA72782	Bone collagen
XV[c]	2220 ± 44	2140–2340	2230	AA72775	Bone collagen
XV[c]	2237 ± 46	2150–2340	2230	AA72789	Bone collagen
XV[c]	2244 ± 45	2150–2340	2240	AA72783	Bone collagen
XV[c]	2302 ± 78	2120–2700	2320	AA69315	Bone collagen
XV[c]	2472 ± 48	2370–2720	2560	AA69314	Bone collagen
XV[c]	2500 ± 46	2380–2740	2580	AA72785	Bone collagen
XV[c]	2508 ± 46	2380–2750	2590	AA72778	Bone collagen

Continued

TABLE 12.5 Radiocarbon Dates from Homestead Cave (Age Estimates Are Listed Chronologically Within Stratigraphic Units)—Cont'd

Stratum	^{14}C Age (yr BP)	Cal Age (yr BP)	Median Cal Age	Lab. No.	Material
XV[c]	2551 ± 39	2490–2760	2630	AA72788	Bone collagen
XV[c]	2553 ± 46	2490–2960	2630	AA72776	Bone collagen
XV[c]	2559 ± 46	2490–2760	2640	AA72773	Bone collagen
XV[c]	2722 ± 39	2750–2920	2820	AA72786	Bone collagen
XV[c]	2850 ± 48	2850–3140	2970	AA72781	Bone collagen
XV[c]	3031 ± 48	3080–3360	3230	AA72780	Bone collagen
XV[c]	4531 ± 54	4580–5440	5170	AA72787	Bone collagen
XIV[b]	2850 ± 50	2850–3080	2970	Beta103692	30 g artiodactyl pellets
XIII[b]	3480 ± 40	3630–3880	3760	Beta101878	30 g artiodactyl pellets
XII[b]	3400 ± 60	3550–3830	3650	Beta63179	Wood/charcoal
XI[d]	4450 ± 40	4880–5290	5100	CAMS70101	1 artiodactyl pellet
XI[d]	4750 ± 40	5330–5590	5510	CAMS70102	1 artiodactyl pellet
X[b]	5330 ± 65	5950–6270	6110	AA14822	1 artiodactyl pellet
IX[d]	5400 ± 40	6020–6290	6220	CAMS70103	1 artiodactyl pellet
IX[d]	6270 ± 50	7020–7300	7200	CAMS70104	1 artiodactyl pellet
VIII[d]	6190 ± 50	6960–7180	7090	CAMS70105	1 artiodactyl pellet

VIII[d]	6200 ± 40	6990–7240	7090	CAMS70106	1 artiodactyl pellet
VII[c]	6160 ± 35	6960–7160	7070	CAMS134591	Bone collagen
VII[d]	6160 ± 85	6850–7260	7060	AA14824	1 artiodactyl pellet
VII[c]	6165 ± 40	6950–7170	7070	CAMS134580	Bone collagen
VII[b]	6185 ± 105	6760–7310	7080	AA14825	1 artiodactyl pellet
VII[c]	6245 ± 40	7020–7260	7180	CAMS136730	Bone collagen
VII[c]	6275 ± 35	7030–7280	7210	CAMS136729	Bone collagen
VII[c]	6345 ± 35	7170–7410	7280	CAMS134586	Bone collagen
VII[c]	6345 ± 40	7170–7410	7280	CAMS134583	Bone collagen
VII[c]	6355 ± 40	7180–7420	7290	CAMS134581	Bone collagen
VII[c]	6370 ± 50	7180–7420	7310	CAMS136733	Bone collagen
VII[c]	6395 ± 40	7260–7420	7330	CAMS134589	Bone collagen
VII[c]	6435 ± 40	7280–7430	7360	CAMS136732	Bone collagen
VII[c]	6440 ± 35	7290–7430	7370	CAMS136731	Bone collagen
VII[c]	6455 ± 35	7290–7430	7370	CAMS134588	Bone collagen
VII[c]	6505 ± 35	7320–7480	7430	CAMS134590	Bone collagen
VII[c]	6625 ± 35	7440–7550	7520	CAMS134587	Bone collagen
VII[c]	6625 ± 45	7440–7580	7510	CAMS134584	Bone collagen
VII[c]	6675 ± 35	7480–7610	7540	CAMS134582	Bone collagen

Continued

TABLE 12.5 Radiocarbon Dates from Homestead Cave (Age Estimates Are Listed Chronologically Within Stratigraphic Units)—Cont'd

Stratum	^{14}C Age (yr BP)	Cal Age (yr BP)	Median Cal Age	Lab. No.	Material
VII[c]	6685 ± 40	7480–7620	7550	CAMS136728	Bone collagen
VII[c]	6735 ± 40	7520–7670	7600	CAMS136734	Bone collagen
VII[c]	6830 ± 35	7590–7720	7590	CAMS134585	Bone collagen
VII[c]	7005 ± 40	7740–7940	7850	CAMS136735	Bone collagen
VI[b]	7120 ± 70	7790–8150	7950	AA14826	1 artiodactyl pellet
V[b]	8230 ± 70	9020–9410	9200	AA16810	1 artiodactyl pellet
IV[b]	6600 ± 40	7430–7570	7500	CAMS70108	1 artiodactyl pellet
IV[b]	8040 ± 50	8720–9030	8910	CAMS70107	1 artiodactyl pellet
IV[b]	8195 ± 85	9000–9420	9170	AA14823	1 artiodactyl pellet
III[d]	8450 ± 40	9420–9530	9480	CAMS71147	1 artiodactyl pellet
III[d]	9650 ± 40	10,880–11,190	9910	CAMS71148	1 artiodactyl pellet
II[c]	7075 ± 35	7840–7970	7900	CAMS134592	Bone collagen
II[c]	8480 ± 35	9460–9540	9500	CAMS134594	Bone collagen
II[b]	8520 ± 80	9400–9680	9510	AA14821	1 *Celtis* endocarp
II[c]	8615 ± 35	9530–9660	9560	CAMS141271	Bone collagen
II[e]	8675 ± 235	9120–10,270	9750	–	*Neotoma* fec. pellet(s)

