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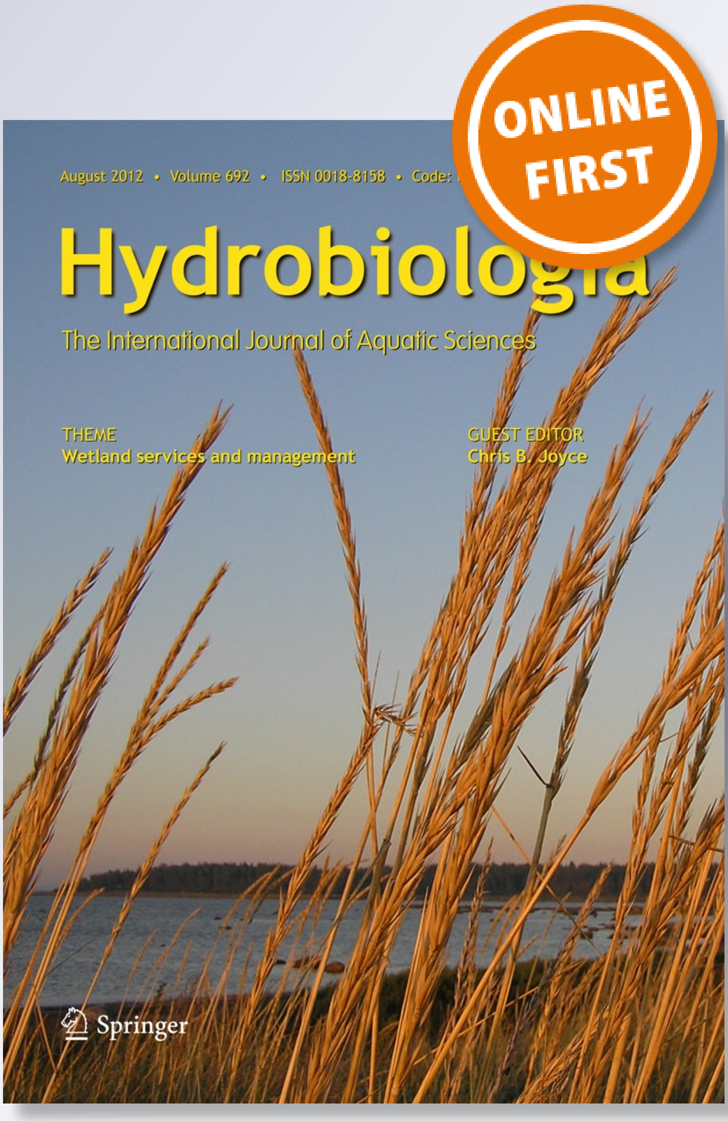

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PRIMARY RESEARCH PAPER

Substratum associations and depth distribution of benthic invertebrates in saline Walker Lake, Nevada, USA

David B. Herbst · **R. Bruce Medhurst** ·
Scott W. Roberts · **Robert Jellison**

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Abstract Walker Lake, a terminal salt lake in western Nevada, is undergoing rapid changes because of falling lake level and rising salinity, affecting the potential habitat of benthic invertebrates that supply food to native fish and birds. Benthic invertebrate surveys were conducted within different substratum size classes and macrophyte beds in the nearshore littoral shallows (<1 m) and in the deeper offshore littoral (2–10 m) and profundal (>10 m) zones of the lake. Samples were dominated by the chironomid midges *Cricotopus ornatus* and *Tanypus grodhausi*; the damselfly *Enallagma clausum*; and an oligochaete worm of the genus *Monopylephorus*. Midges showed distinct depth preferences, with *Cricotopus* found primarily in the shallow littoral, and *Tanypus* found in the lower littoral and profundal regions. *Enallagma* occurred throughout the littoral region but was reduced in abundance below 10 m. *Cricotopus* and *Enallagma* were most abundant on cobble rock substratum and macrophytes. Sand and small gravel substrata supported few invertebrates except oligochaetes, which were most common in shallow littoral areas. The extent of *Ruppia* beds was determined using hydroacoustic sounding and showed that these beds were most well-developed in a zone from 1.25 to 5 m depth. The estimated area of productive shallow littoral zone habitat at different lake levels showed that coverage was lowest near the current surface elevation. Rising lake levels would result in expansion of suitable habitat area, and while falling levels could also expand nearshore habitat, this would likely occur on areas of poorer substratum quality and under high salinities that may inhibit growth.

Keywords Walker Lake · Saline lakes · Substratum preference · Depth distribution · Lentic benthos · Benthic invertebrates · Littoral zone

Introduction

Substratum preferences and depth distribution of benthic invertebrates in salt lakes can provide important insights to features that influence the suitability of habitats among different lakes or as lake levels change (Herbst, 1990; Herbst & Bradley, 1993; Verschuren et al., 2000). Protection from wave action or fish and other predators, food quantity and quality, oxygen requirements, competition for food and space, and body morphology are among the factors that affect where benthic invertebrates reside in littoral and sublittoral environments (Ward, 1992). Defining these relations for a benthic community gives a spatial

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D. B. Herbst (✉) · R. B. Medhurst · S. W. Roberts · R. Jellison
Sierra Nevada Aquatic Research Laboratory, University of California, 1016 Mt. Morrison Road, Mammoth Lakes, CA 93546, USA
e-mail: herbst@lifesci.ucsb.edu

description that can be used to show potential food web relations, frame habitat requirements, identify vulnerabilities to habitat alteration, and design monitoring programs.

