J Insect Conserv
DOI 10.1007/s10841-013-9568-6

ORIGINAL PAPER

Defining salinity limits on the survival and growth of benthic insects for the conservation management of saline Walker Lake, Nevada, USA

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Received: 9 November 2012 / Accepted: 7 April 2013

Abstract Walker Lake, Nevada, a saline desert lake, has been undergoing loss of stream inflows, lowering of lake level, and concentration of dissolved salts for over a century due to agricultural diversions of water. This lake is or has been inhabited by native fish and visited by many species of waterbirds that depend on productive invertebrate life for food resources. The extent to which salinity limits the present and future viability of resident invertebrate fauna was evaluated using salt-tolerance bioassays and studies of salinity effects on growth and behavior in larval stages of the midges *Cricotopus ornatus* and *Tanypus grodhausi*, and nymphs of the damselfly *Enallagmaclausum*. We found that salinities into and above a range of 20–25 g/L present either lethal limits or sublethal inhibitions to survival and growth that will eliminate or substantially reduce the current community of common benthic invertebrates. All species survived best at salinities below the current ambient level, suggesting these populations are already under stress. The 72-h LC-50 for *Cricotopus* was 25 g/L, and while mature damselfly nymphs were somewhat more tolerant, early instars survived for only short times in increased salinity. Damselflies also grew more slowly and fed less when salinity increased from 20 to 30 g/L. A conservation level for the lake that incorporates survival of native fish and recovers diversity and viability of invertebrate life should be within the range of 10–15 g/L salinity of Walker Lake water.

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Keywords Salinity tolerance · Walker Lake · *Enallagma clausum* · *Cricotopus ornatus* · *Tanypus grodhausi* · Salt lake conservation

Introduction

Saline terminal lakes throughout the world are endangered ecosystems, threatened by falling levels, decreasing size, and rising salinity due to diversions of inflowing streams for agriculture and growing urban populations (Williams 1993, 2002). Saline lake ecosystems often support endemic species and abundant populations of salt-adapted forms of fish, waterbirds, aquatic invertebrates, plants, algae and microbial life. With few large perennial saline lakes remaining, conservation of these contracting habitats is essential to protecting their rare aquatic life and for maintaining links among separated metapopulations and along migratory bird pathways. Although volume and salinity typically have a history of fluctuation within and between these types of lakes, the stress of rising salinity from continual loss of freshwater inflow places physiological constraints on aquatic organisms that can only be relieved by returning stream flows that offset evaporative losses. The invertebrates and fish of saline lakes are usually osmoregulators, so determining the amount of water required to sustain terminal salt lakes ecosystems can be evaluated in part by knowing how much salt concentration aquatic life can withstand.

Walker Lake is a closed basin saline–alkaline lake in west central Nevada and is the terminus of the Walker River. The lake level and salinity of Walker Lake are closely tied to fluctuations in the input of freshwater from the Walker River, which is primarily composed of snowmelt from mountain ranges in eastern California and

Published online: 23 April 2013

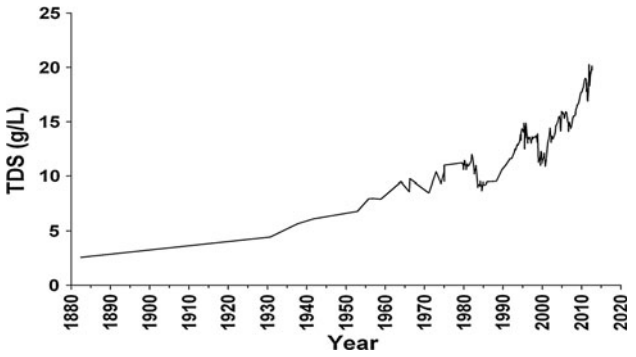

Fig. 1 Total dissolved solids (TDS) measured in Walker Lake from 1882 through 2012 (based on USGS National Water Information System data, Lopes and Smith 2007, and this study for recent measures)