II[b]	8790 ± 90	9560–10,160	9840	AA14820	1 *Celtis* endocarp
II[b]	8830 ± 240	9400–10,520	9910	Beta63438	*Celtis* endocarps
II[c]	9295 ± 40	10,370–10,590	10,500	CAMS141278	Bone collagen
II[c]	9370 ± 35	10,510–10,690	10,600	CAMS141279	Bone collagen
II[c]	9380 ± 35	10,520–10,690	10,610	CAMS141280	Bone collagen
II[c]	9405 ± 45	10,520–10,740	10,640	CAMS141274	Bone collagen
II[c]	9475 ± 40	10,580–11,070	10,720	CAMS134595	Bone collagen
II[c]	9515 ± 40	10,660–11,080	10,830	CAMS141272	Bone collagen
II[c]	9835 ± 40	11,200–11,310	11,240	CAMS134597	Bone collagen
II[c]	10,165 ± 40	11,700–12,310	11,860	CAMS141275	Bone collagen
II[c]	10,195 ± 40	11,750–12,080	11,900	CAMS141276	Bone collagen
II[c]	10,200 ± 40	11,750–12,080	11,900	CAMS141273	Bone collagen
II[c]	10,235 ± 40	11,800–12,130	11,970	CAMS134596	Bone collagen
II[c]	10,255 ± 35	11,830–12,140	12,010	CAMS141277	Bone collagen
II[c]	10,310 ± 40	11,960–12,380	12,110	CAMS134593	Bone collagen
II[c]	10,395 ± 40	12,070–12,420	12,270	CAMS134598	Bone collagen
Ib-5 cm[b,f]	10,160 ± 85	11,400–12,120	11,810	AA14819	1 *Neotoma* fec. pellet
Ib-5 cm[e]	10,235 ± 180	11,340–12,550	11,980	–	*Neotoma* fec. pellet(s)
Ib-5 cm[b]	10,350 ± 80	11,940–12,440	12,210	AA14818	1 *Neotoma* fec. pellet

Continued

TABLE 12.5 Radiocarbon Dates from Homestead Cave (Age Estimates Are Listed Chronologically Within Stratigraphic Units)—Cont'd

Stratum	^{14}C Age (yr BP)	Cal Age (yr BP)	Median Cal Age	Lab. No.	Material
I-middle[b]	10,910 ± 60	12,700–12,940	12,780	Beta72205	Bone collagen
Ia-5 cm[b]	11,065 ± 105	12,730–13,090	12,950	AA14817	2 *Neotoma* fec. pellets
Ia-5 cm[e]	11,168 ± 208	12,710–13,410	13,030	–	*Neotoma* fec. pellet(s)
Ia-5 cm[b]	11,181 ± 85	12,810–13,210	13,140	AA16808	1 *Neotoma* fec. pellet
Ia-5 cm[b]	11,263 ± 85	12,960–13,310	13,130	AA16809	1 *Neotoma* fec. pellet
Ia-5 cm[b]	11,270 ± 135	12,820–13,390	13,130	AA14816	1 *Neotoma* fec. pellet

[a] *At two s.d. range calculated using CALIB 7.1.*

[b] *Dates from individual* Neotoma *or artiodactyl fecal pellets collected from the face of the mapped profile at approximately the middle of each stratigraphic unit (from Madsen, 2000).*

[c] *Dates from bone collagen from kangaroo rat (*Dipodomys *spp.) femora (from Terry and Novak, 2015).*

[d] *Dates obtained by Larry Benson from processed artiodactyl fecal pellets in an amalgam of all pellets from a particular stratigraphic unit (from Broughton et al., 2008).*

[e] *Dates were presumably on* Neotoma *fecal pellets obtained by Felisa Smith collected from processed pellets in an amalgam of all the pellets from a particular stratigraphic unit (from Smith and Betancourt, 2013).*

[f] *Dates for Stratum Ib and Stratum Ia were taken from the upper and lower 5 cm of the unit, respectively.*

provided a date range of 12.2–11.8 cal ka BP. The undisturbed microlaminae in Stratum I suggest the age of these fecal pellets can be used to date the associated faunal remains.

A substantial sample of fish was also derived from Stratum II at Homestead Cave and 21 radiocarbon dates for that unit (Terry and Novak, 2015) span the period from 12.3 to 9.5 cal ka BP (excluding an anomalous late date of 7.9 cal ka BP). That range encompasses the Gilbert episode that culminated at ~11.6 cal ka BP. Stratum II was excavated as a single unit without further sampling of materials from the profile as in Stratum I.