The benthic environment of Walker Lake consists of mud deposits in the profundal zone, beds of the rooted macrophyte *Ruppia maritima* L. (widgeon grass) growing with epiphytic filamentous algae *Cladophora glomerata* (L.) Kuetzing in the nearshore and offshore littoral zone, and mixed sand, gravel–pebble, and cobble rock deposits in shallow littoral regions. Some rock formations at this lake include stromatolite deposits (Osborne et al., 1982). The studies reported here provide a quantitative set of shallow littoral (defined here as eulittoral at <1 m; according to Wetzel, 2001), and sublittoral samples (defined here as infralittoral at 2–8 m, and as profundal at 10–16 m), from combined early and late summer surveys (June and September), and stratified by the substratum types. These data establish baseline conditions for monitoring further changes in the environment of Walker Lake. Surveys of the distribution and abundance of benthic invertebrates also provides background on the availability of benthic food resources to the native fish of the lake—the tui chub (*Siphateles bicolor* Cope) and Lahontan cutthroat trout (*Oncorhynchus clarki henshawi* Gill & Jordan). Since the late nineteenth century the lake level has declined over 49 m and concentrated in salinity from 2.5 to 19 g/l total dissolved solutes. The population of trout native to Walker Lake was lost when spawning runs in the Walker River were depleted by low flows in the 1940s–1950s. The lake was re-stocked with hatchery-raised trout, but these also have failed to persist. Agricultural diversions remain unabated and lake levels continue to fall. The US Fish and Wildlife Service is leading a cutthroat trout recovery program which includes Walker Lake and is linked to restoring lake level and sustaining food resources (USFWS, 2010). The tui chub continues to survive in Walker Lake, but may be extirpated if salinities rise further or the food web is disrupted. Walker is one of only four large terminal saline lakes that remain of the ancient Pleistocene lake systems of the western Great Basin—the others being Pyramid in Nevada, Mono in California, and Abert in Oregon. Conservation management of their distinctive native biological communities should be a priority for preserving these rare ecosystems. As with these other alkaline saline lakes, Walker has a chemical composition composed of a mix of sodium, chloride, sulfate, and carbonate (Cooper & Koch, 1984), that are an important determinant of the potential species inhabiting this lake (Herbst, 2001).

The objective of this study was to survey the habitat preferences for different substratum features and depth profiles among the present-day benthic invertebrates of Walker Lake. Description of the availability of preferred habitat types and distribution will be useful in understanding how benthic invertebrate production might respond to changing lake levels that are caused by diversion of inflow from the Walker River.

Methods

Environmental setting

Walker Lake is a large, deep (~23 m in 2012), terminal salt lake in western Nevada (Table 1; and Jellison, unpublished data). In the summer of 2007 when sampling occurred, salinity was 15.6–16.4 g/l, increasing slightly as lake elevation declined from 1200.0 m in early June to 1199.2 m in late October. Water clarity (Secchi depth) was high (6–10 m) in summer and somewhat lower (3–5 m) throughout winter and spring when a modest phytoplankton bloom occurred under conditions of increased nitrogen availability and less zooplankton grazing. Nearshore and epilimnetic summer temperatures ranged from 20 to 25°C, with a thermocline deepening from 7 to 12 m. During summer stratification the epilimnion has dissolved oxygen in the range of 6.7–8.7 mg/l, but the hypolimnion becomes anoxic. The lake is monomictic, with turnover occurring usually in October, followed by winter holomixis.

Eulittoral sampling

During early summer (mid-June), and late summer (mid-September) of 2007, samples were collected from the shallow littoral zone in less than 1 m at four locations around the lake (SW, SE, NE, and NW; Fig. 1; Table 1). At each location, different substrata were sought to obtain 12 samples representing the range of conditions found at that site. We identified four dominant types: sand (<2 mm), gravel mixed with pebble (2–65 mm range), cobble (65–250 mm

Table 1 Walker Lake environmental setting and sample stations in 2007

Surface elevation, June–September	1200.0–1199.4 m
Surface area of lake at 1,200 m	132.4 km^2
Salinity, summer average	16 g/l and rising as the lake drops
Maximum depth	26 m
Thermocline, summer average[a]	10 m
Temperature in summer, nearshore	20–25°C
Secchi depth, winter[a]	3–5 m
Secchi depth, summer[a]	6–10 m
Ammonium, epilimnion[a]	<0.05 mg/l
Ammonium, hypolimnion late summer[a]	∼0.5 mg/l
Nitrate, epilimnion[a]	0.05 mg/l winter to <0.02 mg/l summer
Chl a, pelagic epilimnion[a]	3–4 mg/m^3 spring, 1–1.5 mg/m^3 summer
Dissolved oxygen, epilimnion[a]	6.7–8.7 mg/l

Sample station and name	Latitude	Longitude
SW: Sportsmans Beach	38.690556	−118.76575
SE: Dunes road access from East road	38.645139	−118.6685
NE: East road at Army 11 RR sign	38.7225	−118.669528
NW: 20-mile Beach	38.7535	−118.758347

[a] *Source*: R. Jellison, unpublished data

range), and beds of filamentous algae usually mixed with the macrophyte *Ruppia maritima* (often entwined, but sometimes found separately). A total of 96 littoral samples were collected with the 1-m depth zone, over a range from 7 to 100 cm, consisting of 35 from sand, 33 from macrophytes beds, 16 from cobble, and 12 from gravel–pebble.

Sand and gravel–pebble substrata were sampled using a bucket from which the bottom had been removed (20 cm diameter), that was placed over the sample area, and pushed into the substratum. Surface substratum materials including invertebrates were then removed with repeated sweeps of a fine-mesh aquarium net (0.1 mm mesh) over and through the stirred substrata. These repeated sweeps were placed in a bucket of clean water and with further stirring, the lighter fraction containing invertebrates was poured through the fine-mesh net and the collected material then preserved in 90% ethanol. Rose Bengal stain was added to enhance contrast for later sample sorting in the laboratory.

Cobble substrata were sampled individually by transfer of whole rocks into a fine-mesh aquarium net held underwater and brought quickly to the surface so few if any invertebrates could escape. All material washed from the rock surface was then transferred as above into a fine-mesh collecting net and preserved. Cobble dimensions were recorded as length (L, longest axis), width (W, maximum perpendicular axis), and circumference (C, longest perimeter in LW plane). Median size of cobbles was 120 × 85 cm, length × width. These were used to calculate the areal two-dimensional surface area of each rock as length x width rectangular area corrected for rounded shape by the ratio of circumference to maximum possible perimeter [$= (L \times W) \times (C/(2L + 2W))$], and used to compute density per area for associated invertebrates. Given the distribution of substrata around the lake, densities on each substratum could be used to estimate lakewide abundance and areas of high and low productivity.