western Nevada. From Walker Lake sediment cores, Bradbury et al. (1989) present evidence that over the past 30,000 years, Walker Lake has varied from a deeper, fresher lake to complete desiccation due to climatic, geomorphic, and tectonic events. Since the mid-1800 s, agricultural diversions and reservoir construction in the Walker Basin have resulted in a reduction of lake surface elevation by about 48 meters and an increase of total dissolved solids (TDS) from 2.5 to nearly 20 g/L TDS salinity at present (Fig. 1). This increase in salinity exceeded the survival of Lahontan cutthroat trout, *Salmo clarki henshawi* (Bigelow et al. 2010) and could have further cascading effects through the food web from benthic macroinvertebrates to the surviving tui chub (*Siphateles bicolor*) and waterbirds feeding at the lake.

As of September 2012, Walker Lake has a surface elevation of 1,196 m, a maximum depth of 22 m, pH of 9.43, and TDS content of 19.73 g/L. Lake water salts are dominated by sodium, chloride, sulfate, and carbonates (NDEP 2004; Yuan et al. 2006, and Table 1). Recent studies of Walker Lake include descriptions of limnological setting and benthic invertebrate distribution and abundance (Herbst et al. 2013), and bathymetric profiles (Lopes and Smith 2007).

The aim of the studies reported here was to define the upper limit of salt tolerance for the three most common benthic insects inhabiting Walker Lake, Nevada (*Enallagma clausum*, *Cricotopus ornatus*, and *Tanypus grodhausi*) using mortality bioassays in natural lake water. These insects are important as food resources to native fish in the lake and a variety of migratory and breeding birds. Walker Lake has been losing stream inflows to agricultural irrigation diversions for over a century but there is an opportunity to reverse this trend through recently initiated purchasing of water rights to secure lake inflows and efforts to conserve water through agricultural practices and crops that require less water (National Fish and Wildlife Foundation, www.nfwf.org/wb/). Bioassays of survival and growth of these insects provides an indication of what salinity range supports lake productivity, and identifies management levels that could achieve sustainable ecosystem conservation. The use of LC-50 bioassays has been shown to be a good proxy for determining the upper limit for field survival of aquatic invertebrates in natural waters (Kefford et al. 2004).

Table 1 Major ion chemical composition of Walker Lake water

	Molar (%)
Ca^{+2}	0.06
Mg^{+2}	1.79
Na^{+}	51.10
HCO_3^{-}	8.81
CO_3^{-2}	4.32
Cl^{-}	25.01
SO_4^{-2}	8.90

Average values from NDEP measured 1994–2004 (NDEP 2004, Yuan et al. 2006)

Methods

Salinity tolerance bioassays

A series of solutions were prepared consisting of filtered Walker Lake water spanning a gradient of salinity concentrations in order to establish acute-response mortality (LC-50, or concentrations required to cause 50 % mortality at 72 h) for three of the dominant invertebrates inhabiting Walker Lake: *C. ornatus*, *T. grodhausi*, and *E. clausum* (genus name only used from here). Exposure of these organisms to a range of salinity concentrations below and above current levels served to mimic conditions of the recent past with a higher lake level and fresher water as well as that of a possible future where continued draw down of lake level would create saltier conditions. Long term growth bioassays and feeding studies were also conducted on the damselfly *Enallagma* to determine how salinity concentrations both above and below current levels influence growth rate and productivity.

Water from Walker Lake was filtered through a 250 μm filter and collected in 20 L carboys, and was aerated in ice chests during transport to the Sierra Nevada Aquatic Research Laboratory in Mammoth Lakes, CA (1.5 h distance). Elevated salinity concentrations were achieved through evaporation of ambient water in a shallow wading pool exposed to direct sun. An Oakton conductivity meter (pH/Con10) was used to monitor conductivity during evaporation. Serial dilutions of concentrated water were prepared and measured to estimate actual concentrations. Once conductivity had reached approximately 150 mS, water was collected from the evaporating pool and vacuum filtered through GF/F glass fiber filters.