12.6.2 Summary and Deposition of the Homestead Cave Fishes

A total of 11 freshwater species, represented by 14,866 specimens, were identified from Homestead Cave (Table 12.6). Several lines of evidence suggest that owls were the agents that deposited the cave fauna: owl pellet cones were observed on the floor of the cave when the excavation began; the deposits contain numerous owl pellets; and many of the bones themselves, including fish bones from Stratum I, still have pellet material adhering to them. Evidence for human and carnivore involvement in the accumulation of the fauna is sparse, and no evidence exists for water-laid deposits (Grayson, 1998; Madsen, 2000). Moreover, quantitative analyses of skeletal part representation, bone fragmentation, and surface digestive damage of the Homestead Cave fish, in comparison to those variables derived from fish remains from modern owl pellets and many other depositional agents (humans, coyote [*Canis latrans*], diurnal raptors), strongly implicate large owls as the primary source of the fish materials in this site (Broughton et al., 2006).

Only two of the raptor taxa identified in the lower strata (I–III) of the deposit (Livingston, 2000; Wolfe and Broughton, 2016), routinely roost and nest in deep, open caves; Barn Owl (*Tyto alba*) and Great Horned Owl (*Bubo virginianus*). Although these owls mainly eat small mammals, they will scavenge fish carcasses and take fish exposed in very shallow water (Errington et al., 1940; Gallup, 1949; Bogiatto et al., 2006; Broughton et al., 2006). The maximum prey size that *B. virginianus*, the larger of the two species, can carry whole is ~1.5 kg (Marti, K., 1997, personal communication). As noted earlier, many of the fish specimens recovered from the cave come from very large individuals (>~2.6 kg estimated live weight; Broughton, 2000c). This evidence suggests that the owls did not take such fish whole, out of deep water, but instead scavenged them as parts. The maximum distance from roost to foraging areas reported for the owls is 5.6 km (Smith, 1971; Marti et al., 2005). Thus, aquatic habitats that supported fish, and that at least occasionally experienced substantial die-offs, likely existed within a radius of ~6 km or less from the cave during the periods of fish bone deposition.

TABLE 12.6 Numbers of Identified Fish Specimens per Taxon by Stratum, Homestead Cave[a]

	Stratum																					
Taxon	*I*	*Ia*	*Ib*	*I–II*	*II*	*III*	*IV*	*V*	*VI*	*VII*	*VIII*	*IX*	*X*	*XI*	*XII*	*XIII*	*XIV*	*XV*	*XVI*	*XVII*	*XVIII*	Total
Salmoninae	701	258	23	–	21	2	6	1	2	1	–	1	–	–	2	1	1	–	1	–	1	1022
cf. *Salvelinus confluentus*	1	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Oncorhynchus cf. *clarkii*	40	20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	60
Oncorhynchus clarkii	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Prosopium sp.	945	5944	449	–	111	19	32	–	10	6	3	5	2	2	–	1	4	–	–	2	1	7536
Prosopium cf. *spilonotus*	79	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	84
Prosopium spilonotus	27	10	3	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	41
P. spilonotus/ abyssicola	93	87	2	–	14	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	198
Prosopium abyssicola	2	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8
Prosopium gemmifer	225	499	37	–	15	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	778
Cypriniformes	1167	471	58	–	44	10	28	4	19	10	8	22	13	45	224	48	23	1	7	38	5	2245
Cyprinidae	34	35	3	–	3	3	5	–	1	1	–	1	–	2	14	4	2	–	–	12	–	120

Gila atraria	443	191	26	–	12	7	17	1	13	10	3	14	6	13	59	40	17	2	20	63	1	958
Richardsonius balteatus	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Catostomus sp.	900	299	24	–	19	4	20	2	7	6	7	5	2	3	25	6	9	2	1	2	–	1343
Catostomus ardens	134	22	7	–	2	–	4	–	1	1	–	1	–	–	5	1	1	–	–	–	–	179
Pantosteus virescens	–	–	–	–	–	–	–	–	1	–	–	3	1	–	–	–	–	–	–	–	–	5
Cottus sp.	53	178	9	–	13	5	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	259
Cottus cf. *bairdii*	0	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Cottus bairdii	2	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6
C. extensus/ echinatus	3	9	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14
Cottus extensus	0	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5
Total	4850	8045	641	1	257	51	114	8	54	36	21	52	24	65	330	101	57	5	29	117	8	14,866

[a] *Specimens identified are from the 1/4″ and 1/8″ sample fractions from Homestead Cave; nomenclature follows Eschmeyer (2015). The osteological criteria used to identify these specimens are discussed in Broughton (2000b,c).*

12.6.3 Strontium Ratios, the Homestead Fishes, and Paleolake Levels

Strontium has four stable isotopes and the ratios of two them, ^{87}Sr and ^{86}Sr, are widely used as tracers in geological analyses. In the context of lake level analyses, it has been established that ^{87}Sr/^{86}Sr ratios of lake water are identical to the ratio of any carbonate (eg, tufa, shell) or apatite (eg, fish bone) growing in that water—the ^{87}Sr/^{86}Sr ratio of paleowaters can thus be reconstructed from analysis of these materials (Quade, 2000a,b; see also Hart et al., 2004). To reconstruct paleolake levels from ^{87}Sr/^{86}Sr ratios of fossil material requires either: (1) lake systems with multiple basins, each fed by rivers with unique ^{87}Sr/^{86}Sr ratios, as in Lake Bonneville; or (2) inflowing rivers in which the ^{87}Sr/^{86}Sr ratios change with recharge fluctuations. The main rivers in this setting are the Bear (^{87}Sr/^{86}Sr $=$ 0.71926) in the north and the Beaver/Sevier (^{87}Sr/^{86}Sr $=$ 0.7074) in the south (Jones and Faure, 1972; Bouchard, 1997). Analysis of tufas and shell from the high (Provo and Bonneville) shorelines shows that the ^{87}Sr/^{86}Sr ratios of paleolake waters in an integrated Lake Bonneville were 0.7114–0.7119, which represents some average of all values of rivers feeding into the lake (Quade, 2000a).