Beds of the macrophyte *Ruppia maritima* (widgeon grass) and associated epiphytic filamentous algae were sampled using a 4 × 5 cm fine-mesh aquarium net. Macrophytes were not strictly epibenthic but formed strands suspended in the water column from the rooted base of the plant. These were sampled by detaching the *Ruppia* at the base of the plant and sweeping the sample net from this point up through the overlying column of water to collect the strand of plant material within that volume. This material was then placed in a bucket and sorted in shallow white pans to separate and remove most of the algae-plant material before preservation of the remnant invertebrates. Density of the associated invertebrates was expressed as numbers per area of the net opening (0.0125 m^2)—as the projected areal cover sampled from the bottom attachment point to the water surface. All algae-plant material removed was squeeze-dried (water wrung-out by hand) to remove adherent water, and wet-weighed with a Pesola spring-scale. This represented a varied height of macrophytes strands from 5 to 75 cm above the benthic surface, and a water volume as the product of sample depth and net area.

Infralittoral and profundal sampling

Deeper offshore samples were collected from a boat using an Ekman grab (15 × 15 cm opening) along west and east transects from shore toward the central lake basin, taking duplicates at each depth of 2, 4, 6, 8, 10, 12, 14, and 16 m on 16–17 June, and 24 October 2007 (Fig. 1). Sample processing consisted of placing each dredge sample in a bucket of clean water, stirring and pouring off the light organic fraction through a fine-mesh aquarium net. Most of the invertebrates were present in this fraction and these were then preserved in collection jars in 90% ethanol. The heavier inorganic substratum fraction and macrophytes strands remaining in the bucket were then inspected in shallow white pans until all invertebrates were picked out and placed in the collection jars.

Laboratory processing of samples

Samples were either sorted in their entirety, removing and identifying each invertebrate found, or subsamples were taken using a Folsom rotating drum splitter to handle samples with high invertebrate densities or large amounts of remnant plant debris and detritus. Counts of larvae and pupae were made for midges (chironomidae) present, and for larval versus adult forms of dytiscidae (beetles) and corixidae (water boatmen). Identifications were possible to the species level in most cases.

Macrophyte surveys

The extensive beds of *Ruppia* likely represent a significant proportion of the lake's primary production and directly affect the benthic macroinvertebrate community and tui chub population by providing habitat, food, and refuge. Changes in the extent and productivity of these beds accompanying salinity and lake levels changes will thereby affect ecosystem processes and trophic relationships including those of the cutthroat trout. Hydroacoustic surveys of *Ruppia* distribution were conducted using a 200 kHz, digital 6° splitbeam echosounder (BioSonics, Inc.; Model DT-X). Positional data were acquired with a differential GPS unit (JRC-Corp. D-GPS212) linked with the Biosonics surface unit for direct integration with the echograms via a field computer (Panasonic Toughbook CF30) running Biosonic's visual acquisition software (Visual Acquisition Ver. 5.0). The echosounder was factory calibrated and checked in situ using a standard tungsten-carbide sphere. The acquisition threshold was set at the maximum sensitivity, -130 dB, to allow maximum flexibility in post-processing. The transducer was deployed amidship on the gunwale of a 5-m boat in a vertical orientation with the face of the unit 0.25 cm below the surface of the water. The ping rate was 5 pings per second with pulse duration of 0.4 ms. Twenty-four transects were taken perpendicular to shore at $\sim$2 km intervals around the lake. Transects were begun at a depth beyond the growth of macrophytes ($\sim$10 m depth) and run directly toward shore at 1.0–2.0 m s^{-1} yielding sample points at approximately 20–40 cm intervals. Along the western edge of the lake, 12 transects averaged 270 m length, 7 on the east shore averaged 420 m, and 5 ranged from 1,100 to 3,500 m in the shallow northern and southern portions of the lake. Post-processing of recordings were converted from Biosonic's raw dt4 format to Sonar5-Pro's format with Sonar5-Pro's (Ver. 6.0.1) built in conversion utility with a time varied gain function of 40 log R and phase file included. Transducer-specific parameters were extracted from the raw Biosonic's file and measured environmental parameters (temperature, salinity, pH) used to calculate the absorption coefficient and sound speed appropriate for Walker Lake water. The amplitude echogram threshold was set to -100 dB well below the range of targets of interest.

The bottom was delineated using Sonar5-Pro's bottom detection algorithms in which the echogram is pre-processed with low pass running mean filter with a sample height of 1 and a width of 5 pings. An image analysis algorithm in which the sonogram was searched from top to bottom with a detection threshold of -30 dB provided the most consistent results in

