

Ostracode endemism in Bear Lake, Utah and Idaho

Jordon Bright

Department of Geology, Box 4099, Northern Arizona University, Flagstaff, Arizona 86011, USA

ABSTRACT

Bear Lake, Utah and Idaho, is one of only a few lakes worldwide with endemic ostracode species. In most lakes, ostracode species distributions vary systematically with depth, but in Bear Lake, there is a distinct boundary in the abundances of cosmopolitan and endemic valves in surface sediments at ~7 m water depth. This boundary seems to coincide with the depth distribution of endemic fish, indicating a biological rather than environmental control on ostracode species distributions. The cosmopolitan versus endemic ostracode species distribution persisted through time in Bear Lake and in a neighboring wetland.

The endemic ostracode fauna in Bear Lake implies a complex ecosystem that evolved in a hydrologically stable, but not invariant, environmental setting that was long lived. Long-lived (geologic time scale) hydrologic stability implies the lake persisted for hundreds of thousands of years despite climate variability that likely involved times when effective moisture and lake levels were lower than today. The hydrologic budget of the lake is dominated by snowpack meltwater, as it likely was during past climates. The fractured and karstic bedrock in the Bear Lake catchment sustains local stream flow through the dry summer and sustains stream and ground-water flow to the lake during dry years, buffering the lake hydrology from climate variability and providing a stable environment for the evolution of endemic species.

INTRODUCTION

Bear Lake, Utah and Idaho, is an interesting lake for several reasons. It is one of the most long-lived extant lakes in North America, if not *the* most long-lived extant lake on the continent (Bright et al., 2006; Colman, 2006). The limestone- and dolomite-rich watershed surrounding the lake generates an unusual water chemistry within the lake (Dean et al., 2007, this volume). Throughout much of the Holocene (and other relatively arid, Holocene-like climates) Bear Lake has precipitated aragonite as the dominant carbonate mineral (Bright et al., 2006; Dean et al., 2006, Dean, this volume), which is also unusual for a high-altitude, northern temperate lake (Dean et al., 2007). Bear Lake

also contains four endemic fish species (Sigler and Sigler, 1996), which, excluding the Great Lakes basin (Smith, 1981; Smith and Todd, 1984; Reed et al., 1998), is the largest number of endemic fishes in any extant North American lake. Recent studies have suggested that the speciation of the Bear Lake whitefish is a recent event, and may still be occurring today (Vuorinen et al., 1998; Toline et al., 1999; Miller, 2006).

Bear Lake also contains an endemic deep-water ostracode fauna. Cosmopolitan ostracodes are uncommon in the lake and are primarily restricted to the shallowest littoral zone or lake margins, which again is unusual. Lakes normally exhibit an ostracode distribution associated with environmental change along a depth gradient from the lake margin through the littoral zone and

into the hypolimnion (e.g., Kitchell and Clark, 1979; Mourguiart and Montenegro, 2002). These biofacies owe their existence to changes in species productivity along the depth gradient. Segments of the gradient may include wetlands, springs, and the upper, middle, sublittoral, and profundal zones. Rather than having a continuum of ostracode species assemblages from the lake margins into the profundal zone, modern Bear Lake exhibits an apparent and relatively abrupt change in the ostracode species assemblage at a water depth of ~7 m. This paper investigates the ostracode distributions, both modern and ancient, within Bear Lake and the surrounding area, and provides two hypotheses to explain those distributions.

BACKGROUND

Bear Lake

Bear Lake is an oligotrophic, alkaline (pH ~8.4; Dean et al., 2007, this volume) lake straddling the Utah-Idaho border (Fig. 1). The lake resides in a half-graben situated between the Bear River Range and the Bear Lake Plateau. The lake's elevation is ~1805 m above sea level and it has a surface area of ~287 km², a volume of ~8.1 × 10⁹ m³, and a maximum depth of ~65 m. Geophysical studies show a thick sedimentary sequence below the lake (Denny and Colman, 2003), with sediments possibly as old as 6 Ma (Colman, 2006).

Bear Lake's outline is smooth, without any prominent coves or bays (Smart, 1958). The littoral zone is rocky and exposed to persistent wind and wave action. Rooted plants are able to grow only in the most protected shore areas (Smart, 1958; Lamarra et al., 1986). The deepest area of the lake (~65 m) is on the eastern side between North and South Eden Canyons (Fig. 1). The lake bottom slopes 0.3° to 0.5° toward this deepest point. The bottom of Bear Lake is very flat and regular with distinctive sediment characteristics. Sandy lake-bottom sediments extend out to a water depth of ~12 m. A sand-silt bottom is prevalent between water depths of ~12 and ~30 m, and a silt-marl bottom is prevalent at water depths >~30 m (Smart, 1958).

Local climate is characterized by a mean annual temperature (MAT) near the lake of ~6 °C and a mean annual precipitation (MAP) of ~316 mm (MAT and MAP are long-term averages (16–95 yr) from Lifton, Idaho, Bear Lake State Park, and Laketown, Utah; <http://wrcc.sage.dri.edu/summary/climsmid> and [/climsmut.html](http://wrcc.sage.dri.edu/summary/climsmut)). Annual precipitation throughout the region is dominated by snow. Summers are warm and dry. Evaporation rates at Bear Lake are poorly known. Type A pan measurements at Lifton, Idaho, place the evaporation rate near 1000 mm yr⁻¹ (www.wrcc.dri.edu/CLIMATEDATA.html), but a more intensive evaporation study at the lake suggests that the rate may be closer to ~600 mm yr⁻¹ (Amayreh, 1995).

The catchment area of Bear Lake contains numerous flowing springs, wetlands, small to moderate-sized streams, and the Bear River. The streams and springs on the west side of Bear Lake are cold and dilute (total dissolved solids [TDS] ~250–350 mg

L⁻¹), whereas those on the east side are primarily cold and more saline (TDS ~400–2000 mg L⁻¹) (Bright, this volume). A small hot spring complex (47 °C) discharges at the northeast corner of the lake (Fig. 1). The TDS of Bear River base flow was 550 mg L⁻¹ during the summer of 2000.

Since ca. A.D. 1912, flow from the Bear River has been seasonally diverted into Mud Lake and from there into Bear Lake for storage and then withdrawn for irrigation and power generation. The diversion of Bear River water into Bear Lake both reduced the lake's TDS and changed its solute composition by dramatically increasing the alk:Ca ratio (Dean et al., 2007, this volume). Bear Lake's TDS was ~1100 mg L⁻¹ ca. 1912 (Birdsey, 1989) and is ~550 mg L⁻¹ today. Prior to Bear River diversion, local inflow, including direct precipitation, was sufficient to maintain limited outflow (McConnell et al., 1957). A hydrologic balance model developed by Lamarra et al. (1986) suggests that Bear Lake would have overflowed throughout the 1970s and into the early 1980s if the lake had been left in its natural state.

The Mud Lake wetlands were sustained by local stream flow as well as by spring and diffuse groundwater discharge from the surrounding highlands prior to Bear River diversion. In the past, Mud Lake water may have entered Bear Lake through the sandbar that divides the two water bodies (McConnell et al., 1957). The sandbar was reinforced during the 1912 Bear River diversion and Mud Lake water now enters Bear Lake through an inlet gate near Lifton. Groundwater exchange through the sandbar between Mud Lake and Bear Lake probably still occurs, however.

Ostracode Ecology

Ostracodes are microscopic, aquatic, bivalved crustaceans. Their life cycles depend, in part, on environmental parameters that link species occurrences to climate and hydrology. They are sensitive to three primary environmental factors: (1) chemical hydrology (hydrochemistry), including both the general solute composition, but especially the total carbonate alkalinity (alk) to calcium ratio (alk/Ca), and, secondarily, the total dissolved solids (TDS) (Forester, 1983; Smith, 1993; Curry, 1999); (2) physical hydrology, including the general setting, e.g., lakes, springs, and streams (Curry, 1999), as well as the nature and variability of the setting's water properties (e.g., permanence), and of its ground-, surface-, and atmospheric-water interchange; and (3) water temperature as determined by the annual water-temperature profile derived from the resident air masses and/or by the groundwater flow path(s) (Forester, 1985, 1991a; Roca and Wansard, 1997). A study by Curry (1999) did not show any significant correlation between water temperature and the distributions of several common North American ostracode species, however.

Ostracode occurrences in lakes are primarily linked to climate through their coupled water-air-temperature dependent biogeographic distributions and their effective-moisture driven hydrochemical requirements (Delorme, 1969; DeDecker, 1981; Forester, 1987) and are secondarily linked to physical hydrology. A lake's physical hydrology can significantly modify the climate

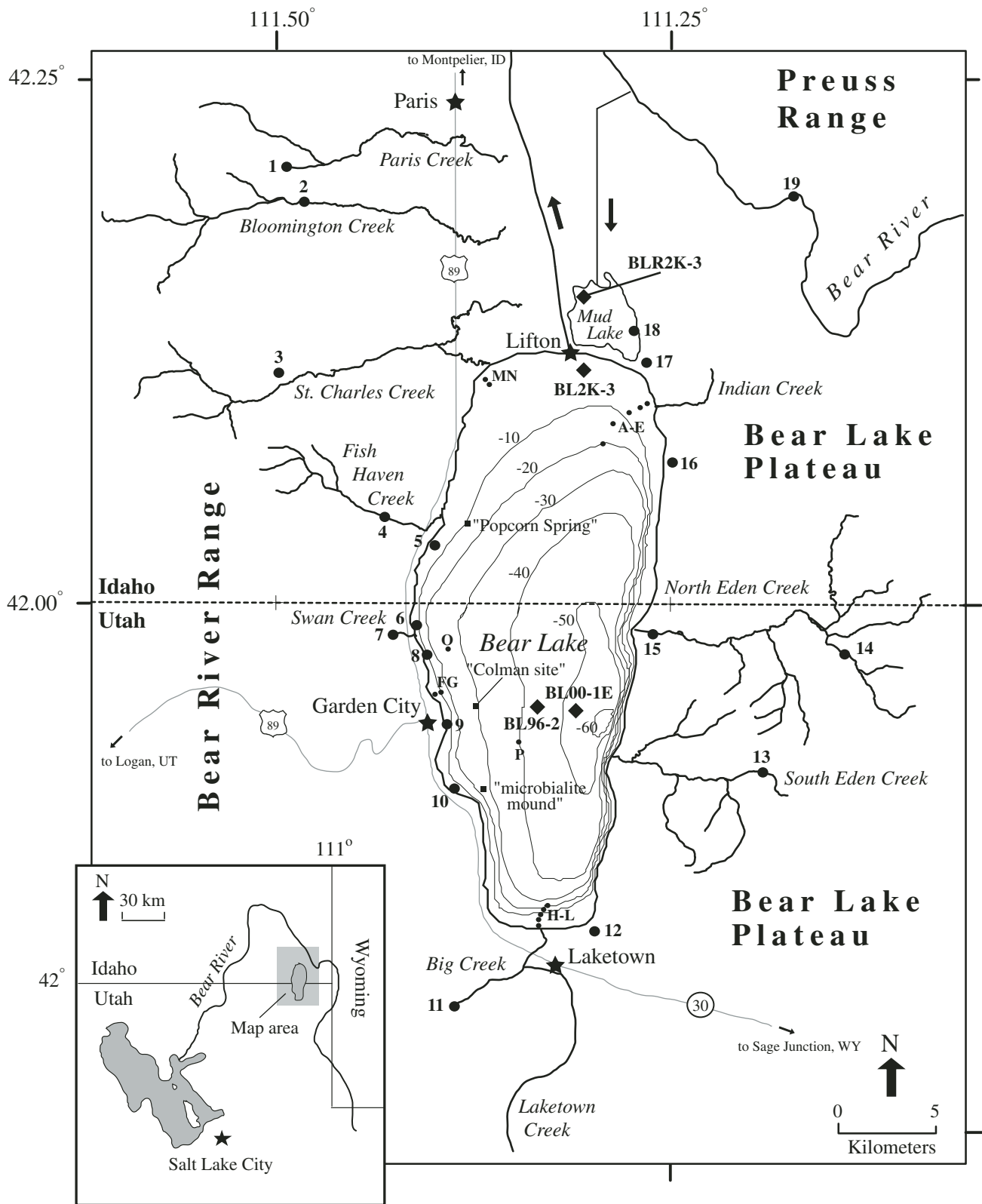


Figure 1. Bear Lake locality map. Bathymetry lines are in 10 m increments. Numbered sites and site P were sampled for ostracodes from 1999 to 2004. Lake sites A–O were sampled for ostracodes in 1999. Core localities labeled BLR2K-3, BL2K-3, BL96-2, and BL00-1E. Sites P, “Colman site”, and “Popcorn Spring” are methane seeps. “Microbialite mound” is a probable sublacustrine spring.

signature by, for example, groundwater through-flow or changes in the relative contributions of multiple groundwater sources (Smith et al., 2002a).