During the terminal Pleistocene when Lake Bonneville dropped below the Old River Bed threshold at 1390 m, it segmented and the ^{87}Sr/^{86}Sr ratio of at least some component water bodies shifted toward the value of local river inputs. This “splitting” event is clearly recorded in the ^{87}Sr/^{86}Sr ratios of carbonates associated with the smaller terminal Pleistocene lake in the southern basin. Shells from the southern basin filled by paleolake Gunnison have low ratios (0.7098), consistent with input from the Sevier/Beaver River. Tufa and shell from the northern basin collected from what was interpreted as the Gilbert shoreline give ratios of 0.7120–0.7144 (see Oviatt (2014) for discussion on the lack of evidence for a basin-wide Gilbert shoreline). Mass balance estimates from modern rivers suggest that these elevated ratios are not the result of isolation of the northern basin from the southern rivers (Bouchard, 1997). Instead, the ^{87}Sr/^{86}Sr ratio of the Bear River, the main source of Sr in the northern basin, may have shifted toward higher values as the lake dropped. Although the exact causes are unclear, the key point here is that lower Gilbert shoreline elevations (ie, ~1300 m) in the northern basin yield consistently higher ^{87}Sr/^{86}Sr ratios (0.7120–0.7144) than those of the higher, integrated lake (0.7114–0.7119) (Quade, 2000a).

The lake level in which the Stratum I fish lived can be broadly estimated by the ^{87}Sr/^{86}Sr ratios of six Stratum I fish specimens. All the fish analyzed, including *C. ardens*, *G. atraria*, and *O. clarkii* returned ^{87}Sr/^{86}Sr ratios between 0.7125 and 0.7129 (Broughton et al., 2000; Quade, 2000b). These values are markedly distinct from those of high-shoreline tufas and shell (0.7114–0.7119), and are close to values from materials derived from Gilbert shoreline features. The presence of freshwater fish taxa with such high

$^{87}Sr/^{86}Sr$ ratios implies the presence of a relatively shallow but freshwater lake within the raptor foraging radius (~6 km) of the cave between 13.1 and 11.8 cal ka BP.

12.6.4 Change in Fish Size

The demographic structure of vertebrate populations is determined by age-specific patterns of fertility and mortality. Variation in these parameters can not only mechanically alter the distribution and abundance of individuals across age classes in a population, but can provide the selective context for the emergence and persistence of different life history strategies (eg, Gadgil and Bossert, 1970; Stearns, 1992; Charnov, 1993). In the context of intermountain fishes, Smith (1981) developed a specific model linking intraspecific variation in life-history strategies to local regimes of habitat stability and adult mortality. This model, consistent with general predictions from life history theory (eg, Roff, 1984; Charnov, 1993), has implications for change in fish-body size in populations that endure high rates of adult mortality:

> *Many intermountain minnows, suckers, and trouts are selected locally for large size by increased adult survival and consequent late reproduction in large habitats. Annual fluctuations that reduce habitats seasonally, thus causing heavy mortality, lead to persistence of phenotypes that reproduce early at the expense of later growth … When adult mortality is low individuals leave more descendants by growing larger and producing more young over several seasons.*
>
> (Smith, 1981, pp. 126, 162)

Positive relationships between habitat size, as a measure of environmental stability, and maximum adult size have been documented in many western fish species (Smith, 1981), including several of the cypriniform taxa represented at Homestead Cave, namely, *G. atraria* and *P. virescens*. Insofar as the Homestead fish assemblage resulted from a progression of die-offs and elevated levels of adult mortality associated with ever increasing temperature and salinity we anticipate a shift to smaller-sized fishes across the period over which the lake lost its fish.

Vertebrae from Cypriniformes identified from Stratum Ia and Ib were selected for analysis of size change (Table 12.7). The maximum diameters of vertebral centra, as a measure of size, differ distinctively between Stratum Ia and Ib; the later deposit (Ib) has a smaller maximum size and exhibits a significantly smaller mean size than Stratum Ia (Mann–Whitney $U = 8546.5$, $P < 0.05$). Since the cypriniform vertebrae were not differentiated below the order level, it is possible that this decrease in size is reflecting species composition change—for instance, increasing proportional abundances of the smaller *G. atraria* relative to the larger *C. ardens*. However, no significant difference occurs in the relative abundance of these taxa between Stratum Ia and Ib ($X^2 = 1.09$, $P = 0.30$).

TABLE 12.7 Vertebral Widths (mm) of the Stratum I Cypriniformes

Stratum	*N*	Mean[a]	Range	Standard Deviation
Ia	365	4.40	1.26–9.20	1.46
Ib	56	4.02	1.74–7.62	1.38

[a] *As a frame of reference, the mean vertebral widths of a modern 450 mm SL* Catostomus ardens *and a 202 mm SL* P. virescens *are 8.76 and 2.84 mm, respectively.*

Since fish size changed in the direction predicted for conditions of elevated adult mortality, the fauna appears to have accumulated over a period of time long enough for size change to occur, that is, over several episodes of substantial mortality, perhaps seasonally as the lake trended downwards.