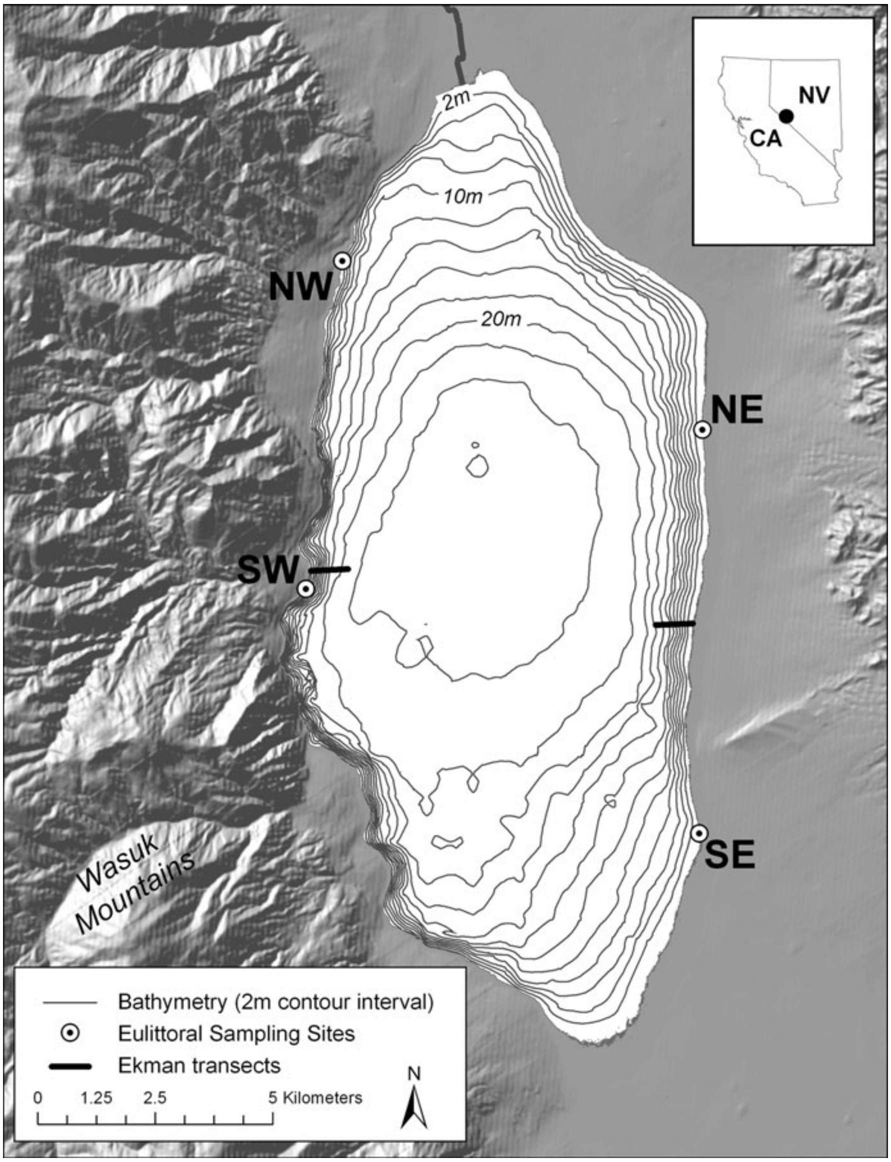

Fig. 1 Map of Walker Lake showing locations of benthic eulittoral sample stations, and bars on lake show west and east Ekman grab transects of 2007. Morphometry and depth profiles relative to surface elevation of 1,200 m in 2007. Walker River enters at north end. *Inset* shows California and Nevada and location of lake

preliminary analysis of various echograms. However, the automated bottom detection algorithm required extensive manual editing as the strength of echoes from dense macrophytes sometimes exceeded −30 dB and the signal was often fully attenuated (no echo recorded) in the shallow dense beds. Except in a few areas with prominent well-defined bottom anomalies and along steep portions of western cliffs, the bottom depth of Walker Lake changes gradually. Thus, strong echoes (>−30 dB) from dense macrophytes are almost always visually apparent and in these cases, the bottom line was manually drawn between well-defined bottom signals. Pings in which the signal was fully attenuated by dense algae or echoes absent for other unknown reasons were omitted from the analysis. The vertical extent of the macrophytes was determined with the same algorithm except with a threshold of −65 dB. Although lower thresholds are sometimes used, we found this resulted in too much noise from macroinvertebrates and other features (e.g., small bubbles and floating algal clumps) to be practical.

The height of vegetative growth increased as depth decreased along a given transect with growth often extending to the surface in waters <5 m depth. The transducer was fixed at 0.25 m depth and near-field distortions typically extend 0.6–1.0 beyond that. For this reason, we only collected and analyzed data from 1.25 m depth and below. Because the full height of *Ruppia* in the upper water column (0–1.25 m depth) could not be measured by the echosounder, a more accurate but still conservative adjusted mean height was calculated by assuming that the tops of those plants extended half-way into that upper layer. Further inshore at depths of 0–1.25 m, macrophyte density was often reduced or absent due to the nearshore energetic wave zone.

Area of eulittoral habitat at different lake levels

The area of shallow littoral habitat within the upper 2-m depth zone for rising or receding lake level was calculated from the relation between lake elevation and lake surface area developed from Walker Lake bathymetry and mapping produced in 2006 (Lopes & Smith, 2007). This assumes that this area can be used to define the zone within which benthos are usually most abundant and diverse at any lake level, including most of the larger and emerging *Enallagma*, and nearly all *Cricotopus* and other saline lake invertebrates.

Results

From the 96 eulittoral and 31 sublittoral samples collected in 2007, 10 different invertebrate taxa were found, of which only four could be considered abundant (thousands per square meter) and had distinctive habitat preferences (Fig. 2)—the midges *Cricotopus* (*Sylvestris* group) *ornatus* Meigen and *Tanypus grodhausi* Sublette, the damselfly *Enallagma clausum* Morse, and an the oligochaete worm of the genus *Monopylephorus* Levinsen. In the shallow littoral, adults and larvae of the dytiscid water beetle *Hygrotus masculinus* Crotch were fairly common at some sites (50 m^{-2} on average), but all other taxa densities averaged below 10 m^{-2}—the water boatman *Corisella decolor* Uhler, the water beetle *Laccobius* (larvae only), and various dipteran larvae including the alkali fly *Ephydra hians* Say, the biting midge *Culicoides*, and the deer fly *Chrysops*. While we found abundant valves of several types of ostracods, we never detected living specimens in any samples. Our sampling also confirmed the disappearance of the amphipod *Hyalella* (reported in abundance in the 1970s–1980s; Herbst, pers. obs., and M. Sevon, unpublished report of the Nevada Division of Wildlife). Previous unpublished records of midges *Chironomus* and *Pelopia* could not be confirmed, although we found a few head capsules of *Chironomus* in deeper samples. Earlier identifications as *Pelopia* should be considered to be *Tanypus* since these genera are synonymous.