MATERIALS AND METHODS

The ostracode data come from numerous grab samples from springs and wetlands around the lake, ~30 Eckman surface grab samples from the lake floor, and four lake sediment cores, BLR2K-3, BL2K-3, BL96-2, and BL00-1 (Fig. 1). The lake-bottom sediment recovered in the Eckman sampler was typically stiff gray mud overlain by a thin (up to a few cm thick) layer of light-tan oozy mud. The tan mud was collected into Ziplock® baggies for further processing. Core BL96-2 was taken with a Kullenberg corer (Kullenberg, 1947), whereas BLR2K-3 and BL2002-4 were taken with a UWITEC piston corer (Mondsee, Austria), with a core diameter of 5 cm. Core BL00-1 was taken with the GLAD800 (Global Lake Drilling to 800 m) drill rig (<http://www.dosecc.org/html/glad800.html>). Radiocarbon ages for cores BLR2K-3, BL2K-3, and BL96-2 are presented in Colman et al. (this volume). The chronology for core BL00-1 is presented in Colman et al. (2006, 2007) and Kaufman et al. (this volume). Cores BLR2K-3, BL2K-3, and BL96-2 were sampled at ~3–4 cm intervals and each sample was ~1 cm thick. Core BL00-1 was sampled at ~1 m intervals and each sample was ~3 cm thick. All sediment samples were processed to concentrate ostracodes using a standard protocol developed for the calcareous microfossil laboratory at the U.S. Geological Survey in Denver, Colorado (Forester, 1988). The process involved disaggregating the sample by soaking for ~1 week in a weak detergent (Calgon®) solution. Solutions containing stubborn sediments were frozen and thawed repeatedly. Once processed, the sand-sized residue (>150 µm) was size sorted and adult ostracode valves were identified to species when possible and counted. Surface samples were processed following the same protocol and species presence was noted.

RESULTS

Cosmopolitan ostracode species are common and diverse in springs and wetlands throughout North America and are generally well known with an established taxonomy (e.g., Furtos, 1933; Delorme, 1971, 1970a, 1970b, 1970c, 1970d; Forester et al., 2006). Cosmopolitan ostracode species inhabit the springs and wetlands in the Bear Lake catchment (Table 1). These habitats contain *Cypridopsis vidua* and *Limnocythere itasca* in the wetlands, *Candona acuminata* around the orifices of springs, and *Cavernocypris wardi* in cold springs and groundwater settings. As expected, sites with composite hydrologic sources, for example springs discharging into wetlands, have diverse assemblages reflecting the hydrologic heterogeneity.

Cosmopolitan ostracode taxa are also common in the upper littoral zone of Bear Lake. For example, at the Bear Lake Training Center site (site 10; Table 1, Fig. 1), the ostracode species

assemblage is diverse, with 11 species living in a small spring that emerged ~3 m lakeward from the shoreline during recent low lake levels. In 2003, the lake regressed farther and the spring discharge expanded lakeward across the former littoral zone. *Herpetocypris brevicaudata* appeared in the 2003 collections, even though it was absent in prior year collections, and it is now common in several exposed shoreline and former littoral zone springs (Table 1). Small numbers of empty cosmopolitan ostracode valves and empty endemic species valves occur together in lake sediment samples out to ~7 m water depth (Table 2). Valves of cosmopolitan species are also rarely found at deeper depths in the lake, but they all appear to be transported shells (poor preservation, single, often juvenile valves).

Empty valves of the endemic species (Fig. 2) are extremely abundant in the surface-sediment samples at water depths >7 m (Table 2), often constituting most of the sand-sized fraction. The ostracode fauna in the most recent lake-bottom sediments is composed of eight candonid species, two limnocytherid species, and one unidentified taxon (Fig. 2). The unknown taxon is a cyprid, but its relationship to other cyprids is not understood. The endemic ostracode species diversity is highest in deeper water (Table 2). It is unclear if the increased diversity is an accurate representation of live distributions, or if empty ostracode valves have simply been reworked to deeper parts of the lake, however. The lack of modern sediment in water depths <30 m (Colman, 2006; Dean et al., 2006) indicates that sediment reworking is an important process in this lake and likely alters the postmortem distribution of ostracode valves. The rarity or absence of ostracode soft body parts in the modern lake sediment variously implies limited present-day productivity (perhaps due to extinction associated with the Bear River diversion), rapid decomposition of soft parts, and/or endemic ostracode populations that normally have a patchy distribution. The possibility of a patchy distribution is supported by abundant soft-part-bearing ostracode carapaces in a sediment sample taken from a large methane seep at 40 m water depth (site P; Fig. 1). Most of the bottom samples reported here were collected in <20 m water depth in an attempt to find live cosmopolitan ostracodes in the littoral zone. Sampling was limited ($n = 4$) in the 24–38 m depth zone where Smart (1958) reported a peak in ostracode concentrations. With the one exception, no live ostracodes were recovered at the few deep-water sample sites. Live ostracodes were recovered at the 40-m-deep methane seep on the first attempt, however. Other possible methane seep locations within the lake are known and further sampling is necessary to determine if the endemic ostracode distributions are linked to these seeps.

The present-day spatial relation between the cosmopolitan and endemic ostracodes is also evident in the fossil record. The stratigraphic distribution of the most common cosmopolitan ostracodes, those with an abundance of 1% or more, and all occurrences of the endemic ostracodes are shown in Figures 3, 4, 5, and 6 for cores BLR2K-3, BL2K-3, BL96-2, and BL00-1, respectively.

Core BLR2K-3 from Mud Lake (Fig. 1) is dominated by cosmopolitan ostracode taxa (Fig. 3). Approximately 75% of the ostracodes counted in the samples from BLR2K-3 are *Limnocythere*

itasca and *Physocypria globula*, and ~15% are *Candona caudata* and *Potamocypris* sp. Core BL2K-3 was taken from the north end of Bear Lake in ~4 m of water (Fig. 1). Ostracode composition fluctuates between being cosmopolitan-dominated and endemic-dominated, with the exception of *Physocypria globula*, which occurs throughout the samples (Fig. 4). Core BL96-2 from the central part of the lake (~40 m water depth; Fig. 1) contains endemic ostracode species only (Fig. 5). Seven of the endemic candonids, the two species of limnocytherids, and the unknown taxon from the modern lake-bottom samples are present (Fig. 5). Seventy-eight percent of the valves in BL96-2 are from just two candonid species (*Candona* sp. 1 and 2; Fig. 2), and 96% of the valves are from four candonids and one limnocytherid species. Core BL00-1, taken in ~50 m of water near the deepest part of

the lake (Fig. 1), contains primarily endemic species. Six of the endemic candonids, one of the limnocytherids, and the unknown taxon are present. The cosmopolitan species *Cytherissa lacustris* is also intermittently present (Fig. 6).

DISCUSSION

Continental surface water (e.g., lakes, wetlands) is ephemeral over geologic time scales. Pluvial lakes of late Pleistocene age in the western and southwestern United States persisted for few tens of thousands of years (e.g., Benson et al., 1990; Lowenstein et al., 1999; Cohen et al., 2000; Garcia and Stokes, 2006). The Great Lakes of the Midwest have been in their current configuration for less than ~18,000 yr, since the retreat of the last

TABLE 1. OSTRACODE SPECIES SURROUNDING BEAR LAKE

Site (Fig. 1)	Lat. (°N)	Long. (°W)	Ostracodes Genus-species
Paris Spring			
1	42.206	111.498	<i>Cavernocypris wardi</i> , <i>Prionocypris canadensis</i>
Jarvis Spring			
2	42.191	111.483	<i>Cavernocypris wardi</i> , <i>Cypria ophthalmica</i> , <i>Candona sigmoides</i> , <i>Strandesia</i> sp.
Blue Pond Spring			
3	42.105	111.495	<i>Candona acuminata</i> , <i>Candona sigmoides</i> , <i>Cavernocypris wardi</i> , <i>Cypria ophthalmica</i> , <i>Strandesia deltoidea</i>
Sadducee Spring			
4	42.051	111.460	<i>Cavernocypris wardi</i> , <i>Strandesia</i> sp.
"South Fish Haven" littoral zone spring			
5	42.026	111.402	<i>Herpetocypris brevicaudata</i> , <i>Ilyocypris bradyi</i> , <i>Cypridopsis vidua</i> , <i>Heterocypris incongruens</i> , <i>Strandesia meadensis</i> , <i>Cavernocypris wardi</i> , <i>Cypridopsis okeechobei</i>
"Swan Creek north" littoral zone spring			
6	41.985	111.406	<i>Herpetocypris brevicaudata</i> , <i>Cypridopsis vidua</i> , <i>Ilyocypris bradyi</i> , <i>Limnocythere itasca</i> , <i>Strandesia meadensis</i> , <i>Candona stagnalis</i> , <i>Physocypria</i> sp.
Swan Creek Spring			
7	42.985	111.427	<i>Candocyprinotus ovatus</i>
Littoral zone beach seeps near Swan Creek			
8	41.978	111.402	<i>Herpetocypris brevicaudata</i> , <i>Ilyocypris bradyi</i> , <i>Candona</i> sp., <i>Heterocypris incongruens</i> , <i>Limnocythere itasca</i> , <i>Physocypria</i> sp., <i>Cypridopsis vidua</i>
Spring discharge onto beach at Garden City			
9	41.944	111.390	<i>Herpetocypris brevicaudata</i> , <i>Ilyocypris bradyi</i> , <i>Candona</i> sp., <i>Heterocypris incongruens</i> , <i>Limnocythere itasca</i> , <i>Physocypria</i> sp., <i>Cypridopsis vidua</i>
"Bear Lake Training Center" littoral zone spring			
10	41.915	111.389	<i>Candona acuminata</i> , <i>Candona stagnalis</i> , <i>Candona caudata</i> , <i>Candona candida</i> , <i>Cavernocypris wardi</i> , <i>Cypridopsis vidua</i> , <i>Physocypria globula</i> , <i>Strandesia meadensis</i> , <i>Potamocypris unicaudata</i> , <i>Limnocythere itasca</i> , <i>Herpetocypris brevicaudata</i>
Big Spring			
11	41.809	111.389	<i>Ilyocypris bradyi</i> , <i>Cypria ophthalmica</i> , <i>Cypridopsis okeechobei</i> , <i>Candona acuminata</i> , <i>Candona sigmoides</i> , <i>Candona</i> sp., <i>Strandesia</i> sp.
Falula Spring			
12	41.842	111.302	<i>Cavernocypris wardi</i> , <i>Candona acuminata</i> , <i>Cypria ophthalmica</i> , <i>Ilyocypris bradyi</i>
Seep, South Eden Canyon			
13	41.921	111.192	<i>Cavernocypris wardi</i> , <i>Ilyocypris bradyi</i> , <i>Heterocypris fretensis</i> , <i>Heterocypris incongruens</i> , <i>Candona sigmoides</i> , <i>Candona stagnalis</i> , <i>Candona acuminata</i> , <i>Cypridopsis vidua</i> , <i>Potamocypris</i> sp., <i>Strandesia</i> sp., <i>Cyclocypris</i> spp.
Spring, North Eden Canyon			
14	41.997	111.140	<i>Cavernocypris wardi</i> , <i>Strandesia</i> sp., <i>Candona sigmoides</i>
North Eden Creek			
15	41.986	111.255	<i>Cavernocypris wardi</i> , <i>Ilyocypris bradyi</i> , <i>Cyclocypris ampla</i> , <i>Candona stagnalis</i> , <i>Candona acuminata</i> , <i>Cypria ophthalmica</i>
"Cedars and Shade" spring			
16	42.075	111.250	<i>Cavernocypris wardi</i> , <i>Ilyocypris bradyi</i> , <i>Candona sigmoides</i>
Mud Lake Hot Spring			
17	42.115	111.264	<i>Candona compressa</i> , <i>Ilyocypris bradyi</i> , <i>Heterocypris fretensis</i> , <i>Heterocypris incongruens</i> , <i>Darwinula stevensoni</i> , <i>Darwinula</i> sp.
Mud Lake			
18	42.125	111.264	<i>Candona acuminata</i> , <i>Candona stagnalis</i> , <i>Candona caudata</i> , <i>Cypridopsis vidua</i> , <i>Physocypria globula</i> , <i>Cyclocypris serena</i> , <i>Heterocypris fretensis</i> , <i>Potamocypris unicaudata</i> , <i>Potamocypris</i> sp., <i>Limnocythere itasca</i>
Bear River at Harer gauge, ID			
19	42.195	111.166	<i>Candona acuminata</i> , <i>Candona distincta</i> , <i>Candona stagnalis</i> , <i>Candona caudata</i> , <i>Cavernocypris wardi</i> , <i>Cypria ophthalmica</i> , <i>Ilyocypris bradyi</i> , <i>Cypridopsis vidua</i> , <i>Limnocythere inopinata</i> , <i>Limnocythere paraornata</i> , <i>Pelocypris albomaculata</i> , <i>Physocypria globula</i> , <i>Cyclocypris serena</i> , <i>Cyclocypris laevis</i> , <i>Strandesia</i> sp.

Note: Lat.—latitude; Long.—longitude. Locations in quotations are common names.