12.6.5 Change in Taxonomic Abundances

Change in the relative abundance of fish taxa that can and cannot tolerate elevated water temperature or total dissolved solids, especially salinity, can also inform on lake-level fluctuations across the period represented by the Stratum I deposits. Of the taxa represented at the cave, *O. clarkii* and *G. atraria* are the most tolerant of higher salinities—up to ~19,000 mg/L total dissolved solids (Westenfelder et al., 1988; Nelson and Flickinger, 1992; Dickerson and Vinyard, 1999; Wright, 2009) and these taxa are significantly overrepresented in Stratum Ib, compared to Stratum Ia ($X^2 = 4.31$, $P < 0.05$; Table 12.8). The fishes from the deposit that are tolerant of warmer (>~27°C) water temperatures, *C. ardens* and *G. atraria* (Beitinger et al., 2000; Broughton, 2000c; and references therein) are significantly overrepresented in Stratum Ib as well ($X^2 = 7.41$, $P \ll 0.01$; Table 12.8). These changes are consistent with other data that suggest the assemblage resulted from a series of die-offs as salinity and temperature exceeded the tolerances of the various taxa making up the Lake Bonneville fauna.

12.6.6 Fish Die-Offs of Terminal Pleistocene Lake Bonneville: 13.1–11.8 cal ka BP

The fish materials from Homestead Cave are clearly concentrated in Stratum I (Table 12.4)—they account for over 26% of the vertebrate assemblage in this unit but comprise, in most cases, far less than 1% of the fauna in the higher strata. To further pinpoint the stratigraphic break in the cave deposits, after which fish remains became far less abundant, we examined the distribution of fish materials within Stratum I itself. In the bulk sediment sample taken from the lower 10 cm of the 30-cm-thick Stratum I, fish comprise

TABLE 12.8 Numbers of Identified Specimens for Salinity- and Temperature-Tolerant and Intolerant Fish Taxa from Stratum I, Homestead Cave

	Stratum		Stratum	
Taxon	*Ia*	%	*Ib*	%
Salinity tolerant				
Gila atraria	226	3.0	29	4.9
Salmoninae	279	3.7	23	3.9
Total	505	6.7	52	8.9
Salinity intolerant				
Prosopium	6551	86.5	491	84.2
Catostomus	321	4.2	31	5.3
Cottus	197	2.6	9	1.5
Total	7069	93.3	531	91.1
Temperature tolerant				
Gila atraria	226	3	29	5.0
Catostomus	321	4.2	31	5.3
Total	547	7.2	60	10.3
Temperature intolerant				
Prosopium	6551	86.5	491	84.2
Salmoninae	279	3.7	23	4.0
Cottus	197	2.6	9	1.5
Total	7027	92.8	523	89.7

23.5% (807 of 3434 specimens) of the entire vertebrate faunal assemblage. By contrast, fish comprise only 0.02% (10 of 3896 specimens) of the vertebrate materials from the upper 10 cm—a figure very similar, with several noteworthy exceptions, to the relative abundance of fishes throughout the rest of the column. The difference in the frequencies of fish and nonfish vertebrate specimens across these divisions is highly significant ($X^2 = 955.34$, $P \ll 0.0001$). Fish remains are essentially absent from the upper one-third of Stratum I and are confined to Stratum Ia and the lowest microlaminae of Stratum Ib. The die-offs of the Lake Bonneville fishes thus appear to have begun at about 13.1 cal ka BP but ended prior to ~11.8 cal ka BP.

Occupancy of a shallow-elevation lake (or lakes) perhaps near the Gilbert episode altitude or lower is suggested from $^{87}Sr/^{86}Sr$ ratios of the Stratum I fish, and the data on size and relative taxonomic abundance suggest the fauna resulted from a series of die-offs that occurred when the lake dropped near this level. Insofar as fish deposition began at 13.1 cal ka but stopped no later than 11.8 cal ka, the Stratum I fauna was most likely derived from Lake Bonneville during the final centuries of the regressive phase and from the postregressive phase when lake elevations were near those of modern Great Salt Lake. Most notably, it is at this time when the brackish tolerant ostracod species, *Limnocythere sappaensis*, first appears in the Lake Bonneville sequence and is indicative of lower lake levels and increases in water temperature and salinity (Oviatt, 2015b). Brine shrimp (*A. franciscana*) cysts and pellets that mark hypersaline conditions do not, however, appear until after the Gilbert episode during the earliest Holocene (11.5–10.2 ka BP).

12.6.7 Fish Recolonize the Gilbert Episode Lake

Although fish are largely absent from the upper portion of Stratum Ib, as noted earlier, suggesting fish were eliminated from the lake sometime before ~11.8 cal ka, fish are present again in the Stratum II deposit (NISP = 257), and comprise 3.0% of the vertebrate fauna from that unit. These materials thus appear to represent a return of fish to the lake basin. Recent research suggests that Gilbert episode lake levels peaked at 11.6 cal ka BP (Oviatt, 2014) and that date is bracketed by the 21 radiocarbon assays from Stratum II at Homestead Cave that range from 12.3 to 9.5 cal ka BP. Stratum II thus includes the Gilbert episode lake but also the first two millennia (11.5–9.5 cal ka BP) of the hypersaline Great Salt Lake.

Analyses of ostracodes from Gilbert episode sediments also suggest the lake may have been brackish, again based largely on the presence of *L. sappaensis*, although that taxon occurs in waters with a range of total dissolved solids between about 500 and 10,000 mg/L. Water at the very low end of this range (<~1000 mg/L is fresh water) would have been tolerable for the entire Lake Bonneville fish fauna and the more salinity-tolerant taxa (ie, *O. clarkii*, *G. atraria*) would have been able to readily withstand values at the high end (Nelson and Flickinger, 1992; Weber-Scannell and Duffy, 2007; Wright, 2009). Indeed, both *O. clarkii* and *Siphateles bicolor* (Tui Chub) survive in Walker Lake, Nevada, where total dissolved solids heavy in sodium have ranged from 13,000 and 19,000 mg/L since the 1990s. (Tui Chub is a close relative of Utah Chub with similar adaptations and histories.) Many other minnows readily tolerate water in excess of 4000 mg/L (Pimentel and Buckley, 1983; Nelson and Flickinger, 1992).