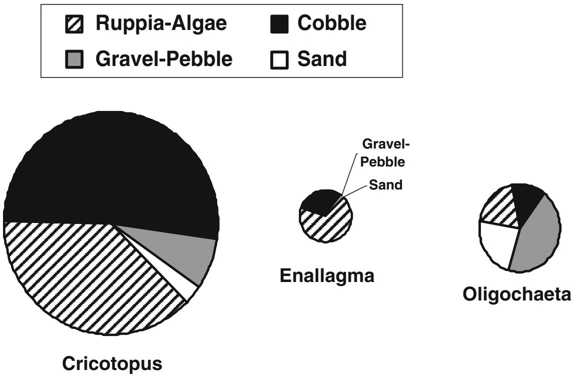

Fig. 2 Eulittoral habitat preferences of dominant benthic invertebrate taxa of this zone according to the relative abundance on each substratum. Area of pie charts scaled to average abundance over all substratum types. Actual mean densities by substratum for each shown in Fig. 3

The orthoclad midge *Cricotopus ornatus* was the most abundant invertebrate of the eulittoral zone (Figs. 2, 3), with a mean density of about 15,700 m^{-2} averaged over all substratum types, and there was a marked decline in abundance with depth in the infralittoral zone, and was absent in most samples of the profundal zone at 10 m or deeper (Fig. 4). This midge was most abundant on cobble at a mean density of nearly 35,000 m^{-2}, and in macrophytes at 25,000 m^{-2}. Densities on sand and gravel–pebble substrata were only about 2,000–5,000 m^{-2}, respectively. Pupae of this species became most abundant in the September samples with a mean density of 259 m^{-2} in 71% of samples compared to June collections of 56 m^{-2} in just 27% of samples, corresponding to an observed early autumn emergence of adults.

In contrast to *Cricotopus*, the Tanypod midge *Tanypus grodhausi* was abundant only in the deeper infralittoral and profundal samples (mean density of nearly 15,000 m^{-2} across depths), and was scarce in the shallow littoral zone, being found in less than 20% of samples at only about 100 m^{-2} on average (Fig. 4). *Tanypus* showed no clear preference for macrophytes/

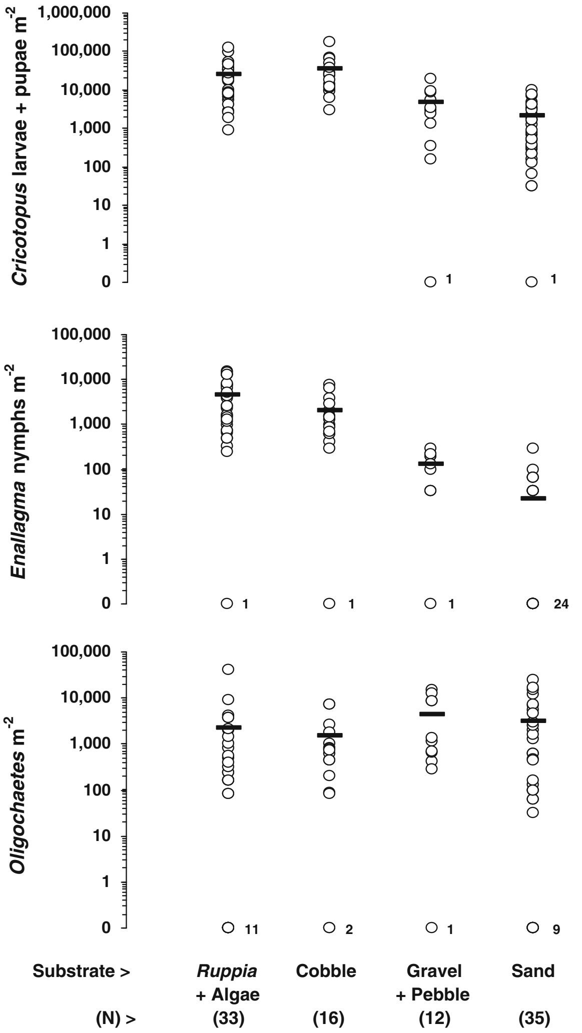

Fig. 3 Standing stock densities of benthic invertebrates on different eulittoral substrata. Separate samples from June and September 2007 shown as *circles*, and means as *horizontal bars* (note log scale). *Cricotopus* on *upper panel*, *Enallagma* on *center panel*, *Monopylephorus* oligochaetes on *lower panel*. Number of total samples on each substratum shown below each type, and number of absences on each type shown next to zero density point for each taxon

algae cover in infralittoral samples and persisted in high abundance even at depths below 10 m.

Damselfly nymphs in shallow littoral samples were most common in macrophytes/algae beds (4,500 m^{-2}) and cobble rocks (2,000 m^{-2}), but appeared to avoid sand and gravel–pebble where densities were only 21–130 m^{-2}, respectively, and were absent on almost 70% of sand samples (Figs. 2, 3). Nymphs were of near-equal abundance in the shallow littoral zone and at infralittoral depths of 2–8 m (Fig. 4, mean densities over all substrata of about 1,900 and 2,600 m^{-2}, respectively), but none below the eulittoral were larger than 7–8 mm whereas eulittoral nymphs covered a broad size range up to the 15–20 mm mature size. In deeper water of 10 m or below, densities dropped to about 600 m^{-2}, significantly less than overall littoral densities with or without sand habitat included ($P < 0.0002$ unequal variance two-tailed t test). Nymphs in the infralittoral were most often associated with macrophytes beds. This may be due in part to the fact that most of the profundal samples lacked *Ruppia* whereas moderate infralittoral depths (2–8 m) were dominated by *Ruppia* beds, and nymphs were most abundant in this zone. The range of densities in the eulittoral zone in terms of volume of macrophytes sampled (as opposed to areal estimates of Fig. 3) were an average of about 184,000 per cubic meter for