The relationship between specific conductance (conductivity), specific gravity, and TDS was established to prepare Walker Lake water for bioassays. A range of salinities at, above, and below a concentration of 20 g/L TDS (near ambient conditions at the time of this study) was selected for bioassays (10, 15, 20, 25, 30, 40, 50, and 75 g/L TDS). For salinity concentrations above ambient, evaporated lake water and filtered lake water were mixed to the equivalent conductivity or specific gravity. For concentrations below ambient, distilled water was mixed with filtered lake water. Calibrated hydrometers were used to measure the specific gravity of each solution at 20 °C and the relationship specific gravity = 0.0008 × TDS +1.0014 used to prepare test solutions (when the conductivity meter was out of range). Aerated test solutions were stored in a temperature controlled chamber at 20 °C where bioassays were conducted.

For use in the salinity tolerance bioassays and the growth experiments, *Enallagma* and *Cricotopus* specimens were collected from stirred sediments using fine-mesh aquarium nets in the littoral zone of western lake shores during the summer of 2009. *Tanypus* specimens were collected offshore using an Ekman dredge at depths of 2, 6, 10, and 16 m. Specimens were transported from Walker Lake to the laboratory in 5-gallon buckets of Walker Lake water. During transport, buckets containing specimens were kept aerated and cool in ice chests. Upon return to the laboratory, fifty *Enallagma* nymphs of mixed sizes (1.5–17 mm body length) were randomly assigned to treatment salinity concentrations of 10, 15, 20, 25, 30, 35, 40, 50 g/L. Each of the 400 *Enallagma* nymphs was placed in an individual container containing 50 mL of test solution without food. *Cricotopus* larvae of mixed sizes (1–7 mm) were exposed as groups of 20 each in 50 mL of test solution, also without food, at salinity concentrations of 10, 15, 20, 25, 30, 35, 40, 50 g/L (7 replicate groups per salinity for 140 total *Cricotopus*). Thirty *Tanypus* larvae of mixed size (1–9 mm) were exposed at each salinity concentration of 15, 25, 50, and 75 g/L, with individual larvae placed in 10 mL of test solution with no food. The bioassay salinity range used for each species was determined after preliminary range-finding tests showed levels where all or none of exposed specimens survived.

All *Enallagma*, *Cricotopus*, and *Tanypus* bioassays were exposed to treatment salinities for 120 h in an incubator on a daily light dark hour cycle of 12:12 at 20 °C (this is within the range of summer littoral temperature in Walker Lake). Specimens were examined for mortality at 12, 24, 48, 72, 96, and 120 h (*Enallagma*) or at 12, 24, 48, 72, and 120 h (*Cricotopus* and *Tanypus*). Bioassay culture dish solutions were replaced with fresh aerated water at each check, covered with lids to prevent evaporation, and had a large surface-to-volume for gas exchange. Mortality was defined as a lack of response to tactile stimulation with a blunt probe. Individuals that were determined to be dead were counted and their extended body length was measured to 0.05 mm using an ocular micrometer. The body lengths of all test specimens still surviving at 120 h were then measured after quick immersion in boiling water (for full body extension).