Although the sample size of fish bone from Stratum II is considerably smaller than that from Stratum I, the assemblage is nonetheless represented by 7 of the 11 species identified from the latter unit. This suggests that nearly the entire Lake Bonneville fish fauna may have recolonized the basin during the deposition of the Gilbert-aged sediments of Stratum II. It is possible, however, that the fish in Stratum II owe their presence to limited mixing with Stratum I.

The mixing issue can, however, be directly addressed through an examination of the relative taxonomic abundance of the Stratum I and II faunas. Insofar as taxa more resilient to high water temperature and salinity were able to establish larger populations during the interval including the Gilbert episode, its regressive phase, and the emergence of Great Salt Lake, the resulting Stratum II fauna should exhibit higher relative frequencies of these fishes. If, on the other hand, the fish materials from Stratum II were derived from mixing with Stratum I, we would not expect such differences.

Chi-square tests document significant increases in the relative abundance of temperature- and salinity-tolerant fish in Stratum II compared to both Stratum Ia and Ib (Tables 12.9 and 12.10). Moreover, a significant linear increase (using Cochran's test of linear trends; see Cannon, 2001) in the relative abundance of temperature- and salinity-tolerant fish specimens is indicated across the full sequence of Stratum Ia, Ib, and II (Table 12.10). These analyses strongly suggest that the Stratum II fish materials did not result from bioturbative mixing but were instead derived from the foraging behavior of owls using fish that resulted from die-offs of the Gilbert episode lake(s).

12.6.8 Lake Level Fluctuations of Great Salt Lake

The Holocene history of Great Salt Lake remains poorly understood, although recent summaries of the limited available data suggest the lake may not have exceeded much above historic period altitudes (about 1280 m) over the last ~10.2 ka years (Oviatt, 2014; Oviatt et al., 2015). Several lake transgressions during the Holocene have, however, been proposed based in part on inferred climatic conditions and limited core and shoreline data (eg, Currey et al., 1984; Murchison, 1989b; Madsen et al., 2001). Most recently, Patrickson et al. (2010) suggested an early Holocene highstand at 1360 m based on a 7.51 ± 0.04 ^{14}C ka BP (8.2–8.4 cal ka BP) date from Stansbury Island lacustrine sediments, although others interpret the deposit as colluvial (Oviatt et al., 2015). Late Holocene transgressions have also been proposed, most notably one between ~3.2 and 2.0 cal ka BP that may have transgressed to a highstand of 1287 m and flooded the Great Salt Lake Desert (Mehringer, 1985; McKenzie and Eberli, 1987; Murchison, 1989b). A transgression near ~1.0 cal ka BP has also been inferred from shoreline data (ie, the "Fremont beach") that suggest the lake reached an elevation of ~1283 m (Currey et al., 1984; Murchison, 1989b; Currey, 1990; Madsen et al., 2001); this episode may be associated with increased precipitation and is synchronous with the agriculturally based, Fremont cultural complex of the eastern Great Basin and Colorado Plateau (Madsen and Simms, 1998).

TABLE 12.9 Numbers of Identified Specimens for Salinity- and Temperature-Tolerant and Intolerant Fish Taxa from Stratum II, Homestead Cave

	Stratum	
Taxon	*II*	**%**
Salinity tolerant		
Gila atraria	15	7.1
Salmoninae	21	9.9
Total	36	16.9
Salinity intolerant		
Prosopium	141	66.2
Catostomus	21	9.9
Cottus	15	7.0
Total	177	83.1
Temperature tolerant		
Gila atraria	15	7.0
Catostomus	21	9.9
Total	36	16.9
Temperature intolerant		
Prosopium	141	66.2
Salmoninae	21	9.9
Cottus	15	7.0
Total	177	83.1

The *G. atraria* (Utah Chub) record from Homestead Cave provides an additional source of information on the Holocene history of Great Salt Lake (Broughton et al., 2000). Although *G. atraria* has never inhabited Great Salt Lake historically, this species is tolerant of relatively high salinity levels and warm-water temperatures and is the only member of the Lake Bonneville fauna that now occupies low-elevation creeks, springs, and marshes of the northern Bonneville basin. However, based on genetic analyses of modern populations of *G. atraria* in the region, Rosenfeld (1991, p. 89) suggested that during wetter periods of the Holocene, Great Salt Lake may have become sufficiently diluted to support this species. Since Great Salt Lake sediment cores

TABLE 12.10 **Chi-Square Test Statistics for Comparisons of the Abundance of Temperature- and Salinity-Tolerant and Intolerant Taxa for Strata I and II, Homestead Cave**

	Strata		
Taxonomic Abundance Groups	*Ia and II*	*Ib and II*	*Ia, Ib, and II*[a]
Temperature tol./intol.	28.02*	6.43***	31.87*
Salinity tol./intol.	33.56*	10.11**	31.90*

*Significant at $P<0.0005$.
**Significant at $P<0.001$.
***Significant at $P<0.01$.
[a] *Test statistic is for the linear trend component of the total chi-square (see Cannon, 2001).*

show no late Holocene gaps in deposition of brine shrimp, it is possible that fish moved within plumes of freshwater that entered the basin from input rivers to the east and floated west above the higher density hypersaline core of Great Salt Lake. Even if *G. atraria* could not have invaded Great Salt Lake during wetter cycles, the extent of local fresh water marshes should have varied with regional moisture and the elevation of the lake. In any case, change in the Holocene abundance of *G. atraria* near the cave should be linked to higher elevations of Great Salt Lake.