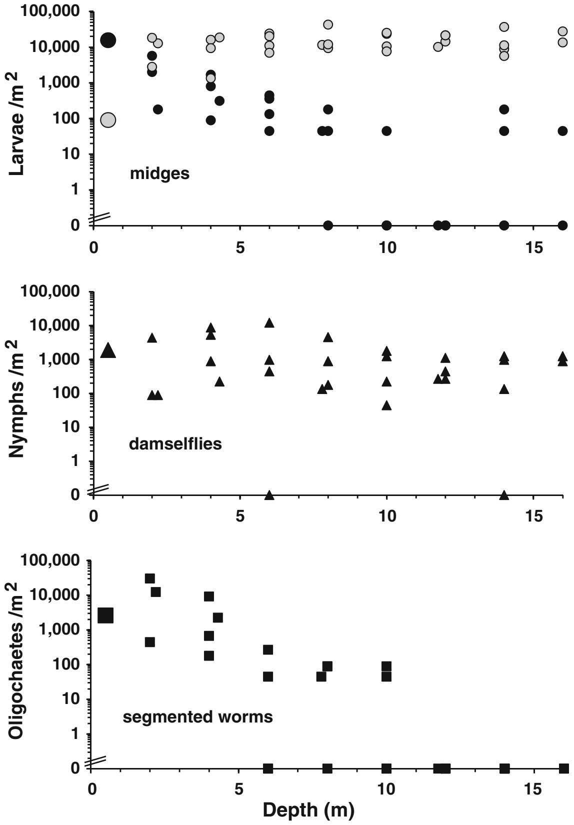

Fig. 4 Depth distribution of density for benthic invertebrates in Walker Lake samples from June and September 2007. Enlarged point between 0 and 1 m depth shows the mean eulittoral density for contrast. *Upper panel* shows midges (*Cricotopus* in *black* and *Tanypus* in *gray*); *middle panel*, *Enallagma*; and *lower panel*, *Monopylephorus* oligochaetes. Break in log scale at zero to indicate actual absences

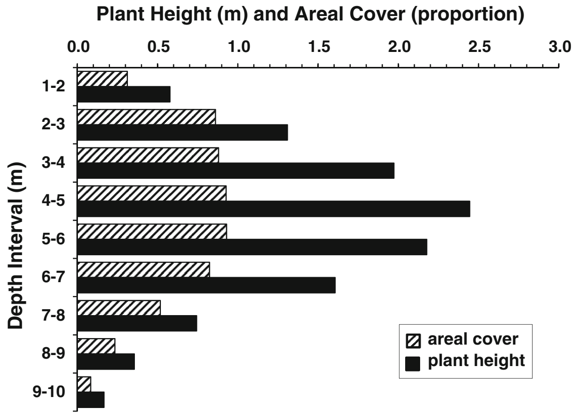

Fig. 5 Distribution of macrophytes by average proportion of areal cover and adjusted average height over depth intervals to 10 m. Adjusted estimate of average plant height assumes that the tops of *Ruppia* extend halfway into the upper 1.25 m of the water column. Depth layer 1–2 m begins at 1.25 m, the limit of hydroacoustic resolution

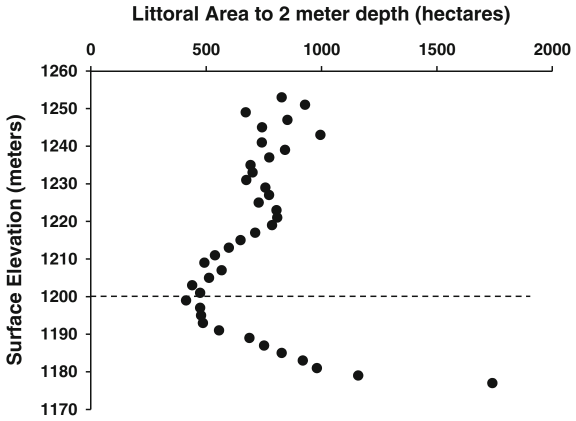

Fig. 6 Littoral habitat area within 0–2 m depth zone at different lake surface elevations of Walker Lake (based on data of Lopes & Smith, 2007). *Dashed line* shows 2007 surface elevation at 1,200 m

Cricotopus larvae and 26,000 for *Enallagma* nymphs (and ca. 18,000 and 4,000 per kg wet weight of vegetation-algae, respectively).

Oligochaetes were abundant in eulittoral samples (average density >2,600 m^{-2}), but in contrast to *Cricotopus* and *Enallagma*, they were most often associated with gravel–pebble substrata and sand (Figs. 2, 3). While abundant in the upper infralittoral at 2–4 m, they declined at 6–10 m, and were found in only a single sample deeper than this (Fig. 4).

Hydroacoustic surveys of macrophytes showed areal coverage in the turbulent high energy 1.25–2 m depth layer ranged from 11 to 65% with a lakewide mean of 31% (Fig. 5). The lakewide mean of areal coverage then increased to 82–93% between 2 and 7 m depth after which it declined to 52% at 7–8 m, 23% at 8–9 m, and just 8% in the 9–10 m depth layer. The lakewide average of adjusted *Ruppia* heights ranged from 0.6 m in the 1.25–2 m zone to 2.4 m tall for plants rooted at 4–5 depth before declining to 0.2 m in the deepest layer (9–10 m). However, a significant portion (35–56%) of the plants rooted at depths less than 5 m deep extended to the water surface. Visual assessments indicated that shallower than 1.25 m depth a zone of energetic wave action reduced or eliminated the macrophyte cover, especially in sandy areas.

Habitat area of the littoral zone within a 2-m depth profile at varied lake elevations was found to cover least area at 2007 lake levels around 1,200 m surface elevation (Fig. 6). Only 400–500 hectares of littoral habitat within the 2-m depth zone exists between the 2007 elevation and the present day (1196.6 m as of April 2012). Sonar images from the bathymetric studies of Walker Lake suggest that the availability of rocky habitat including cobble rubble and larger boulders diminish with depth (Lopes & Smith, 2007, p. 17, Fig. 9), but are evident in abundance above the present lake level.