Effect of salinity on growth rates and prey consumption of *Enallagma*

In order to maximize growth potential and minimize early instar mortality, *Enallagma* of moderate size between 7 and 13 mm length were selected for growth studies. Forty *Enallagma* specimens each were exposed to 10, 20, and 30 g/L salinity concentrations for 15 days in an incubator set at L:D 12:12 at 20 °C. At the beginning of the experiment, each of the 120 *Enallagma* subjects was placed in an individual container containing 50 mL of solution and was provided ten midges (*Cricotopus*) as food. Every 5 days (day 5 and day 10), one-half of the solution in each container (25 mL) was removed and replaced with fresh aerated solution. This was accomplished by drawing down half the solution of each container with a pipette while simultaneously removing dead midge parts. Then, fresh solution was immediately placed in the container using a pipette, bringing the solution volume back up to 50 mL. To ensure equal opportunity for growth among all *Enallagma*, additional live midges were made available to *Enallagma* nymphs to replace those that had died or been consumed. A total of 50 live midges were available to each *Enallagma* over the course of the experiment: 10 midges initial and the other 40 at 3–5 day intervals so live prey were always available. On days 6 and 14, the feeding rate of each *Enallagma* nymph was determined assuming the number of midges consumed was the difference between midges provided at the beginning of each trial and the number of midges found remaining or dead at the end of the 24 h period of availability. The experiment was concluded on day 15 when the body length of each test *Enallagma* nymph was measured and placed in separate aluminum pans for oven drying at 60 °C for 24 h. After 24 h, the dry weight of each *Enallagma* specimen was recorded as the final weight over the growth period. The dry weight of each *Enallagma* at the beginning of the experiment was determined from initial live length based on a length to weight regression: weight (mg) = 0.0088 ×length (mm)$^{2.3619}$, and the difference in final and initial weights over the time interval used to calculate growth rates. Survivoring nymphs at the end of the experiment were 36, 39, and 33 at 10, 20, and 30 g/L, respectively.

Results

Salinity tolerance bioassays

We found differing tolerances of salinity for *Enallagma*, *Cricotopus*, and *Tanypus* (Figs. 2, 3, 4). By examining the

observed percent mortality for all salinity treatments over time for each taxa, we were able to calculate the lethal concentration of salinity that causes mortality in fifty percent of the population at 72 h of exposure (i.e. LC-50). *Cricotopus*, with an LC-50 at 72 h of 25 g/L, had the lowest tolerance for salinity, followed by *Enallagma* at 42 g/L, and *Tanypus* at 59 g/L. The salinity tolerance of *Enallagma* nymphs also depends on the size and development of the individual. At a salinity concentration of 50 g/L, mortality of smaller *Enallagma* nymphs occurred earlier than among later instar larger nymphs in the same treatment (Fig. 5). All nymphs smaller than about 8 mm died before 72 h, so this sensitivity of early life stages shows that the population as a whole is more sensitive to salinity increase than indicated by the mixed-population of nymphs exposed in the bioassay. Sustained survival of *Enallagma* nymphs appears possible only below about 30 g/L (Fig. 2). Similarly, survival of more than half of *Cricotopus* larvae exposed beyond 72 h occurs only below 25–30 g/L (Fig. 3), but there is still much higher rate of mortality at this level than at lower salinities.

Effect of salinity on growth rates and prey consumption of *Enallagma*

Growth rates in units of biomass were calculated based on the difference between the measured dry weights of *Enallagma* nymphs at the end of the experiment and the regression-derived dry weights based on measured lengths of *Enallagma* nymphs taken at the beginning of the experiment. The rate of growth of *Enallagma* nymphs diminishes with increased salinity to 30 g/L (Fig. 6). *Enallagma* exposed to salinity concentrations of 30 g/L had a significantly lower growth rate, in length and weight, than the growth rate of *Enallagma* nymphs exposed to salinity concentrations of 20 and 10 g/L ($p < 0.001$ for both length and weight between 30 and either 10 or 20 g/L). The feeding rate of *Enallagma*, measured as the number of midges consumed per day, is also diminished at higher salinity. *Enallagma* exposed to salinity concentrations of 30 g/L had a significantly slower feeding rate than *Enallagma* exposed to salinity concentrations of 20 or 10 g/L ($p < 0.001$ in both cases, Fig. 7).