TABLE 2. OSTRACODES FROM BEAR LAKE SURFACE SEDIMENT

Site (Fig. 1)	Lat. (°N)	Long. (°W)	Depth (m)	Endemic ostracodes (see Fig. 2)		Cosmopolitan ostracodes Genus-species
				Genus-species	Genus-species	
Bear Lake off Indian Creek						
A	42.094	111.263	1.0	<i>Candona</i> sp. 2		<i>Ilyocypris bradyi</i>
B	42.094	111.264	4.0	<i>Candona</i> sp. 2		<i>Physocypris</i> sp.
C	42.090	111.275	7.0	<i>Candona</i> spp. 1-7, <i>Limnocythere</i> spp. 1 and 2, unidentified genus		<i>Ilyocypris bradyi</i>
D	42.087	111.280	14.5	<i>Candona</i> spp. 1, 2, and 4, <i>Limnocythere</i> spp. 1 and 2		none
E	42.083	111.284	20.0	<i>Candona</i> spp. 1-8, <i>Limnocythere</i> spp. 1 and 2, unidentified genus		rare <i>Ilyocypris bradyi</i> , <i>Physocypris</i> sp.
Bear Lake, bay south of marina						
F	N.D.	N.D.	2.0	<i>Candona</i> sp. 2, <i>Limnocythere</i> sp. 2		<i>Ilyocypris bradyi</i>
G	N.D.	N.D.	5.0	<i>Candona</i> spp. 1 and 2, <i>Limnocythere</i> sp. 2		<i>Ilyocypris bradyi</i> , <i>Cypridopsis vidua</i>
Bear Lake off Big Creek						
H	41.846	111.337	1.5	none		fragments of ostracodes
I	41.848	111.337	3.5	none		fragments of ostracodes
J	41.852	111.334	6.5	<i>Candona</i> spp. 1-4, <i>Candona</i> sp. 6-8, <i>Limnocythere</i> spp. 1 and 2		<i>Physocypris</i> sp., <i>Cypridopsis vidua</i> , <i>Cyclocypris</i> sp.
K	41.857	111.329	15.0	<i>Candona</i> spp. 1-4, <i>Candona</i> sp. 8, <i>Limnocythere</i> spp. 1 and 2, unidentified genus		none
L	41.860	111.326	25.0	<i>Candona</i> spp. 1-5, <i>Candona</i> sp. 7, <i>Limnocythere</i> spp. 1 and 2, unidentified genus		none
Bear Lake northwest corner						
M	42.105	111.369	2.0	rare <i>Candona</i> sp. 2		
N	42.098	111.362	4.5	<i>Candona</i> spp. 1, 2, and 5, <i>Limnocythere</i> sp. 2		<i>Physocypris</i> sp., <i>Ilyocypris bradyi</i> , <i>Cypridopsis vidua</i> , <i>Cyclocypris</i> sp.
Bear Lake east of Swan Creek						
O	N.D.	N.D.	24.0	<i>Candona</i> spp. 1-7, <i>Limnocythere</i> spp. 1 and 2		none
Sublacustrine methane seep						
P	41.937	111.342	40.0	<i>Candona</i> spp. 1-7, <i>Limnocythere</i> sp. 1, unidentified genus		none

Note: Lat.—latitude; Long.—longitude; N.D.—no data; all ostracode valves at sites A-O were empty, with preservation ranging from pristine to encrusted. Encrusted valves were more common in shallow water. Live ostracodes were recovered only at site P.

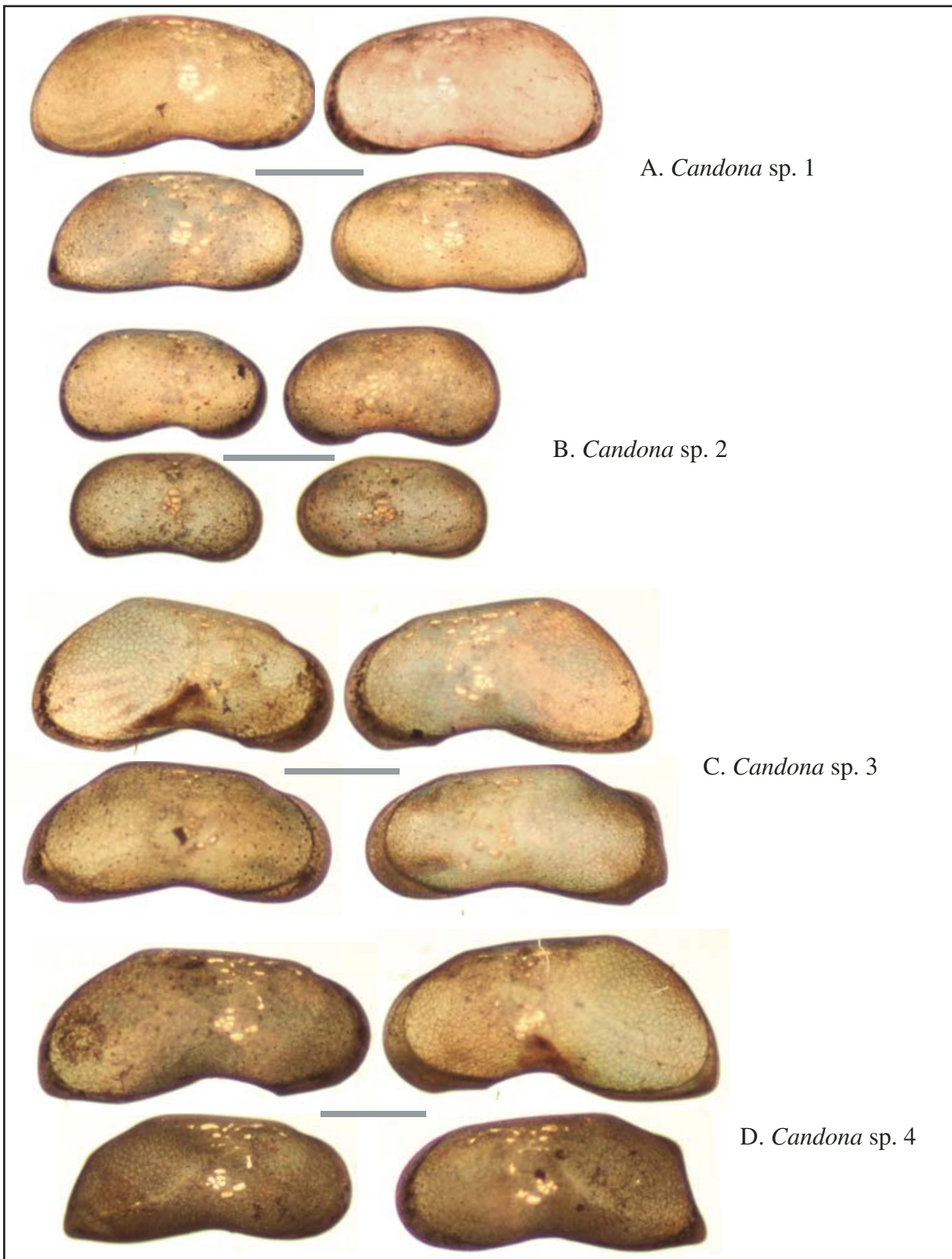


Figure 2 (continued on following three pages). Endemic Bear Lake ostracode fauna and two cosmopolitan ostracodes photographed under transmitted light. Groupings A–K are from an Eckman lake-bottom sample taken in ~30 m of water, and are endemic to the lake. Grouping L is from a grab sample taken at Jarvis Spring (Site 2; Fig. 1). Grouping M is from a late Pleistocene aged deposit from Térapa, Sonora, Mexico. Valve placement is identical for each image grouping. Upper left—male right valve; upper right—male left valve; lower left—female right valve; lower right—female left valve. All images are external lateral views taken on a Leica DMLP microscope using a Cannon EOS Rebel XT digital camera. Scale bar in each grouping—0.5 mm.

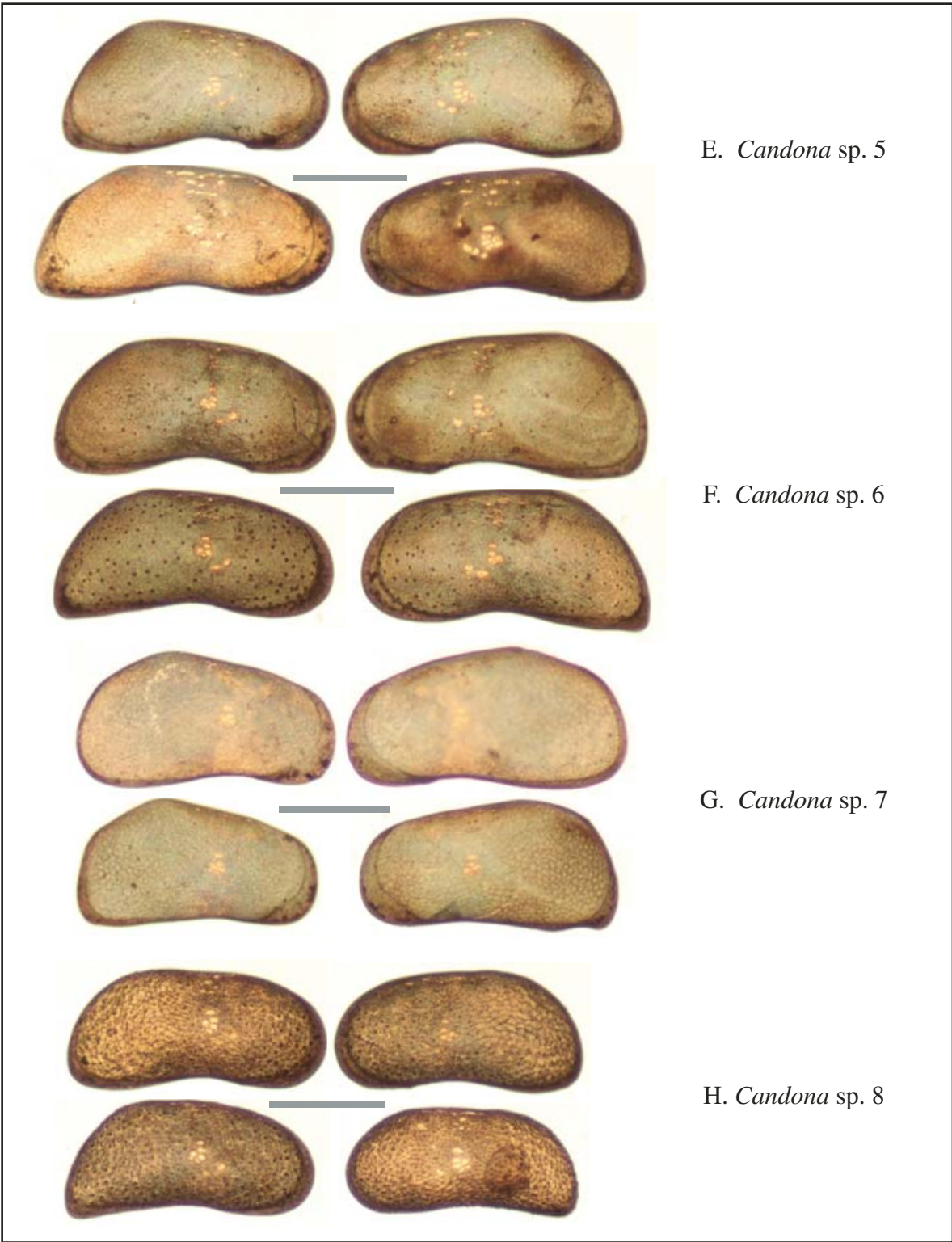


Figure 2 (continued).



Figure 2 (continued).



Figure 2 (continued).

continental glaciers (e.g., Calkin and Feenstra, 1985; Colman et al., 1994; Lewis et al., 1994; Breckenridge, 2007). Groundwater discharge habitats (e.g., springs, wetlands) are susceptible to changes in the elevation of the local water table, which in turn is controlled by wet and dry cycles that operate on annual, decadal, century, and millennial scales (e.g., Quade et al., 1995, 1998; Fritz et al., 2000; St. George and Nielson, 2002). Cosmopolitan ostracodes (and other) species are those that are widespread and have adapted to ephemeral or variable habitats, giving them an advantage over species that have not. Important adaptive traits might include the ability of an individual to withstand desiccation, or the ability to generate large numbers of eggs or offspring that are easily transported from one location to another or that are capable of surviving adverse conditions (e.g., McLay, 1978a, 1978b). Ostracode (and other) species with poor dispersal mechanisms, low reproductive rates, or a limited home range would be more susceptible to extinction during adverse conditions (Cohen and Johnson, 1987). It seems plausible that once evolved, cosmopolitan species may *require* habitat variability in order to trigger key life phases (e.g., mating or egg hatching). For example, the spring thaw may trigger the hatching of *Candona candida* eggs, and seasonal fluctuations in salinity appear to be important in the life cycle of *Candona rawsoni*, because it is not found in lakes or ponds that lack that particular characteristic (Forester, 1987).

At the other extreme of continental aquatic habitats are geologically long-lived lakes. These lakes are unique in that they persist for hundreds of thousands to millions of years and experience large-scale changes in climate, lake chemistries, and lake levels (Frogley et al., 2002). Extant lakes that fall into this category are Lake Baikal, Lake Tanganyika, Lake Malawi, and several others (Frogley et al., 2002). These ancient lakes harbor incredible species diversity and are host to many endemic species (Martens and Schön, 1999).