Materials representing the Lake Bonneville fish fauna occur in extremely low frequencies above Stratum II and likely owe their presence in those contexts to limited mixing. However, the *G. atraria* materials in these upper strata may be derived not only from limited mixing with Stratum I and II but also from Holocene-aged scavenging by owls. If owls deposited substantial numbers of *G. atraria* during Holocene transgression–regression cycles of Great Salt Lake, then major frequency peaks of *G. atraria* within the cave deposits should signal them. These data cannot be used to estimate the absolute elevations of the lake and may be more sensitive at registering highstands that were persistent over extended periods—that would allow sustained fish colonizations—rather than highly ephemeral (eg, seasonal) ones that may have even briefly reached considerable altitudes. In other words, high amplitude fluctuations even with high average depths would preclude fish occupation of the lake. The Holocene sequence of deposits at Homestead Cave (Strata III–XVIII) is constrained by 67 radiocarbon dates that span the period from 9.9 to 0.7 cal ka BP (Table 12.5).

G. atraria shows two main peaks in both absolute abundance and density (*G. atraria* NISP/L) in the Holocene strata at the cave, first within Stratum XII and second within Strata XVI and XVII (Table 12.6; Fig. 12.11). These strata provided radiocarbon dates of 3.6, and 1.1 and 0.9 cal ka BP, respectively. Insofar as the chub record is reflecting periods of sustained higher

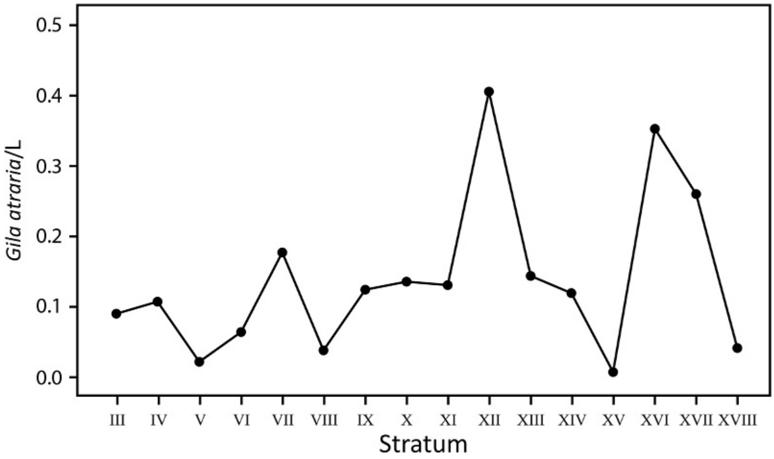

FIG. 12.11 Density (NISP/L) of Utah Chub (*Gila atraria*) by stratum (exclusive of Strata I and II) at Homestead Cave. Specimens identified as "Cyprinidae" are included with *Gila atraria* here because that species represents well over 99% of the identified cyprinids at Homestead Cave.

levels of Great Salt Lake, it suggests that such transgressions were limited to the late Holocene. Moreover, the dates associated with the chub spikes align with previous suggestions based on core and shoreline data for highstands between ~3.4 and ~2.0 cal ka, and again near 1.0 cal ka.

No suggestion occurs from the fish record, however, for a post-Gilbert early Holocene (8.4–8.2 cal ka BP) highstand of Great Salt Lake—strata IV through VI date to this period and chub densities are consistently low in these units. This conclusion was also reached by recent summaries of the shoreline, outcrop, and offshore deposition data and may have paleoclimatic implications (Oviatt et al., 2015). Although climate models and paleoclimatic proxy data from the Bonneville basin and adjacent areas indicate enhanced seasonality and warm and dry summer conditions during the early Holocene (eg, Broughton, et al., 2008; Doner, 2009; Moser and Kimball, 2009; Lundeen et al., 2013), many small mammal and plant macrofossil records have been read to suggest cooler and moister climate at this time (eg, Grayson, 1998, 2000, 2011; Rhode, 2000; Schmitt et al., 2002; Schmitt and Lupo, 2012). Oviatt et al. (2015) have recently proposed a reconciliation of these apparent inconsistencies. Specifically, they suggested that early Holocene climate was dry, but Lake Bonneville-derived groundwater—trapped in the fractured limestone of small interior basin ranges—was steadily discharged, feeding local plant communities at this time. The release of water stored in Homestead Knoll, for instance, may have been enough to produce localized, mesic refugia of early Holocene age for plant and small mammal communities, but insufficient to produce a sustained lake transgression.

Not only is this hypothesis consistent with the Homestead fish record that shows no indication of a post-Gilbert highstand during the early Holocene, but it accords well with our current understanding of Holocene variation in artiodactyl populations in the region. The primary taxa that occur in the Bonneville basin are mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and bighorn sheep (*Ovis canadensis*), and it is unlikely that the restricted spatial extent of groundwater-fed vegetation in the early Holocene would have been enough to affect substantial improvements in the overall quality and quantity of forage to the wide-ranging artiodactyl herds. The high seasonality and dry climate of the early Holocene is, thus, anticipated to have depressed regional artiodactyl population densities.