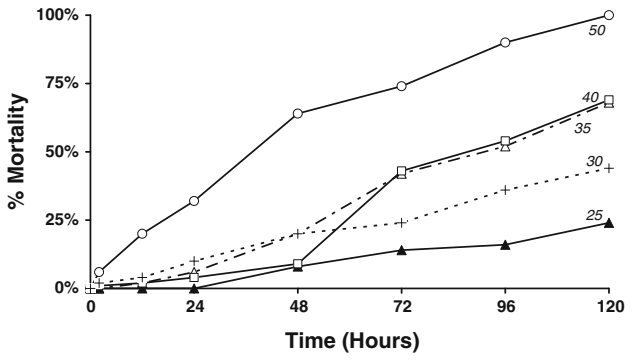

Fig. 2 *Enallagma* salinity tolerance bioassays—percent mortality for each treatment per time. *open circles* 50 mg/L, *open squares* 40 mg/L, *open triangles* 35 mg/L, + 30 mg/L, *filled triangles* 25 mg/L

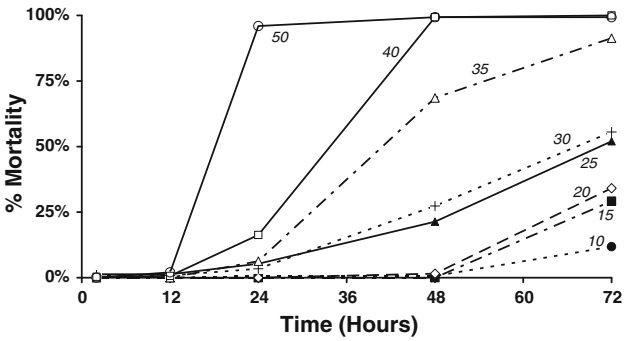

Fig. 3 *Cricotopus* salinity tolerance bioassays—percent mortality for each treatment per time. *Open circles* 50 mg/L, *open squares* 40 mg/L, *open triangles* 35 mg/L, + 30 mg/L, *filled triangles* 25 mg/L, *open diamonds* 20 mg/L, *filled squares* 15 mg/L, *filled circles* 10 mg/L

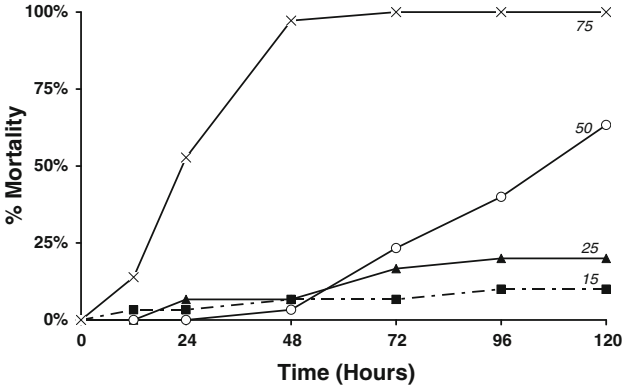

Fig. 4 *Tanypus* salinity tolerance bioassays—percent mortality for each treatment per time. $X = 75$ mg/L, *open circles* 50 mg/L, *filled triangles* 25 mg/L, *filled square* 15 mg/L

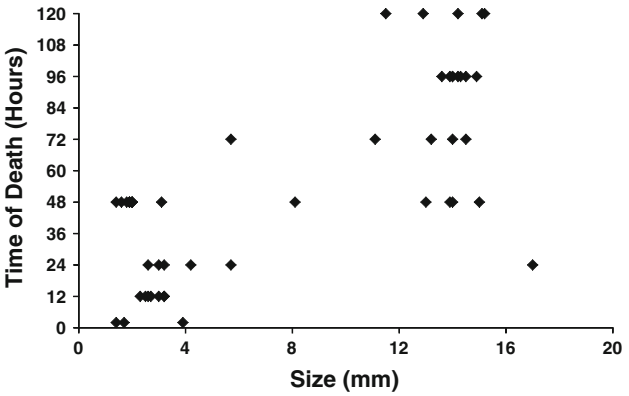

Fig. 5 Distribution of *Enallagma* sizes at time of death on exposure to 50 g/L salinity Walker Lake water