Leading theories pertaining to the development of endemic species in these lakes include long-term stability (e.g., Cohen and Johnson, 1987), repeated speciation and extinction within the lake system (McCune, 1987), and repeated immigration

events (Martens and Schön, 1999). The development of complex ecosystems and associated endemic species may be a time-dependent phenomenon, with a few thousand years of stability likely insufficient to produce endemism (e.g., Forester, 1991b; Wells et al., 1999; Smith et al., 2002b). Stability for many tens to hundreds of thousands of years and gene pool isolation are thought to be necessary to evolve endemic populations (e.g., Martens, 1997). Large pluvial lakes in western North America (Forester, 1987) and the Great Lakes in the Midwest (Forester et al., 1994) were (are) presumably stable environments for a few thousand years, yet, with the exception of Lake Bonneville, did (do) not contain endemic ostracode species. Lake Bonneville is interesting in that several of the fossil ostracode taxa found in its sediments are very similar to those from the profundal zone of Bear Lake (Spencer et al., 1984). Similarly, several of the fossil fish species found in Lake Bonneville sediments are presently living in, and are endemic to, Bear Lake (Sigler and Sigler, 1987, 1996; Broughton, 2000). Bear Lake, with its continuous history (cf. Balch et al., 2005, and Bright et al., 2006) is likely the source of the endemic species (e.g., Miller, 2006).

The necessity of long-term stability in the development of endemism has been countered by debate on the origin of endemic cichlid fish species in Lakes Victoria and Malawi of East Africa, the cisco species flock of the Great Lakes, and the whitefish complex of Bear Lake, Utah and Idaho. Lake Victoria contains over 500 endemic cichlid fish species (Verheyen et al., 2003). Complete desiccation of the lake ~15,000 yr ago implies that the lake's endemic diversity has evolved since that time (Johnson et al., 1996; Stager et al., 2004), although competing theories do exist (Verheyen et al., 2003; Rutaisire et al., 2004). In Lake Malawi, the >200 endemic cichlid fish species that inhabit the rocky shore zone and islands of the lake may have developed very recently, as little as 200–300 yr ago (Owen et al., 1990). In recent history the Great Lakes contained as many as eight endemic cisco (*Coregonus*) species (Smith, 1981; Smith and Todd, 1984; Todd and Smith, 1992). The evolution of the Great Lakes ciscoes is thought to have occurred recently, since

the last retreat of continental glaciers from the Great Lakes basins ~15,000 yr ago (Smith, 1981; Bailey and Smith, 1981; Reed et al., 1998). And at Bear Lake, genetic studies on its endemic whitefish suggest a recent divergence between the three whitefish species (Vuorinen et al., 1998; Miller, 2006). Bones of two of the Bear Lake endemic whitefish (*Prosopium gemmifer* [Bonneville cisco] and *P. spilonotus* [Bonneville whitefish]) have been found in the earliest deposits of Lake Bonneville (Stansbury phase; Smith et al., 1968) and are likely ~20,000 yr old (Broughton, 2000), indicating speciation by at least that time. Bones from all three endemic Bear Lake whitefish have been identified from Lake Bonneville sediments that were deposited 10,160–11,270 ^{14}C yr

B.P. (~11,700–13,500 cal yr B.P.; Broughton, 2000), indicating that all three species were established by at least that time. The apparent lack of *Prosopium abyssicola* (Bear Lake whitefish) in the older Lake Bonneville sediments may be due to several factors, the most simplistic being that specimens of *P. abyssicola* have yet to be found (or correctly identified) in the older sediments, or more controversially, that *P. abyssicola* had not yet speciated and arrived later in the Lake Bonneville sequence.

Forester (1991b) suggested that endemic lacustrine ostracodes evolve because biologic selection pressures exceed physical selection pressures in lakes where stable environmental conditions persist over long time intervals. Biologic selection pressures involve

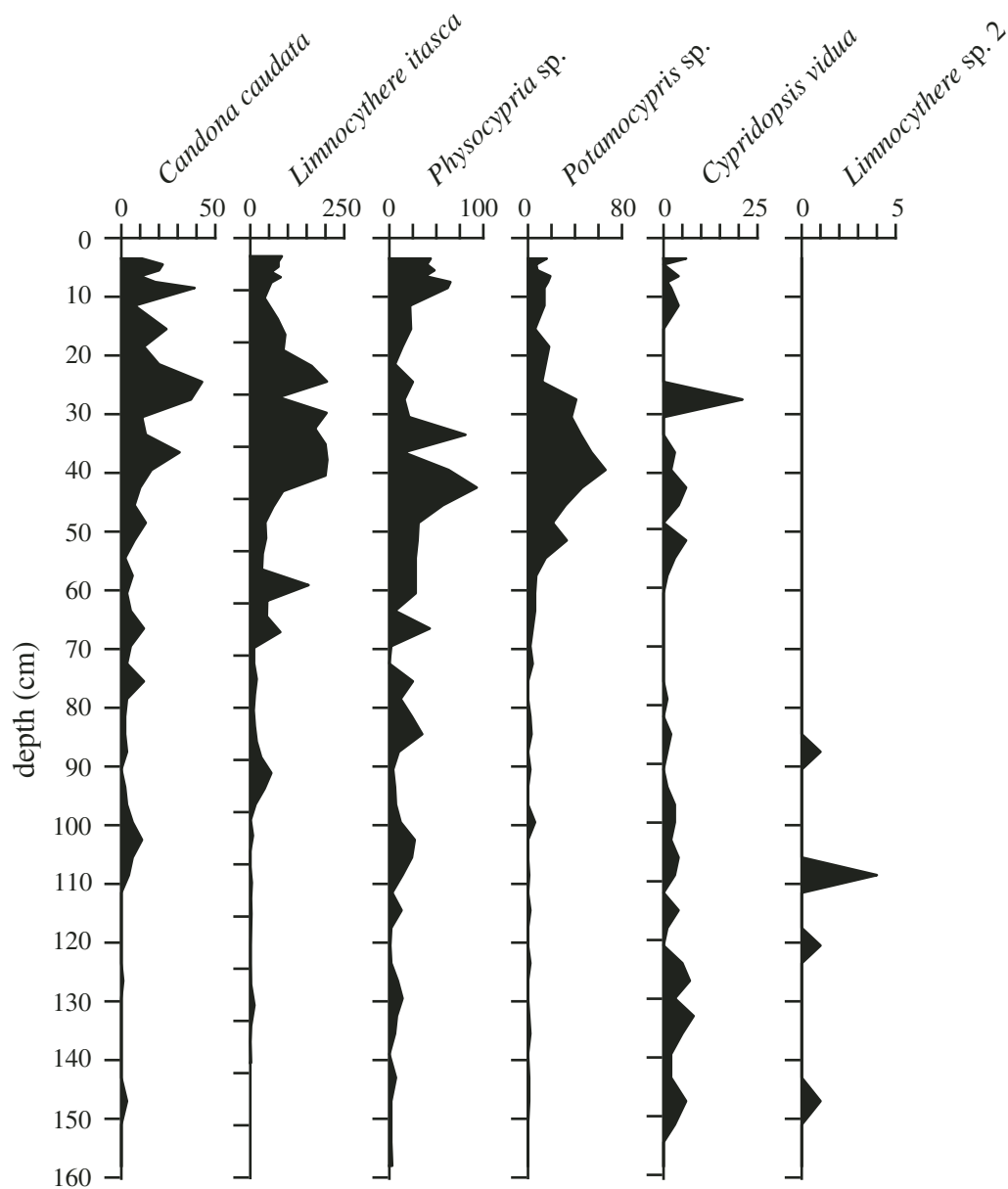


Figure 3. Stratigraphic distribution of common cosmopolitan and all endemic ostracodes in core BLR2K-3. Abundance is reported in valves per gram of sediment.

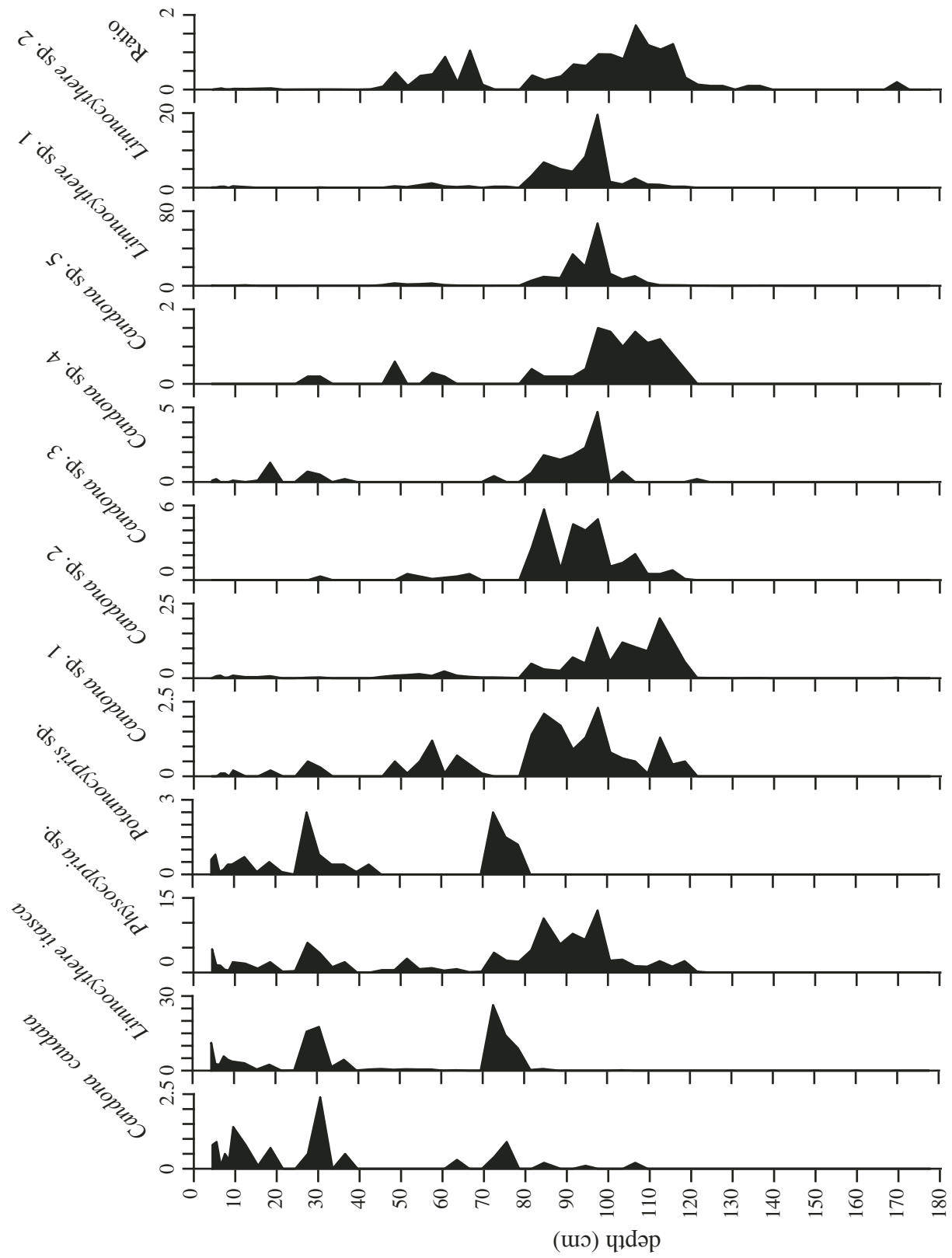


Figure 4. Stratigraphic distribution of common cosmopolitan and all endemic ostracodes in core BL2K-3. Abundance is reported as one-tenth of the actual valves per gram of sediment.

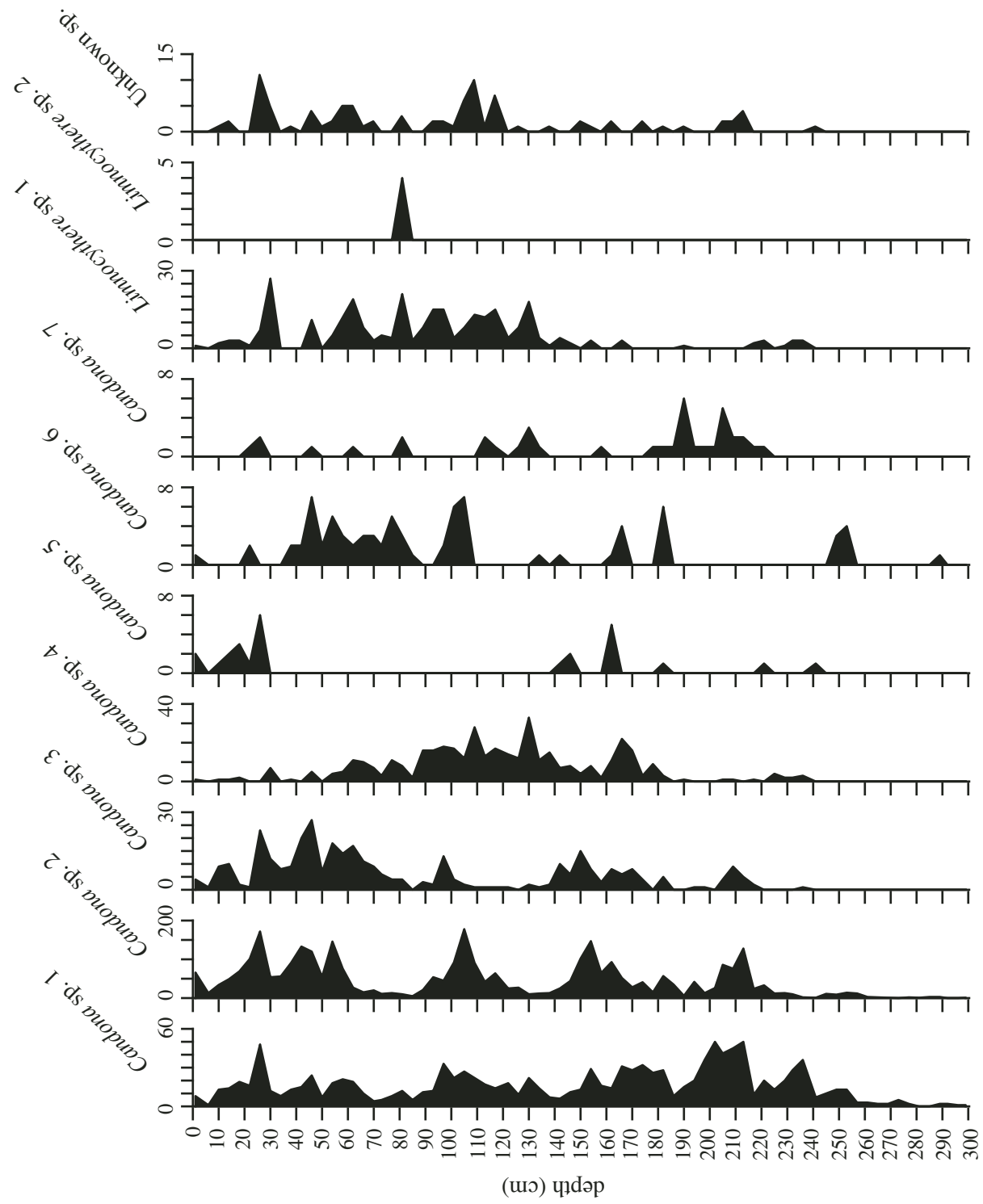


Figure 5. Stratigraphic distribution of endemic ostracodes in core BL96-2; no cosmopolitan ostracodes were found in this core. Abundance is reported in valves per gram of sediment.