Discussion

The benthic invertebrates of Walker Lake show distinct associations for depth and substratum distribution. The dominant midges of the lake inhabit different depth zones, with *Cricotopus* in the shallow eulittoral, and *Tanypus* in the deeper infralittoral and profundal zones. In field and lab settings we observed *Cricotopus* to be the primary prey of the large benthic insect predator, the damselfly *Enallagma*, which ranges over much of both littoral and sublittoral areas. The importance of stable habitats in the shallow wave-exposed eulittoral zone was evident for *Cricotopus* and *Enallagma* in showing preference for rocky cobble substrata, or macrophytes beds. These may also serve as habitat refugia from predation by visual predators such as fish and diving birds. Cobble provides a growth surface for epibenthic algae including diatoms, cyanobacteria, and filamentous green algae that comprise the littoral algae primary producers. *Cricotopus* inhabits cobble, feeding on the attached periphyton, and often builds cases within the algal matrix where it may also avoid predation by *Enallagma*. The oligochaete *Monopylephorus*, like other burrowing segmented worms, requires fine particles or soft organic substrata within which they move and feed, and these are the types of substrata in Walker Lake where this tubificid worm was found. Tubificids cannot tolerate anoxic conditions and often decline in abundance below the mixing zone of lakes (Brinkhurst, 1974). Intermittent oxygenation of the profundal region of Walker Lake appears to permit only limited survival of oligochaetes and *Enallagma*. *Tanypus grodhausi*, by contrast, is known to thrive in wastewater ponds with high levels of organic decomposition and anoxia (Grodhaus, 1967), similar to the low redox conditions in profundal mud sediments of Walker Lake. Hypolimnetic oxygen depletion has been demonstrated below 10 m depth in Walker Lake during the summer growth season (below thermocline), also limiting the area of the lake that can be inhabited by cutthroat trout and tui chub (Beutel, 2001; Beutel et al., 2001). Few benthic invertebrates can survive anaerobic conditions but *Tanypus* is among the midges that produce hemoglobin, providing oxygen storage capacity to support aerobic metabolism in profundal sediments.

Invertebrates previously documented from benthic habitats of Walker Lake include an abundant population of the amphipod *Hyalella*, observed in the late 1970s and mid-1980s, at lake levels of 1,205–1,210 m, corresponding to salinity of approximately 9–11 g/l (Herbst, pers. obs.). Amphipods are often an important source of nutrition to lake-dwelling trout, and along with other benthic insects such as chironomids and damselflies, were integral to the diet of early life stages of cutthroat trout in Pyramid Lake (Sigler et al., 1983). *Hyalella* were still common at the time cutthroat trout persisted in Walker Lake. Paleolimnologic studies have shown ostracods (e.g. *Limnocythere* spp.) to be abundant over long periods of the Pleistocene and Holocene stratigraphic record of the lake, suggesting high lake levels and low salinity (Bradbury et al., 1989). Shorter periods of higher salinity and low lake levels are also evident in this record in the form of remains of the brine shrimp *Artemia* as recently as 2,000 years ago.

Comparative ecology studies from other lakes suggest many of the benthic taxa in Walker Lake are near physiological limits for survival. At Abert Lake, Oregon, during a rising phase of the lake where it decreased in salinity from over 50 down to 20 g/l, *Hyalella* and *Enallagma* were found to colonize littoral habitats. This lake also became inhabited by oligochaetes (again, *Monopylephorus*), *Chrysops*, *Corisella decolor* and *Hygrotus masculinus* under these conditions of salt dilution (Herbst, 1988), much the same community of present Walker Lake. In higher salinity Mono Lake, in the range of 80–100 g/l salinity, the alkali fly *Ephydra hians* is dominant (as at other alkaline lakes of moderate-to-high salinity) and *Enallagma*, *Hyalella*, midges, oligochaetes and most other Walker Lake benthic invertebrates are absent (Herbst, 1988). At Owens Lake, in nearby eastern California, a lake that desiccated in the 1930s due to stream diversions to supply Los Angeles, periodic flood irrigation of parts of the dry lake bed produce ponds of dilute salinities in the range of 10–20 g/l where both *Cricotopus ornatus* and *Tanypus grodhausi* have been found to thrive, but not above these salinities (Herbst, pers. obs.). In Soap Lake, Washington, *Cricotopus ornatus* and *Tanypus nubifer* Coquillet have been described as abundant at salinities between 15 and 20 g/l, but disappeared in nearby Lake Lenore when salinities declined below about 5 g/l (Wiederholm, 1980). Surveys of saline lakes in Saskatchewan suggest that *Hyalella* is most common in the range of 1–12 g/l, while *Cricotopus ornatus* and *Tanypus nubifer* were found over the range 5–30 g/l but no higher (Timms et al., 1986).

As Pleistocene Lake Lahontan dried, the large remnant lakes it left were Walker, Pyramid, and Winnemucca. Winnemucca was connected with Pyramid but due to stream diversions, dried in the 1930s. As this lake was drying it was visited by G. Evelyn Hutchinson in 1933 who found it inhabited by ephydrid larvae (probably *Ephydra hians*) and the moderately salt-tolerant corixid *Trichocorixa verticalis*, and extensive macrophyte beds which he named as a narrow-leaf *Potomogeton* but more likely was *Ruppia* (Hutchinson, 1937). At this time the salinity of the lake was approximately 40 g/l, and he further reported finding a large number of dead and dried bodies of tui chub stranded along the shore, some 3 m above the lake surface.

The widgeon grass *Ruppia maritima* is generally known from estuarine habitats at salinities less than

25 g/l, but ranges over waters of widely varied chemical composition and salinity in both marine-origin and inland saline waters (Kantrud, 1991). Studies of different *Ruppia* varieties have shown optimal growth in low salinity culture conditions of <10‰ seawater, decreased growth at 15–25‰, and little or no growth beyond 28‰ (Verhoeven, 1989). *Ruppia occidentalis* S. Wats., sometimes called western widgeon grass (Husband & Hickman, 1989), is found in inland lakes of North America, and while mature plants may survive in higher salinities, the variety, salt tolerance, and capacity for flowering and germination have not been established for *Ruppia* in Walker Lake. Where rooted *Ruppia* persists and new recruitment occurs at varied lake levels is also uncertain.