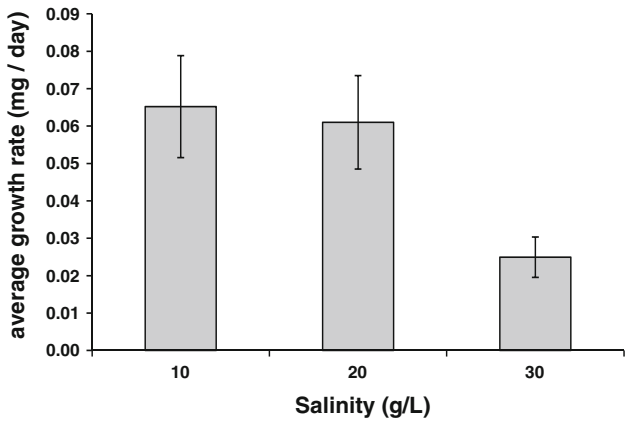

Fig. 6 Average growth rate of *Enallagma* in mg dry weight per day for each salinity concentration. *Error bars* are 95 % confidence intervals

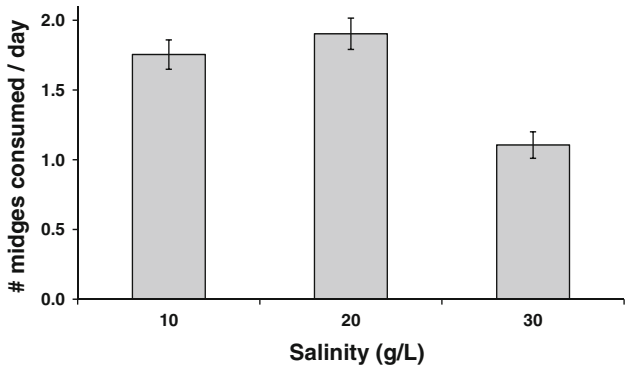

Fig. 7 *Enallagma* feeding rates—average number of midges consumed per day for each salinity concentration. *Error bars* are 95 % confidence intervals

Discussion

The salinity tolerance bioassays reported here indicate that survival of the benthic invertebrates of Walker Lake is near a limit. The midge *C. ornatus*, inhabiting the near-shore shallow littoral zone, appears especially vulnerable, reaching lethal concentrations at just 20–25 g/L for 25–50 % of larvae tested, with mortality rates rising after just 3 days of exposure (Fig. 3). This midge is the primary prey of *Enallagma*, so elimination of *Cricotopus* also threatens the food resource base for the damselfly that is in turn an important food source to fish and birds of the lake ecosystem.

As with many other saline lake invertebrates, *Enallagma* is an osmoregulator, maintaining homeostasis of internal fluid osmotic concentration when external salinities are both more and less concentrated than their blood (Lauer 1969). The results showing diminished survival and growth of *Enallagma* at increased salinity may be due both to the cost of osmoregulation and to lower rates of food consumption. In either case, energy becomes limiting to the growth and survival of *Enallagma* as salinity increases, and there can be no compensation for osmoregulation cost by increased food intake. All nymphs smaller than about 8 mm died before 72 h exposure at 50 g/L (Fig. 5). This early life stage sensitivity shows that the population as a whole is more sensitive to salinity increase than indicated by the mixed-population of nymphs in the salt tolerance bioassay. Sustained survival of mature *Enallagma* nymphs appears possible only below about 30 g/L, but these concentrations cannot be tolerated by the immature nymphs (Fig. 3). Considered together, these data indicate that salinities of 20–25 g/L will become increasingly critical sublethal limits on productivity of these saline lake damselflies.

The deep-water midge *Tanypus* appears to be somewhat more salt tolerant than other benthic insects in Walker Lake (Fig. 4). It showed steady survival at conditions of 25 g/L, but mortalities increased sharply at 50 g/L suggesting some intermediate concentration where salinity would become lethal for long-term survival. It does not survive salt as high as 75 g/L, showing that it is not a member of the hypersaline invertebrate community such as brine flies or brine shrimp, *Ephydra* and *Artemia*.