adaptive strategies related to surviving inter- and intra-species competition (e.g., reproduction, predation). The development of thick shells or spines and other ornamentation, brooding behavior, and extended parental care are examples of adaptations in response to biologic pressures such as predator-prey relationships and mate recognition (e.g., Martens and Schön, 1999). Physical selection pressures involve adaptive strategies and physiologies suited to changing physical and chemical environments. The development of desiccation-resistant eggs and eggs that hatch at random intervals after production (Angell and Hancock, 1989), short life spans that guarantee several populations and egg clutches per year (e.g., Delorme, 1978, 1982), and the ability for some ostracodes to enter

into a state of torpidity when environmental conditions are less than favorable (Delorme and Donald, 1969) are all adaptations to physical selection pressures.

Endemism is presumably favored when biological pressures are at a maximum and when physical selection pressures, such as environmental changes, are relatively invariant and play a secondary role in the survival of the species. Biological and physical selection pressures are interdependent, however. For example, the environmental variability that requires special physical adaptations for success (physical selection) also places limitations on the survival potential for the predators (biological selection) of a given species.

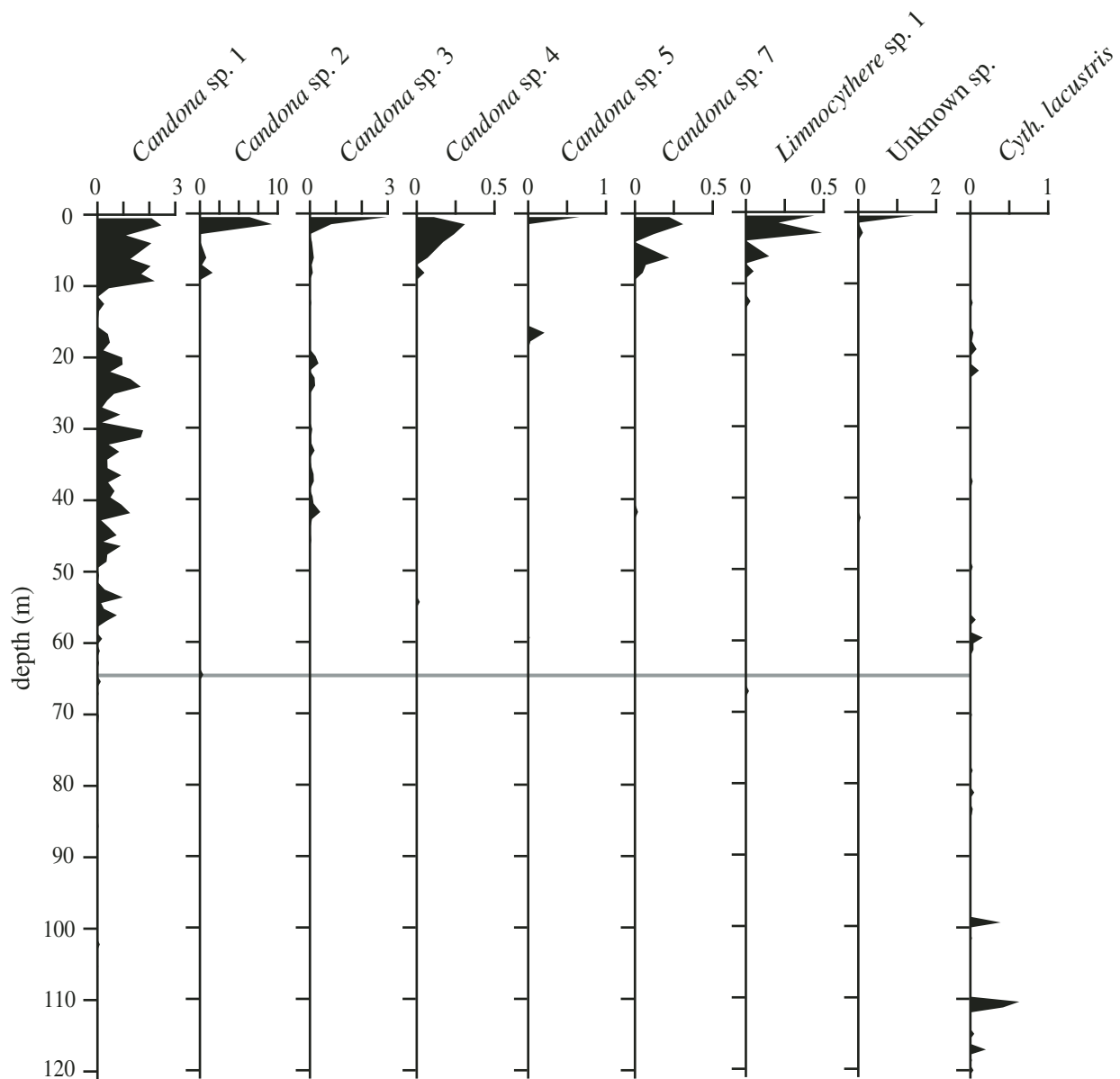


Figure 6. Stratigraphic distribution of endemic ostracodes and *Cytherissa lacustris* in core BL00 1E. Abundance is reported in valves per gram of sediment. Aragonite from ~65 m depth (gray line) generated a U-Th age of ca. 128 ka (Colman et al., 2006, 2007).

An example of an ancient, geologically long lived, lacustrine environment is the Pliocene-aged Glenns Ferry Formation of the western United States. The deep-lake phase of the Glenns Ferry Formation lasted roughly 1 million years (ca. 3.5 to ca. 2.5 Ma; Thompson, 1996; and references therein) and was populated by both endemic and cosmopolitan ostracodes. The endemic ostracodes of the Glenns Ferry Formation resemble contemporaneous cosmopolitan species except for unusual ornamentation such as a large mid-valve spine. Others were highly ornamented relative to typical cosmopolitan continental ostracodes (Forester, 1991b). The ornamented Glenns Ferry Formation endemic taxa populated only the deep lake sediment, whereas cosmopolitan taxa were common in all marginal hydrologic settings. A similar cosmopolitan-endemic ostracode distribution occurs at Bear Lake.

Ostracode Distributions in Bear Lake

Bear Lake is an oligotrophic lake (Wurtsbaugh and Hawkins, 1990). Mean annual whole-lake benthic invertebrate biomass estimates are extremely low, only 0.34 g dry weight per square meter (g dry wt m⁻²), which is the lowest value recorded for a temperate-zone lake (Wurtsbaugh and Hawkins, 1990). Invertebrate biomass estimates for the more productive littoral zone are only slightly higher, but are always less than 1 g dry wt m⁻² (Wurtsbaugh and Hawkins, 1990). Ostracodes, although rare, do constitute a large part of the littoral zone biomass, however (Wurtsbaugh and Hawkins, 1990). The ostracodes reported by Wurtsbaugh and Hawkins (1990) were not identified to species, so it is unknown whether the ostracodes were cosmopolitan or endemic species. Smart (1958) conducted an extensive biologic survey of the bottom sediments of Bear Lake and reported that ostracodes (simply reported as “*Candona* species”) were most abundant in water depths of 24–38 m. The decrease in ostracode abundance at depths greater than ~38 m may be an apparent decrease resulting from sediment resuspension and focusing in the deeper portions of the lake, however (Colman, 2006; Dean et al., 2006). The “*Candona* species” reported by Smart (1958) were not identified to species level and here are assumed to represent the endemic, candonid-rich, profundal assemblage.

It is unclear why cosmopolitan ostracode valves are not found in water depths greater than ~7 m. Live cosmopolitan ostracodes have been clearly identified only from lake marginal springs and the marsh complexes that have developed on the exposed lake floor during the recent low-water years (Table 2). Live endemic ostracodes, and identified as such, have been recovered only from one deep-water methane seep, although they are apparently abundant at water depths of 24–38 m (Smart, 1958). One hypothesis is that cosmopolitan ostracodes do not actively live in the lake at any depth and the lake is inhabited entirely by the endemic fauna. In this scenario the cosmopolitan ostracode valves found in Bear Lake’s littoral zone are reworked from the springs along the lake margins and from marsh sediments that were deposited on the exposed lake floor during previous low lake levels. An alternative hypothesis is that cosmopolitan ostracodes do inhabit

the littoral zone of the lake, but only to a water depth less than 7 m (with empty valves likely being reworked out to ~7 m depth). In either scenario cosmopolitan ostracodes are unable to inhabit the deeper parts of the lake.

The fish distributions within Bear Lake may partially explain the cosmopolitan-endemic ostracode distributions in the lake. Fish densities in Bear Lake are low in water <5 m deep, with native Utah chub and Utah suckers being most numerous throughout the year and endemic juvenile Bear Lake sculpin (*Cottus extensus*) being numerous only during the summer (Wurtsbaugh and Hawkins, 1990). Bear Lake sculpin and Bear Lake whitefish (*Prosopium abyssicola*) are most abundant in water depths >30 m, with adult Bear Lake sculpin abundances increasing in shallower water (~15 m) during the summer. Bear Lake whitefish (*P. spilonotus*) abundances are highest in water depths of ~15–30 m. (Wurtsbaugh and Hawkins, 1990; Kennedy et al., 2006).

Analyses of the gut contents of Bear Lake fish indicate that ostracodes (unidentified taxa) are a large part of the diet of several fish species. Ostracodes constitute 59%–99% of the diet of Bear Lake whitefish and Bear Lake sculpin, both of which are endemic to the lake. The next two most active ostracode predators are juvenile Bonneville whitefish and the Utah sucker (Table 3). The Bonneville whitefish is also endemic to the lake, but the Utah sucker is not (Wurtsbaugh and Hawkins, 1990; Thompson, 2003; Tolentino and Thompson, 2004; Kennedy, 2005; Kennedy et al., 2006). Because the ostracodes from the fish gut analyses were not identified to species, however, the relative abundance of endemic or cosmopolitan ostracode species consumed by the various fish species is unknown. Bear Lake whitefish are substantially more numerous in water depths greater than ~40 m (Kennedy et al., 2006), which implies that the ostracodes they consume are exclusively endemics.

The ecology of the endemic ostracode fauna must involve adaptive strategies that allow them to survive in spite of the oligotrophic nature of the lake and the heavy predation pressure of the endemic fish. One theoretical possibility is that the endemic ostracodes exploit the fish predation and, for example, use the endemic fish as a dispersal mechanism (e.g., Kornicker and Sohn, 1971; Mellors, 1975; Vinyard, 1979; Smith, 1985; Bartholmé et al., 2005). Finding new food resources in a large oligotrophic lake, especially if that food resource has a patchy distribution, would be key to survival. Fish are highly mobile and migrate over large areas of the lake. Exploiting that mobility (actively or passively) would allow the endemic ostracodes (or their eggs) to be dispersed throughout the lake, and from food patch to food patch. Maximum endemic ostracode and fish densities overlap in water depths of ~20–38 m. If fish are a dispersal mechanism for the endemic ostracodes, then it is reasonable to expect that endemic ostracode densities would coincide with high fish densities. Cosmopolitan ostracode species attempting to invade this endemic ecosystem may be unable to cope with the intense predation pressure, or might not have a reproductive strategy compatible with the endemic fish behavior, and would be restricted to lake

marginal springs or the shallowest portions of the littoral zone (<5 m deep) where fish densities are lowest.