In addition to a rich record of small vertebrates, Homestead Cave has also produced a singular high-resolution paleontological record of artiodactyl abundances in the region in the form of fecal pellets. Insofar as the number of fecal pellets deposited in the cave reflect the frequency of artiodactyl visits, and that this is an index of the relative abundance of those animals on the landscape, trends in fecal pellet densities (pellets/L) can be used to track variation in the regional artiodactyl population size.

The late Holocene spikes in chub abundances at Homestead Cave (eg, at 3.6 and 1.0 cal ka) are, in fact, closely aligned with dramatic increases in the density of artiodactyl fecal pellet abundances in the Homestead Cave sediments, the latter likely reflecting moisture-driven increases in regional artiodactyl populations at these times (Broughton et al., 2008). As with the density of chub bones, fecal-pellet densities are noticeably depressed in the early Holocene strata of the cave. Moreover, numerous Great Basin archeological faunas exhibit significant increases in the abundance of artiodactyl specimens at the times that chub bones and fecal pellets increase, suggesting that prehistoric human foragers took full advantage of increasing encounters with large game that resulted from ameliorating climate (Byers and Broughton, 2004; Broughton et al., 2008, 2011).

12.7 SUMMARY AND CONCLUSIONS

The study of Bonneville basin fishes with a comprehensive interpretive approach began with Hubbs and Miller in the mid-20th century. Although they made significant strides in our understanding of regional fish biogeography and paleohydrology, they recognized that a deeper integration with geology and a far richer fish paleontological record would lead to still greater advances. Still, neither we suspect could have envisioned that strontium derived from fish bones could be used to estimate the depth of the water the fish lived in or that DNA extracted from modern tissues could inform on species divergence times and places. They also surely could not have dreamed that generations of owls living in the heart of the Bonneville basin at Homestead Cave had already fortuitously assembled a relatively fine-grained, 13,000-year terminal Pleistocene and Holocene fish sequence that could provide a series of inferences on the dynamics of fish populations in relation to climate-based fluctuations in lake levels.

With these methodological advances, the substantial growth of the fish-fossil record, and increasing interdisciplinary work, our understanding of the dynamics of the late Quaternary ichthyofauna of the Bonneville basin has, indeed, grown. As we report here, the fish remains from 10 Bonneville basin sites dating to the late Pleistocene or early Holocene have now been studied, yielding a total 16,172 identified specimens representing 13 of the 21 species known for the drainage—these data show that the fauna was similar to the modern assemblage from Bear Lake, a cold, deep lake on the Utah–Idaho border.

The conjoined DNA and pre-Bonneville fossil fish records suggest extra-basinal connections that offer insights into the antiquity of the region's unique fish fauna. Although Hubbs and Miller (1948) were tempted to explain many of the Bonneville fish species as arrivals through the outlet at Red Rock Pass, the current data suggest that nearly the entire fish fauna predates Lake Bonneville, but is not as old as the Cache Valley Member of the Salt Lake Formation.

The Homestead Cave fish sequence has provided detailed insights on the nature and dynamics of the Bonneville basin ichthyofauna as lake levels fluctuated over the last ~13,000 years. The subfossil fish bones, accumulated by large owls, were concentrated in the lowest strata of the deposit and are represented by 11 of the 13 species that have been derived from Lake Bonneville sediments. The $^{87}Sr/^{86}Sr$ values from the Stratum I fish suggest they were derived from a low-elevation lake and a significant decrease in the size of cypriniform vertebrae documented across two divisions of Stratum I, suggests the fauna resulted from a process involving a series of die-offs. Taxa tolerant of higher salinities (*O. clarkii* and *G. atraria*) and temperatures (*C. ardens* and *G. atraria*) are more abundant in the upper division of Stratum I than in the lower section of this deposit. The terminal regressive and/or postregressive die-offs of the Lake Bonneville fish fauna appear to have occurred rapidly beginning at ~13.1 cal ka, and fish were eliminated from the lake no later than 11.8 cal ka. A return of nearly the entire Lake Bonneville fish fauna, although skewed to higher abundances of salinity- and temperature-tolerant taxa, occurs in the Stratum II deposits, with dates ranging from 12.3 to 9.5 and is most consistent with recolonization during the Gilbert episode.

No post-Gilbert highstands in the early Holocene are registered in the fauna, but frequency peaks of Utah Chub in the upper strata of the cave imply two prominent late Holocene transgressions of Great Salt Lake, one at ~3.6 cal ka and the other at ~1.0 cal ka. Both periods are associated with apparent expansions of artiodactyl herds in the Bonneville basin and the human hunting of those animals. The final moisture pulse at ~1.0 cal ka is coincident with the agriculturally based Fremont cultural complex of the eastern Great Basin and Colorado Plateau.

ACKNOWLEDGMENTS

We thank Virginia Butler, Charles Oviatt, and John Shroder for very helpful comments on the chapter; James Mead for help with the Smith Creek Cave fauna; Bryce Nielson and Scott Tolentino for providing fish reference specimens from Bear Lake; Marlene Lambert-Tempest for Figs. 12.2 and 12.3; Charles Oviatt for Fig. 12.9; Shawn Miller and Isaac Hart for assistance with Figs. 12.1 and 12.11, respectively; and David Madsen for all his work on the Homestead Cave and Cathedral Cave projects, including the recent compilation of the Homestead radiocarbon dates we present here in Table 12.5. Figs. 12.2–12.7 are reprinted here with permission from the American Society of Ichthyologists and Herpetologists. The Homestead Cave analysis was supported by grants from the Legacy Project, Department of Defense, and Hill Air Force Base.

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