Further increases in salinity of Walker Lake will cause substantial changes in *Enallagma* and *Cricotopus* populations. Increasing salinity levels from 20 to 30 g/L at Walker Lake would inhibit the growth rate of *Enallagma* nymphs and surpass the long-term survival capability of *Cricotopus*. Further increases in salinity into the 25–30 g/L range would likely eliminate *Enallagma* and *Cricotopus* or severely reduce populations from Walker Lake proper, and lake-margin refuge habitats are unknown. We speculate that while the salt tolerance of existing invertebrates and those previously found in the lake may be and has been exceeded (e.g. *Hyalella* and ostracods), others present in the lake now (e.g. *Ephydra hians*) would become more abundant if salinity increases. These are dynamic communities and there is sediment stratigraphy evidence indicating that diatom and crustacean populations also have changed in the past, waxing and waning under varied climate and salinity conditions (Bradbury et al. 1989). The difference in the situation now is that loss of inflow water to upstream diversion could bring a persistent state of higher salinity conditions, and one that is not representative of what would be present under the natural recent climatic regime. Modeling of Walker Lake's hydrologic budget assuming the absence of water diversions has shown the lake level would have changed little and salinity would be around 3,000 mg/L (Milne 1987).

Comparative field studies provide important information to corroborate laboratory bioassays. A previous study of benthic invertebrates under conditions of rising lake levels

at saline-alkaline Abert Lake in Oregon, showed the appearances of *E.clausum* and the amphipod *Hyalella azteca* as salinities declined from a range of 25–35 to 20–25 g/L (Herbst 1988). Galat et al. (1988) reported that in laboratory experiments with benthic invertebrates of Pyramid Lake, *Hyalella* densities were lower at 8 and 11 g/L than at 5.6. *Hyalella* had also been common in Walker Lake in the mid-1970s (Cooper 1985), but disappeared sometime during the 1980s–1990s at around 15 g/L (records of D. Herbst). Recent sampling at Big Soda Lake, just 100 km north of Walker Lake is especially instructive. In June of 2012, near-shore shallow water salinity of Big Soda Lake was near 23 g/L, compared to 19.7 at Walker Lake at the same time. The community composition was quite similar but relative abundance showed that with just this slight difference in salinity, *Cricotopus* comprised over 90 % of benthic invertebrate counts at Walker, while it was less than 1 % at Big Soda (Table 2). *Enallagma* was slightly less common at Big Soda (3.6 % compared to 1.6 %), but *Ephydra hians* (Ephydridae) and larvae of the biting midge *Culicoides* (Ceratopogonidae) were more common, from 1 % or less at Walker to 30.6 and 44.4 % at Big Soda, respectively. Extensive sampling in outflows from natural springs and irrigation on the Owens Lake playa, another alkaline salt lake (about 200 km south of Walker), have also shown that *C. ornatus* larvae are not found above salinities in the range of 20–25 g/L (Herbst, unpublished surveys). Studies of coastal lagoons in Spain have shown this midge inhabiting an even lower salt range, not occurring above about 8 g/L salinity (Cañedo-Argüelles and Rieradevall 2009). These observations are consistent with an inhibitory effect of salinity on the production of the different species that have comprised the Walker Lake benthic invertebrate community, limiting or eliminating taxa as concentration rises over a range of 10–25 g/L, or showing replacement by more saline-tolerant species.

Rising salinities may not be the only limitation for growth and survival of benthic invertebrates due to reduced lake volumes. As the lake surface level of Walker Lake recedes, the amount and type of available habitat will be reduced. Of particular concern is whether or not rock substrates and protective macrophyte bed cover will still be available as habitat for benthic invertebrates when lake surface levels recede (Herbst et al. 2013). Limitations in the availability of cobble substrates in the eulittoral zone shallows have already been observed as lake surface levels receded from 2007 to 2010. Loss of protective cover may further expose littoral invertebrates to mortality due to being dislodged by turbulence from wave action.