The morphology of Bear Lake is likely another factor that contributes to the confinement of cosmopolitan ostracodes to the shallow littoral zone. The large expanses of gently sloping lake bottom means that any fluctuation in lake levels would expose and flood large expanses of Bear Lake's littoral zone. For example, a 4 m decrease in lake level (from full lake) would expose ~30 km² of lake bottom. Cosmopolitan ostracodes adapted to variable habitats (strong colonizers) would likely be restricted to this zone (in the emergent marshes). The endemic deep-water ostracode fauna are apparently unable to exploit the shallow littoral zone and are restricted to the deeper parts of the lake where the impacts of lake-level fluctuations are minimal to nonexistent. In addition to the fish predation pressure, cosmopolitan ostracode species may not be able to invade the deeper parts of the lake due to its comparative stability. As a result of these variables, and probably others, the cosmopolitan-endemic ostracode distribution in Bear Lake mirrors that of the Glenns Ferry Formation.

Ostracode Distribution in Bear Lake Sediment Cores

The same species assemblage distinctions noted in the modern lake sediment also existed in the past. Core BLR2K-3 from Mud Lake contains sediments deposited over the past ~8000 yr, but primarily over the past ~2000 yr (Colman et al., this volume), that are dominated by cosmopolitan ostracodes (Fig. 3). These taxa suggest that Mud Lake was principally a shallow lake and wetland, similar to today. The chemical composition of Mud Lake prior to the 1912 Bear River diversion is unknown, but the near absence of endemic ostracodes in the Mud Lake core indi-

cates that it has been incompatible with their requirements for the last several thousand years.

Core BL2K-3 contains modern sediments deposited at the north end of Bear Lake over the past 3500 yr (Colman et al., this volume). Radiocarbon ages from this core are not in stratigraphic order, suggesting sediment reworking or complications with some of the radiocarbon samples. The problematic radiocarbon data limit the usefulness of this core, but several trends in the ostracode data are apparent (Fig. 4). First, the antithetic behavior of the endemic and cosmopolitan ostracode faunas at this site suggests a species distribution pattern that was similar to the present. Second, any given sediment sample from this core was dominated by either cosmopolitan or endemic ostracodes, but never both, with the exception of *Physocypria* sp. And third, there does not appear to be a faunal gradation between the cosmopolitan and endemic dominated samples. The difference between the two sample types is distinct. The cosmopolitan-rich zones may represent times when the core site was situated in less than ~7 m of water and endemic fish predation was minimal or nonexistent.

Core BL96-2 contains entirely endemic-dominated ostracode assemblages (Fig. 5) from sediments that were deposited over the last ~26,000 yr (Colman et al., this volume). The absence of cosmopolitan taxa in the deep-water setting is atypical of lakes throughout North America with oxygenated hypolimnia. The lack of cosmopolitan species indicates that the lake depth at the core site has never been shallower than ~5 m. This suggests that Bear Lake has never dried out, or never exceeded the environmental tolerances of the endemic ostracode species from the late Wisconsin to the present day.

Core BL00-1 contains sediments that were deposited near the deepest part of the lake over the last 220,000 yr (Kaufman et al., this volume). With one exception, core BL00-1 contains

TABLE 3. OSTRACODE CONSUMPTION BY BEAR LAKE FISH SPECIES

Fish species (size, season)	% Diet	Reference
Bear Lake whitefish (100–150 mm, spring)	99	Thompson, 2003
Bear Lake whitefish (150–200 mm, spring)	90	Thompson, 2003
Bear Lake whitefish (200–250 mm, spring)	73	Thompson, 2003
Bear Lake whitefish (>250 mm, spring)	75	Thompson, 2003
Bear Lake whitefish (100–150 mm, summer)	59	Thompson, 2003
Bear Lake whitefish (150–200 mm, summer)	75	Thompson, 2003
Bear Lake whitefish (200–250 mm, summer)	83	Thompson, 2003
Bear Lake whitefish (>250 mm, summer)	99	Thompson, 2003
Bear Lake sculpin (small)	60	Wurtsbaugh and Hawkins, 1990
Bear Lake sculpin (medium)	68	Wurtsbaugh and Hawkins, 1990
Bear Lake sculpin (large)	73	Wurtsbaugh and Hawkins, 1990
Bonneville whitefish (100–150 mm, spring)	33	Thompson, 2003
Bonneville whitefish (150–200 mm, spring)	14	Thompson, 2003
Bonneville whitefish (200–250 mm, spring)	3	Thompson, 2003
Bonneville whitefish (250–300 mm, spring)	1	Thompson, 2003
Bonneville whitefish (300–350 mm, spring)	3	Thompson, 2003
Bonneville whitefish (>350 mm, spring)	0	Thompson, 2003
Bonneville whitefish (all sizes, summer)	0	Thompson, 2003
Utah sucker (small)	19	Wurtsbaugh and Hawkins, 1990
Utah sucker (large)	38	Wurtsbaugh and Hawkins, 1990
Utah chub	16	Wurtsbaugh and Hawkins, 1990
Carp	6	Wurtsbaugh and Hawkins, 1990
Dace	0	Wurtsbaugh and Hawkins, 1990
Redsides	0	Wurtsbaugh and Hawkins, 1990

Note: Bear Lake whitefish, Bonneville whitefish, and Bear Lake sculpin are endemic to Bear Lake.

entirely endemic species (Fig. 6). Some of the endemic species, but not all (primarily *Candona* sp. 1; Fig. 2A), are found in sediments as old as ca. 130 ka (MIS 5). The core extends through a second glacial-interglacial cycle (to MIS 7), but few whole ostracodes are preserved. Identifiable fragments of *Candona* sp. 1 (Fig. 2A) exist to the bottom of the core, however.

Endemic ostracode species diversity is greatest in the Holocene aragonitic sediments in the upper 10 m of core BL00-1E and in the upper 3 m of core BL96-2 (Figs. 5 and 6). It is unknown whether the higher endemic ostracode diversity in the Holocene sediment is an example of relatively recent ostracode speciation (younger than 15 ka) or whether the lower species diversity in pre-Holocene-aged sediment is due to a preservational bias or some other mechanism.

Cause of Endemism in Bear Lake

The Bear Lake ostracode assemblage contains 11 endemic species, although some of the candonids are morphologically similar to local cosmopolitan taxa and could be ecophenotypes or subspecies of local or other cosmopolitan species (compare Fig. 2A and Figs. 2L and 2M, and compare Fig. 2C with *Candona mendotaensis* from Kitchell and Clark, 1979). The profundal zone of Bear Lake supports more ostracode species than is observed in other large North American lakes. For example, Lake Michigan contains only two ostracode species in the deepest parts of the lake (91–244 m; Buckley, 1975), and rarely more throughout the Holocene (Forester et al., 1994). The endemic Bear Lake ostracodes also exhibit some unusual morphologic features, such as hooked caudal processes, sharp valve margins, and unusual ornamentation (Figs. 2A, 2C, and 2G). However, the morphology and species diversity is less than in the Glenns Ferry Formation sediments (Forester, 1991b) and in other ancient extant lakes such as Lake Baikal or Lake Tanganyika (Mazepova, 1994; Park and Downing, 2000). Bear Lake also supports four species of endemic fish (Sigler and Sigler, 1987, 1996) and perhaps other taxa, but overall the lake does not have a large number of species as is observed in other lakes with endemic faunas. The reduced morphological expression and lower endemic diversity at Bear Lake may result from its oligotrophic state and possibly less complex and variable ecosystems than in other larger endemic-containing lakes (e.g., Lake Baikal or Lake Tanganyika). The reduced endemic diversity at Bear Lake may also be due to its young age and small size relative to lakes like Baikal or Tanganyika.

Bear Lake has been able to produce endemic (ostracode) faunas because of its unique hydrology and chemistry. A possible paleoshoreline is presently submerged under ~22 m of water (Colman, 2006), suggesting that Bear Lake periodically experiences substantial decreases in lake level, decreases that may or may not be climate related (Smoot and Rosenbaum, this volume). Intuitively, Bear Lake should become saline or possibly even go dry during periods of low effective moisture (e.g., the Great Salt Lake; Oviatt et al., 1999; Balch et al., 2005), resulting in the extinction of the endemic fauna. There are no evaporite

deposits or any known high-salinity-tolerant ostracode species in core BL2K-3, BL96-2, or the 120-m-long core to suggest elevated lake TDS during times of maximum aridity (e.g., the middle Holocene, OIS 5e; Dean et al., 2006). Bear Lake may never develop a high TDS water mass during arid climates because the majority of local solute inflow is calcium, magnesium, and bicarbonate (Dean et al., 2007; Bright, this volume). Carbonate precipitation (as aragonite or calcite) removes a large portion of the calcium and bicarbonate from the water column. The degree and rate of solute enrichment within the lake are then limited because the majority of the solute load is lost to carbonate precipitation. Groundwater leakage from the lake removes solutes as well. Additionally, the oxygen isotope ($\delta^{18}\text{O}$) values on bulk sediment from core BL96-2 are lower during the arid middle to late Holocene (ca. 3–5 ka) than during the latest Holocene (younger than 3 ka; Dean et al., 2006). Isotopic depletion during arid climates has been noted in other settings where groundwater is a large component of a lake's hydrologic budget (e.g., Smith et al., 1997; 2002a). A large groundwater influx derived predominantly from the Bear River Range (Bright, this volume) sustains the lake through arid climates and provides a stable and persistent habitat for the biota inhabiting the lake.

Further Research

The ostracode faunas and distribution patterns in Bear Lake provide several intriguing avenues for additional research. Further research should focus on the following: (1) Determining if, or to what extent, the methane seeps within the lake contribute to the health of the endemic ostracode fauna. Ostracodes are a key component in the diets of three of Bear Lake's endemic fish and are an integral part of the lake's food chain. The methane seeps may provide a food source or a refuge for the endemic ostracodes during times of unfavorable chemical and physical conditions. (2) Conducting a thorough sampling of the modern lake sediments, with the ostracodes identified to species level, noting which species are currently living in the lake and their distributions. (3) Identifying which species of ostracodes are being consumed by the various fish species in Bear Lake and determining if there are seasonal or spatial variations in those predation patterns. (4) Documenting soft-part anatomy and studying the genetic material of the endemic ostracodes to determine their evolutionary relationships. Do they represent a recent radiation, or are they more ancient lineages? Some of the species may be ecophenotypes or subspecies of extant local cosmopolitan forms (Fig. 2).

CONCLUSIONS

Bear Lake is contained in a tectonically active basin with a sedimentary record that may extend back nearly 6 m.y. As many as 11 species of endemic ostracodes inhabit Bear Lake, yet cosmopolitan ostracodes have been unable to successfully colonize the lake. The evolutionary reason for the genesis of the endemic ostracodes in Bear Lake is unknown, but may be

related to a combination of environmental stability, fish predation pressure, and the numerous isolated methane seeps within the lake. Extensive fish predation may also play a key role in the endemic-cosmopolitan ostracode distribution in the lake. Bear Lake contains one of the most diverse endemic ecosystems in North America, in spite of its relatively small size and oligotrophic nature. The endemic ostracodes suggest that, in addition to being a long-lived lake, Bear Lake has an environment that has remained relatively stable in spite of large fluctuations in climate, lake chemistry, and lake level. Groundwater that discharges in Bear River Range streams plays a key role in the modern hydrologic balance of Bear Lake and likely has done so through most of its existence. This persistent groundwater variable buffers the lake, to some extent, from the effects of climate change and generates a permanent lacustrine habitat suitable for the generation of endemic species.

ACKNOWLEDGMENTS

Funding for this study was provided by the U.S. Geological Survey's Earth Surface Dynamics Program. Countless conversations with Rick Forester (retired) and Scott Tolentino (Utah Division of Wildlife Resources, Bear Lake Station) have been greatly appreciated. A conversation with Dennis Shiozawa (Brigham Young University) on the development of the endemic Bear Lake whitefish complex was appreciated. Scott Tolentino was instrumental in locating and sampling the sublacustrine methane seep and lake-marginal springs. Reviews by Alison Smith and Brandon Curry contributed greatly to the improvement of this paper.