The damselfly larvae of *Enallagma clausum* were the largest benthic invertebrates found and are known to be an important food resource to trout (e.g., Sigler et al., 1983). Nymphs crawl out of the water, attach to firm substrata and emerge as adults that occupy shoreline areas and hover over emergent beds of *Ruppia* along the shore. During emergence and while mating they may also be especially vulnerable to predation by birds. The presence of *Enallagma* in deep water is unusual, as odonate nymphs are often found only in shallow nearshore regions of lentic habitats where littoral vegetation may afford protection from fish predation (Crowder & Cooper, 1982; Gilinsky, 1984). Infralittoral macrophyte beds may provide refuge from fish predation for *Enallagma*, so the dense infralittoral *Ruppia* in Walker Lake may permit these damselflies to venture into deeper water and suggests that they may be more vulnerable in shallow water where *Ruppia* is less dense. In Pyramid Lake, *Enallagma clausum* has also been found on submerged areas of algae and vegetation (Kennedy, 1917). On the rocky cobble substrata of Walker Lake, damselfly nymphs were found beneath rocks as well as on upper exposed surfaces, and these substrata may also afford the spatial heterogeneity to allow refuge from fish. The integrity of littoral macrophytes is also known to be important to supporting adult damselfly abundance and diversity, and the genus *Enallagma* appears especially sensitive to disturbances of macrophyte beds (Butler & deMaynadier, 2008).

Substratum type and depth play important roles in the structure of benthic communities and distribution of particular species over the lake bottom environment of Walker Lake. Given the distribution and abundance of benthic invertebrates and habitat types of Walker Lake, an illustration of habitat associations and the food web of the benthic community can be proposed here (Fig. 7). With segregation according to mode of feeding and habitat preferences among the primary consumers *Cricotopus*, *Monopylephorus*, and *Tanypus*, there are different food resources utilized (Berg, 1995; Brinkhurst & Gelder, 2001). Early stage Tanypod midges such as *Tanypus* often feed on organic particulates as early instar larvae, then become facultative predators (possibly on oligochaetes). *Cricotopus* is a grazer on epilithic algae (probably diatoms primarily), and oligochaetes feed on organic sediments. Damselfly nymphs range over varied depths and inhabit macrophytes and rocky areas where preferred prey is available. As current environmental conditions change with fluctuating lake level (substratum availability, *Ruppia* production, salinity), this may alter the abundance or viability of these invertebrates, favor expansion of currently rare taxa or colonization by others, shift zonation limits, and change the strength of trophic links. This ecological context for spatial distribution and abundance provides a benchmark for comparing temporal changes as lake level fluctuates.

While littoral habitat area increases at higher or lower lake level, most of the littoral region would occupy favorable substratum and habitat with rising levels, but as lake level declines the substrata would become increasingly composed of unfavorable fine substrata and mud over a large region of shallow slopes as lake levels decline below about 1,190 m (about 6 m below the present 2012 lake level). Although sediment focusing may cleanse eulittoral area and expose rock as lake levels go down, there is likely to be less coarse substratum available at low lake level because (1) these areas are further from source areas of rock along the Wasuk mountain front on the west shore (little rock substratum is present anywhere along the eastern shore), (2) less wave energy can be generated in a smaller lake and more of the bottom area would already be covered by focused sediments, (3) there are less steep slope profiles over much of the lake at levels below 1,190 m, rendering focusing less effective (at slopes less than 4% according to Håkanson, 1981), and (4) we have observed rocks becoming more scarce at study sites over years of falling lake level. As habitat area and

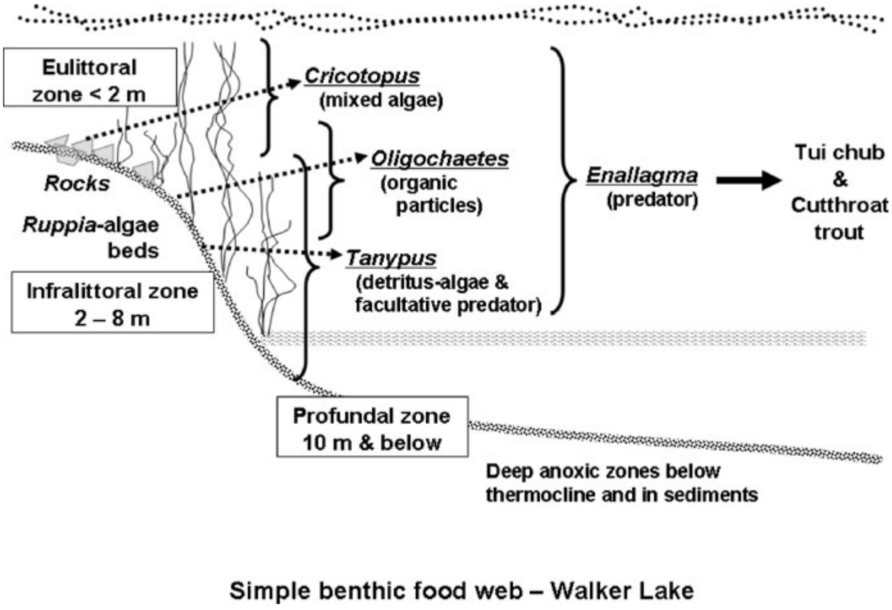

Fig. 7 Benthic food web of Walker Lake indicating dominant taxa under conditions in 2007. Primary feeding habit shown in *parentheses* below names of taxa. Macrophyte *Ruppia* beds indicated by *vertical strands*. Taxa not shown but expected to become important components would be the amphipod *Hyalella* at higher lake levels, and the more salt-tolerant alkali fly *Ephydra hians* at lower lake levels

substratum types change, the greater availability of rock substratum and littoral area above elevation 1,200 m should benefit benthic production, but less rock and salinity limitations on *Ruppia* at lower lake levels could eliminate habitat for the present-day community.

Environmental factors other than spatial structure may also contribute to community composition. These include salinity, redox potential of the sediments, the thermal environment in the littoral zone, nutrient availability, benthic algae productivity, and wave exposure disturbance of different locales. Experiments may provide some insight to the role of these factors, and salinity in particular may be a constraint on the viability of present-day aquatic life in Walker Lake. Predicting the compounding ecological effects of varied lake level on salinity may be examined in terms of the lethal and sublethal effects of varied dissolved solute concentration on survival and growth of the benthic invertebrate community. Together, the physical and chemical habitat conditions dictate the primary drivers of differences and transitions between and within saline lake ecosystems (Herbst, 2001).

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