During salinity tolerance experiments where we held field-collected invertebrates in the laboratory, we made observations of the feeding behaviors and preferences of the midges and *Enallagma*. We found that *Enallagma* fed primarily and most readily on *Cricotopus* though could also feed on *Tanypus* larvae. Large damselfly nymphs also fed on smaller nymphs, showing that cannibalistic behavior was not unusual and could be an important source of nutrition for larger late instar *Enallagma*. *Cricotopus* was observed to feed primarily on mixed benthic algae, whereas *Tanypus* was found to feed on mixed detritus but were also capable of preying on early instar *Enallagma.* Both midges readily scavenged dead and decomposing tissue of invertebrates or fish. The diets of tui chub and Lahontan cutthroat trout in inland saline lakes have an important invertebrate component, including midges, damselflies and amphipods (Cooper 1985; Sigler et al. 1983). These invertebrates are also important in the diets of many of the waterbirds that visit Walker Lake, and indirectly support fish-feeding birds such as white pelicans and double-crested cormorants that are also common. Although other salt-tolerant invertebrates such as brine flies (*Ephydra*) may inhabit a more saline Walker Lake, they are not apt to replace present-day Walker Lake benthic fauna in fish and waterfowl diets because they are smaller and less accessible (attaching to undersides of rocks), though certain shorebirds may benefit.

Although the LC-50 results reported here indicate limits on survival, the sublethal effects on physiological processes, such as decreased growth rate, prolonged development, and/or reduced reproduction, will constrain population viability under salinity stress at concentrations well below the LC-50 limits. Indeed, the better survival observed at salinities below ambient suggest populations are already under stress compared to past lake levels. At even lower salinities, below 10 g/L, the benthic invertebrate community would be more similar to Pyramid Lake and have a more diverse assemblage of organisms. Lower

Table 2 Relative abundance of benthic invertebrates collected from mixed substrata at Big Soda Lake and at Walker Lake in June 2012

Percent relative abundance	6-Jun-12 Walker	7-Jun-12 Big Soda
Cricotopus ornatus	90.6	0.8
Enallagma clausum	3.6	1.6
Oligochaeta	5.1	12.1
Culicoides sp.	1.0	44.4
Ephydra hians	0.2	30.6
Tanypus grodhausi	0.1	3.4
Hygrotus masculinus	0.3	2.6
Laccobius sp.*	+	2.6
Trichocorixa verticalis californica	−	0.8
Chrysops sp.*	+	0.6
Paracoenia sp.*	+	0.4

* All but *Trichocorixa* previously collected at Walker Lake but not on this sample date

salinities would not favor the moderately salt-tolerant fauna of the present lake because more intense predation and competition could either eliminate these taxa or reduce their abundance (Herbst 2001).

Of primary concern in conservation planning for Walker Lake has been the goal of returning Lahontan cutthroat trout to the lake. Salt tolerance studies of this fish have shown survival limited to no more than about 14 g/L, but only with acclimation providing some capability for larger mature fish to survive at this TDS or slightly higher level (Dickerson and Vinyard 1999; Bigelow et al. 2010). Along with the invertebrate salt tolerance bioassays presented here, this argues that an achievable conservation level for restoring a healthy and productive invertebrate and fish community for Walker Lake is in the range of 10–15 g/L total dissolved salts.

Acknowledgments This work was conducted with the support of the Lahontan National Fish Hatchery Complex of the United States Fish and Wildlife Service (Agreement #81332-5-G004, Desert Terminal Lakes Program). We thank program managers Lisa Heki and Stephanie Byers for their enthusiasm for the project and for background information about fish physiology, and Robert Jellison for assistance with salinity calibrations. Helpful edits were also provided by Graham Chisholm. Senator Harry Reid deserves credit for his instrumental role in establishing a conservation program for the saline terminal lakes of Nevada.

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