REFERENCES CITED

- Amayreh, J., 1995, Lake evaporation: A model study [Ph.D. thesis]: Logan, Utah State University, 178 p.
- Angell, R.W., and Hancock, J.W., 1989, Response of eggs of *Heterocypris incongruens* (Ostracoda) to experimental stress: *Journal of Crustacean Biology*, v. 9, p. 381–386, doi: 10.2307/1548561.
- Bailey, R.M., and Smith, G.R., 1981, Origin and geography of the fish fauna of the Laurentian Great Lakes basin: *Canadian Journal of Fisheries and Aquatic Sciences*, v. 38, p. 1539–1561, doi: 10.1139/f81-206.
- Balch, D.P., Cohen, A.S., Schnurrenberger, D.W., Haskell, B.J., Valero Garces, B.L., Beck, J.W., Cheng, H., and Edwards, R.L., 2005, Ecosystem and paleohydrological response to Quaternary climate change in the Bonneville Basin, Utah: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 221, p. 99–122, doi: 10.1016/j.palaeo.2005.01.013.
- Bartholmé, S., Samchyshyna, L., Santer, B., and Lampert, W., 2005, Subitaneous eggs of freshwater copepods pass through fish guts: Survivability, hatchability, and potential ecological implications: *Limnology and Oceanography*, v. 50, p. 923–929.
- Benson, L.V., Currey, D.R., Dorn, R.I., Lajoie, K.R., Oviatt, C.G., Robinson, S.W., Smith, G.I., and Stine, S., 1990, Chronology of expansion and contraction of four Great Basin lake systems during the past 35,000 years: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 78, p. 241–286, doi: 10.1016/0031-0182(90)90217-U.
- Birdsey, P.W., Jr., 1989, The limnology of Bear Lake: A literature review: Salt Lake City, Utah Department of Natural Resources, Publication no. 89-5, 113 p.
- Breckenridge, A., 2007, Lake Superior varve stratigraphy and implications for eastern Lake Agassiz outflow from 10,700 to 8900 cal ybp (9.5–8.0 ¹⁴C ka): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 246, p. 45–61, doi: 10.1016/j.palaeo.2006.10.026.
- Bright, J., 2009, this volume, Isotope and major-ion chemistry of groundwater in Bear Lake Valley, Utah and Idaho, with emphasis on the Bear River Range, in Rosenbaum, J.G., and Kaufman, D.S., eds., *Paleoenvironments of Bear Lake, Utah and Idaho, and its catchment*: Geological Society of America Special Paper 450, doi: 10.1130/2009.2450(04).
- Bright, J., Kaufman, D., Forester, R., and Dean, W., 2006, A continuous 250,000 yr record of oxygen and carbon isotopes in ostracode and bulk-sediment carbonate from Bear Lake, Utah-Idaho: *Quaternary Science Reviews*, v. 25, p. 2258–2270, doi: 10.1016/j.quascirev.2005.12.011.
- Broughton, J.M., 2000, Terminal Pleistocene fish remains from Homestead Cave, Utah, and implications for fish biogeography in the Bonneville Basin: *Copeia*, v. 2000, p. 645–656, doi: 10.1643/0045-8511(2000)000[0645:TPFRFH]2.0.CO;2.
- Buckley, S.B., 1975, Study of post-Pleistocene ostracod distribution in the soft sediments of southern Lake Michigan [Ph.D. thesis]: Urbana-Champaign, University of Illinois, 293 p.
- Calkin, P.E., and Feenstra, B.H., 1985, Evolution of the Erie-Basin Great Lakes, in Karrwo, P.F., and Calkin, P.E., eds., *Quaternary evolution of the Great Lakes*: St. John's, Newfoundland, Geological Association of Canada Special Publication 30, p. 149–170.
- Cohen, A.S., and Johnson, M.R., 1987, Speciation in brooding and poorly dispersing lacustrine organisms: *Palaios*, v. 2, p. 426–435, doi: 10.2307/3514614.
- Cohen, A.S., Palacios-Fest, M.R., Negrini, R.M., Wigand, P.E., and Erbes, D.B., 2000, A paleoclimate record for the past 250,000 years from Summer Lake, Oregon, USA: II. Sedimentology, paleontology and geochemistry: *Journal of Paleolimnology*, v. 24, p. 151–182, doi: 10.1023/A:1008165326401.
- Colman, S.M., 2006, Acoustic stratigraphy of Bear Lake, Utah-Idaho—Late Quaternary sedimentation patterns in a simple half-graben: *Sedimentary Geology*, v. 185, p. 113–125, doi: 10.1016/j.sedgeo.2005.11.022.
- Colman, S.M., Clark, J.A., Clayton, L., Hansel, A.K., and Larsen, C.E., 1994, Deglaciation, lake levels, and meltwater discharge in the Lake Michigan basin: *Quaternary Science Reviews*, v. 13, p. 879–890, doi: 10.1016/0277-3791(94)90007-8.
- Colman, S.M., Kaufman, D.S., Bright, J., Heil, C., King, J.W., Dean, W.E., Rosenbaum, J.G., Forester, R.M., Bischoff, J.L., Perkins, M., and McGeehin, J.P., 2006, Age model for a continuous, ca. 250-ky Quaternary lacustrine record from Bear Lake, Utah-Idaho: *Quaternary Science Reviews*, v. 25, p. 2271–2282, doi: 10.1016/j.quascirev.2005.10.015.
- Colman, S.M., Kaufman, D.S., Bright, J., Heil, C., King, J.W., Dean, W.E., Rosenbaum, J.G., Forester, R.M., Bischoff, J.L., Perkins, M., and McGeehin, J.P., 2007, Corrigendum to “Age model for a continuous, ca. 250-ky Quaternary lacustrine record from Bear Lake, Utah-Idaho”: *Quaternary Science Reviews*, v. 26, p. 1192, doi: 10.1016/j.quascirev.2007.02.006.
- Curry, B.B., 1999, An environmental tolerance index for ostracodes as indicators of physical and chemical factors in aquatic habitats: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 148, p. 51–63, doi: 10.1016/S0031-0182(98)00175-8.
- Dean, W.E., 2009, this volume, Endogenic carbonate sedimentation in Bear Lake, Utah and Idaho, over the last two glacial-interglacial cycles, in Rosenbaum, J.G., and Kaufman, D.S., eds., *Paleoenvironments of Bear Lake, Utah and Idaho, and its catchment*: Geological Society of America Special Paper 450, doi: 10.1130/2009.2450(07).
- Dean, W., Rosenbaum, J., Skipp, G., Colman, S., Forester, R., Liu, A., Simmons, K., and Bischoff, J., 2006, Unusual Holocene and late Pleistocene carbonate sedimentation in Bear Lake, Utah and Idaho, USA: *Sedimentary Geology*, v. 185, p. 93–112, doi: 10.1016/j.sedgeo.2005.11.016.
- Dean, W., Forester, R., Anderson, R., Bright, J., and Simmons, K., 2007, Influence of the diversion of Bear River into Bear Lake (Utah and Idaho) on the environment of deposition of carbonate minerals: Evidence from water and sediments: *Limnology and Oceanography*, v. 52, p. 1094–1111.
- Dean, W., Wurtsbaugh, W., and Lamarra, V., 2009, this volume, Climatic and limnologic setting of Bear Lake, Utah and Idaho, in Rosenbaum, J.G., and Kaufman, D.S., eds., *Paleoenvironments of Bear Lake, Utah and Idaho, and its catchment*: Geological Society of America Special Paper 450, doi: 10.1130/2009.2450(01).
- DeDeckker, P., 1981, Ostracodes of athalassic saline lakes: *Hydrobiologia*, v. 81, p. 131–144, doi: 10.1007/BF00048710.
- Delorme, L.D., 1969, Ostracodes as Quaternary paleoecological indicators: *Canadian Journal of Earth Sciences*, v. 6, p. 1471–1476.
- Delorme, L.D., 1970a, Freshwater ostracodes of Canada: Part I: Subfamily Cypridinae: *Canadian Journal of Zoology*, v. 48, p. 153–168.

- Delorme, L.D., 1970b, Freshwater ostracodes of Canada: Part II: Subfamily Cypridopsinae and Herpetocypridinae, and family Cycloocypridae: Canadian Journal of Zoology, v. 48, p. 253–266, doi: 10.1139/z70-042.
- Delorme, L.D., 1970c, Freshwater ostracodes of Canada: Part III: Family Candonidae: Canadian Journal of Zoology, v. 48, p. 1099–1127, doi: 10.1139/z70-194.
- Delorme, L.D., 1970d, Freshwater ostracodes of Canada: Part IV: Families Ilyocyprididae, Notodromadidae, Darwinulidae, Cytherideidae, and Entocytheridae: Canadian Journal of Zoology, v. 48, p. 1251–1259, doi: 10.1139/z70-214.
- Delorme, L.D., 1971, Freshwater ostracodes of Canada: Part V: Families Limnocytheridae, Loxoconchidae: Canadian Journal of Zoology, v. 49, p. 43–64, doi: 10.1139/z71-009.
- Delorme, L.D., 1978, Distribution of freshwater ostracodes in Lake Erie: Journal of Great Lakes Research, v. 4, p. 216–220.
- Delorme, L.D., 1982, Lake Erie oxygen: The prehistoric record: Canadian Journal of Fisheries and Aquatic Sciences, v. 39, p. 1021–1029, doi: 10.1139/f82-137.
- Delorme, L.D., and Donald, D., 1969, Torpidity of freshwater ostracodes: Canadian Journal of Zoology, v. 47, p. 997–999, doi: 10.1139/z69-160.
- Denny, J.F., and Colman, S.M., 2003, Geophysical survey of Bear Lake, Utah-Idaho, September 2002: U.S. Geological Survey Open-File Report 03-150, CD-ROM.
- Forester, R.M., 1983, Relationship of two lacustrine ostracode species to solute composition and salinity: Implications for paleohydrochemistry: Geology, v. 11, p. 435–439, doi: 10.1130/0091-7613(1983)11<435:ROTLOS>2.0.CO;2.
- Forester, R.M., 1985, *Limnocythere bradburyi* n. sp.: A modern ostracode from central Mexico and a possible Quaternary paleoclimatic indicator: Journal of Paleontology, v. 59, p. 8–20.
- Forester, R.M., 1987, Late Quaternary paleoclimate records from lacustrine ostracodes, in Ruddiman, W.F., and Wright, H.E., Jr., eds., North America and adjacent oceans during the last deglaciation: Boulder, Colorado, Geological Society of America, Geology of North America, v. K-3, p. 261–276.
- Forester, R.M., 1988, Nonmarine calcareous microfossil sample preparation and data acquisition procedures: U.S. Geological Survey Technical Procedure HP-78 R1, p. 1–9.
- Forester, R.M., 1991a, Ostracode assemblages from springs in the western United States: Implications for paleohydrology: Memoirs of the Entomological Society of Canada, v. 155, p. 181–201.
- Forester, R.M., 1991b, Pliocene-climate history of the western United States derived from lacustrine ostracodes: Quaternary Science Reviews, v. 10, p. 133–146, doi: 10.1016/0277-3791(91)90014-L.
- Forester, R.M., Colman, S.M., Reynolds, R.L., and Keigwin, L.D., 1994, Lake Michigan's Late Quaternary limnological and climate history from ostracode, oxygen isotope, and magnetic susceptibility records: Journal of Great Lakes Research, v. 20, p. 93–107.
- Forester, R.M., Smith, A.J., Palmer, D.F., and Curry, B.B., 2006, North American non-marine ostracode database NANODE, Version 1: Kent, Ohio, Kent State University, <http://www.kent.edu/nanode> (accessed January 2008).
- Fritz, S.C., Ito, E., Yu, Z., Laird, K.R., and Engstrom, D.R., 2000, Hydrologic variation in the northern Great Plains during the last two millennia: Quaternary Research, v. 53, p. 175–184, doi: 10.1006/qres.1999.2115.
- Frogley, M.R., Griffiths, H.I., and Martens, K., 2002, Modern and fossil ostracods from ancient lakes, in Holmes, J.A., and Chivas, A.R., eds., The Ostracoda: Applications in Quaternary research: Washington, D.C., American Geophysical Union, Geophysical Monograph 131, p. 167–184.
- Furtos, N.C., 1933, The Ostracoda of Ohio: Columbus, Ohio State University, Ohio Biological Survey 5, Bulletin 29, p. 411–524.
- Garcia, A.F., and Stokes, M., 2006, Late Pleistocene highstand and regression of a small, high altitude pluvial lake, Jakes Valley, central Great Basin, USA: Quaternary Research, v. 65, p. 179–186, doi: 10.1016/j.yqres.2005.08.025.
- Johnson, T.C., Scholz, C.A., Talbot, M.R., Kelts, K., Ricketts, R.D., Ngobi, G., Beuning, K., Ssemmanda, I., and McGill, J.W., 1996, Late Pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes: Science, v. 273, p. 1091–1093, doi: 10.1126/science.273.5278.1091.
- Kaufman, D.S., Bright, J., Dean, W.E., Moser, K., Rosenbaum, J.G., Anderson, R.S., Colman, S.M., Heil, C.W., Jr., Jiménez-Moreno, G., Reheis, M.C., and Simmons, K.R., 2009, this volume, A quarter-million years of paleoenvironmental change at Bear Lake, Utah and Idaho, in Rosenbaum, J.G., and Kaufman, D.S., eds., Paleoenvironments of Bear Lake, Utah and Idaho, and its catchment: Geological Society of America Special Paper 450, doi: 10.1130/2009.2450(14).
- Kennedy, B.M., 2005, Trade-offs in environmental growth conditions and predation risk relate to observed ecological separation between two closely related endemic whitefishes in Bear Lake, Utah/Idaho [M.S. thesis]: Logan, Utah State University, 84 p.
- Kennedy, B.M., Thompson, B.W., and Luecke, C., 2006, Ecological differences between two closely related morphologically similar benthic whitefish (*Prosopium spilonotus* and *Prosopium abyssicola*) in an endemic whitefish complex: Canadian Journal of Fisheries and Aquatic Sciences, v. 63, p. 1700–1709, doi: 10.1139/F06-065.
- Kitchell, J.A., and Clark, D.L., 1979, Distribution, ecology, and taxonomy of recent freshwater Ostracoda of Lake Mendota, Wisconsin: Madison, University of Wisconsin–Madison Natural History Series, no. 1, 24 p.
- Kornicker, L.S., and Sohn, I.G., 1971, Viability of ostracode eggs egested by fish and effect of digestive fluids on ostracode shells—Ecologic and paleoecologic implications, in Oertli, H.J., ed., Colloque sur la paléocéologie des ostracodes, Pau, 20 July 1970: Centre Recherches Pau-SNPA Bulletin, v. 5 (Suppl.), p. 125–135.
- Kullenberg, B., 1947, The piston core sampler: Svenska Hydrografisk-Biologiska Kommissionens Skrifter, v. 3, p. 1–40.
- Lamarra, V., Liff, C., and Carter, J., 1986, Hydrology of Bear Lake basin and its impact on the trophic state of Bear Lake, Utah-Idaho: The Great Basin Naturalist, v. 46, p. 690–705.
- Lewis, C.F.M., Moore, T.C., Jr., Rea, D.K., Dettman, D.L., Smith, A.M., and Mayer, L.A., 1994, Lakes of the Huron Basin: Their record of runoff from the Laurentide ice sheet: Quaternary Science Reviews, v. 13, p. 891–922, doi: 10.1016/0277-3791(94)90008-6.
- Lowenstein, T.K., Li, J., Brown, C., Roberts, S.M., Ku, T.-L., Luo, S., and Yang, W., 1999, 200 k.y. paleoclimate record from Death Valley salt core: Geology, v. 27, p. 3–6, doi: 10.1130/0091-7613(1999)027<0003:KYPRFD>2.3.CO;2.
- Martens, K., 1997, Speciation in ancient lakes: Trends in Ecology and Evolution, v. 12, p. 177–182, doi: 10.1016/S0169-5347(97)01039-2.
- Martens, K., and Schön, I., 1999, Crustacean biodiversity in ancient lakes: A review: Crustaceana, v. 72, p. 899–910, doi: 10.1163/1568540995038807.
- Mazepova, G., 1994, On comparative aspects of ostracod diversity in the Baikalian fauna, in Martens, K., Goddeeris, B., and Coulter, G., eds., Speciation in ancient lakes: Archiv für Hydrobiologie Ergebnisse der Limnologie, v. 44, p. 197–202.
- McConnell, W.J., Clark, W.J., and Sigler, W.F., 1957, Bear Lake: Its fish and fishing: Utah State Department of Fish and Game, Idaho Department of Fish and Game, Wildlife Management Department of Utah State Agricultural College, 76 p.
- McCune, A.R., 1987, Lakes as laboratories of evolution: Endemic fishes and environmental cyclicity: Palaios, v. 2, p. 446–454, doi: 10.2307/3514616.
- McLay, C.L., 1978a, Comparative observations on the ecology of four species of ostracodes living in a temporary freshwater puddle: Canadian Journal of Zoology, v. 56, p. 663–675, doi: 10.1139/z78-094.
- McLay, C.L., 1978b, The population biology of *Cyprinotus carolinensis* and *Herpetocypris reptans* (Crustacea, Ostracoda): Canadian Journal of Zoology, v. 56, p. 1170–1179, doi: 10.1139/z78-161.
- Mellors, W.K., 1975, Selective predation of ephippal *Daphnia* and the resistance of ephippal eggs to digestion: Ecology, v. 56, p. 974–980, doi: 10.2307/1936308.
- Miller, B.A., 2006, The phylogeography of *Prosopium* in western North America [M.S. thesis]: Provo, Brigham Young University, 164 p.
- Mourguiart, P., and Montenegro, M.E., 2002, Climate changes in the Lake Titicaca area: Evidence from ostracode ecology, in Holmes, J.A., and Chivas, A.R., eds., The Ostracoda: Applications in Quaternary Research: Washington, D.C., American Geophysical Union, Geophysical Monograph 131, p. 151–165.
- Oviatt, J.G., Thompson, R.S., Kaufman, D.S., Bright, J., and Forester, R.M., 1999, Reinterpretation of the Burmester core, Bonneville Basin, Utah: Quaternary Research, v. 52, p. 180–184, doi: 10.1006/qres.1999.2058.
- Owen, R.B., Crossley, R., Johnson, T.C., Tweddle, D., Kornfield, I., Davison, S., Eccles, D.H., and Engstrom, D.E., 1990, Major low levels of Lake Malawi and their implications for speciation rates in cichlid fishes: Proceedings of the Royal Society of London, ser. B, Biological Sciences, v. 240, p. 519–553.
- Park, L.E., and Downing, K.F., 2000, Implications of phylogeny reconstruction for ostracod speciation modes in Lake Tanganyika: Advances in Ecological Research, v. 31, p. 303–330, doi: 10.1016/S0065-2504(00)31017-0.

- Quade, J., Mifflin, M.D., Pratt, W.L., McCoy, W., and Burckle, L., 1995, Fossil spring deposits in the southern Great Basin and their implications for changes in water-table levels near Yucca Mountain, Nevada, during Quaternary time: Geological Survey of America Bulletin, v. 107, p. 213–230, doi: 10.1130/0016-7606(1995)107<0213:FSDITS>2.3.CO;2.
- Quade, J., Forester, R.M., Pratt, W.L., and Carter, C., 1998, Black mats, spring-fed streams, and late-Glacial-age recharge in the southern Great Basin: Quaternary Research, v. 49, p. 129–148, doi: 10.1006/qres.1997.1959.
- Reed, K.M., Dorschner, M.O., Todd, T.N., and Phillips, R.B., 1998, Sequence analysis of the mitochondrial DNA control region of ciscoes (genus *Coregonus*): Taxonomic implications for the Great Lakes species flock: Molecular Biology, v. 7, p. 1091–1096.
- Roca, J., and Wansard, G., 1997, Temperature influence on development and calcification of *Herpetocypris brevicaudata* Kaufmann, 1900 (Crustacea: Ostracoda) under experimental conditions: Hydrobiologia, v. 347, p. 91–95, doi: 10.1023/A:1003067218024.
- Rutaisire, J., Booth, A.J., Masebe, C., Nyakaana, S., and Muwanika, V.B., 2004, Evolution of *Labeo victoriamus* predates the Pleistocene desiccation of Lake Victoria: Evidence from mitochondrial DNA sequence variation: South African Journal of Science, v. 100, p. 607–608.
- Sigler, W.F., and Sigler, J.W., 1987, Fishes of the Great Basin: A natural history: Reno, University of Nevada Press, 425 p.
- Sigler, W.F., and Sigler, J.W., 1996, Fishes of Utah: A natural history: Salt Lake City, University of Utah Press, 375 p.
- Smart, E.W., 1958, An ecological study of the bottom fauna of Bear Lake, Idaho and Utah [Ph.D. thesis]: Logan, Utah State University, 88 p.
- Smith, A.J., 1993, Lacustrine ostracodes as hydrochemical indicators in lakes of the north-central United States: Journal of Paleolimnology, v. 8, p. 121–134, doi: 10.1007/BF00119785.
- Smith, A.J., Donovan, J.J., Ito, E., and Engstrom, D.R., 1997, Ground-water processes controlling a prairie lake's response to mid-Holocene drought: Geology, v. 25, p. 391–394, doi: 10.1130/0091-7613(1997)025<0391:GWPCAP>2.3.CO;2.
- Smith, A.J., Donovan, J.J., Ito, E., Engstrom, D.R., and Panek, V.A., 2002a, Climate-driven hydrologic transients in lake sediment records: Multiproxy record of mid-Holocene drought: Quaternary Science Reviews, v. 21, p. 625–646, doi: 10.1016/S0277-3791(01)00041-5.
- Smith, D.G., 1985, Recent range expansion of the freshwater mussel *Anodonta imbecilis* and its relationship to clupeid fish restoration in the Connecticut River system: Freshwater Invertebrate Biology, v. 4, p. 105–108, doi: 10.2307/1467182.
- Smith, G.R., 1981, Late Cenozoic freshwater fishes of North America: Annual Review of Ecology and Systematics, v. 12, p. 163–193, doi: 10.1146/annurev.es.12.110181.001115.
- Smith, G.R., and Todd, T.N., 1984, Evolution of species flocks of fishes in north temperate lakes, in Echelle, A., and Kornfield, I., eds., Evolution of fish species flocks: Orono, University of Maine, Orono Press, p. 45–68.
- Smith, G.R., Stokes, W.L., and Horn, K.F., 1968, Some Late Pleistocene fishes of Lake Bonneville: Copeia, v. 1968, p. 807–816, doi: 10.2307/1441848.
- Smith, G.R., Dowling, T.E., Gobalet, K.W., Lugaski, T., Shiozawa, D.K., and Evans, R.P., 2002b, Biogeography and timing of evolutionary events among Great Basin fishes, in Hershler, R., Madsen, D.B., and Currey, D.R., eds., Great Basin aquatic systems history: Smithsonian Contributions to the Earth Sciences, no. 33, p. 175–234.
- Smoot, J.P., and Rosebaum, J.G., 2009, this volume, Sedimentary constraints on late Quaternary lake-level fluctuations at Bear Lake, Utah and Idaho, in Rosenbaum, J.G., and Kaufman, D.S., eds., Paleoenvironments of Bear Lake, Utah and Idaho, and its catchment: Geological Society of America Special Paper 450, doi: 10.1130/2009.2450(12).
- Spencer, R.J., Baedeker, M.J., Eugster, H.P., Forester, R.M., Goldhaber, M.B., Jones, B.F., Kelts, K.F., McKenzie, J., Madsen, D.B., Rettig, S.L., and Bowser, C.J., 1984, Great Salt Lake, and precursors, Utah: The last 30,000 years: Contributions to Mineralogy and Petrology, v. 86, p. 321–334, doi: 10.1007/BF01187137.
- St. George, S., and Nielson, E., 2002, Hydroclimatic change in southern Manitoba since A.D. 1409 inferred from tree rings: Quaternary Research, v. 58, p. 103–111, doi: 10.1006/qres.2002.2343.
- Stager, J.C., Day, J.J., and Santini, S., 2004, Origin of the superflock of cichlid fishes from Lake Victoria, East Africa: Comment: Science, v. 304, p. 963, doi: 10.1126/science.1091978.
- Thompson, B.W., 2003, An ecological comparison of two endemic species of whitefish in Bear Lake, Utah/Idaho [M.S. thesis]: Logan, Utah State University, 131 p.
- Thompson, R.S., 1996, Pliocene and early Pleistocene environments and climates of the western Snake River Plain, Idaho: Marine Micropaleontology, v. 27, p. 141–156, doi: 10.1016/0377-8398(95)00056-9.
- Thompson, R.S., Whitlock, C., Bartlein, P.J., Harrison, S.P., and Spaulding, W.G., 1993, Climatic changes in the western United States since 18,000 yr B.P., in Wright, H.E., Jr., Kutzbach, J.E., Webb, T., III, Ruddiman, W.F., Street-Perrott, F.A., and Bartlein, P.J., eds., Global climates since the Last Glacial Maximum: Minneapolis, University of Minnesota Press, p. 468–513.
- Todd, T., and Smith, G.R., 1992, A review of differentiation in Great Lakes ciscoes: Polskie Archiwum Hydrobiologii, v. 39, p. 261–267.
- Tolentino, S.A., and Thompson, B.W., 2004, Meristic differences, habitat selectivity and diet separation of *Prosopium spilonotus* and *P. abyssicola*: Annales Zoologici Fennici, v. 41, p. 309–317.
- Toline, C.A., Seamons, T.R., and Davis, C., 1999, Quantification of molecular and morphological differentiation of whitefish taxa in Bear Lake: Salt Lake City, Final Report to the Utah Division of Natural Resources, Project F-47-R, Study 5, 53 p.
- Verheyen, E., Salzburger, W., Snoeks, J., and Meyer, A., 2003, Origin of the superflock of cichlid fishes from Lake Victoria, East Africa: Science, v. 300, p. 325–329, doi: 10.1126/science.1080699.
- Vinyard, G., 1979, An ostracode (*Cypridopsis vidua*) can reduce predation from fish by resisting digestion: American Midland Naturalist, v. 102, p. 188–190, doi: 10.2307/2425084.
- Vuorinen, J.A., Bodaly, R.A., Reist, J.D., and Luczynski, M., 1998, Phylogeny of five *Prosopium* species with comparisons with other Coregonine fishes based on isozyme electrophoresis: Journal of Fish Biology, v. 53, p. 917–927.
- Wells, T.M., Cohen, A.S., Park, L.E., Dettman, D.L., and McKee, B.A., 1999, Ostracode stratigraphy and paleoecology from surficial sediments of Lake Tanganyika, Africa: Journal of Paleolimnology, v. 22, p. 259–276, doi: 10.1023/A:1008046417660.
- Wurtsbaugh, W.A., and Hawkins, C., 1990, Trophic interactions of fish and invertebrates in Bear Lake, Utah/Idaho: Logan, Ecology Center Special Publication, 167 p.

Geological Society of America Special Papers

Ostracode endemism in Bear Lake, Utah and Idaho

Jordon Bright

Geological Society of America Special Papers 2009;450; 197-216
doi:10.1130/2009.2450(08)

E-mail alerting services click www.gsapubs.org/cgi/alerts to receive free e-mail alerts when new articles cite this article

Subscribe click www.gsapubs.org/subscriptions to subscribe to Geological Society of America Special Papers

Permission request click www.geosociety.org/pubs/copyrt.htm#gsa to contact GSA.

Copyright not claimed on content prepared wholly by U.S. government employees within scope of their employment. Individual scientists are hereby granted permission, without fees or further requests to GSA, to use a single figure, a single table, and/or a brief paragraph of text in subsequent works and to make unlimited copies of items in GSA's journals for noncommercial use in classrooms to further education and science. This file may not be posted to any Web site, but authors may post the abstracts only of their articles on their own or their organization's Web site providing the posting includes a reference to the article's full citation. GSA provides this and other forums for the presentation of diverse opinions and positions by scientists worldwide, regardless of their race, citizenship, gender, religion, or political viewpoint. Opinions presented in this publication do not reflect official positions of the Society.

Notes