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Limnology and Food Web Structure of a Large Terminal Ecosystem, Walker Lake (NV, USA)

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ABSTRACT

Walker Lake is a large, terminal, saline lake in the Western Great Basin of the United States. Diversions have greatly reduced river inflow, which has lead to a decrease in lake volume by 75% since the 1880s. As a result there has been a concomitant increase in salinity levels and alteration to biotic community structure. This study provides a contemporary snapshot of the water quality, phytoplankton-zooplankton biomass, and the lake's food web structure. Water quality and zooplankton were sampled monthly (March to October 2007) from six locations at discrete depths. Nutrient concentrations were highly variable (ammonium levels - 0 to 30 ppb, nitrate - 0 to 12 ppb, total and dissolved phosphorus - 500 to 1000 ppb, and soluble reactive phosphorus - 400 to 600 ppb). The food web structure determined from stable isotope measurements (carbon and nitrogen) and stomach contents suggests benthic resources contributed greatly to fisheries energetics.

INTRODUCTION

Large, permanent lakes with high salinity occur infrequently in nature. Walker Lake is one of eight large, hypersaline lakes worldwide. It is one of many terminal lakes remnant of Lake Lahontan, a large lake from the Pleistocene era that began to desiccate roughly 10000 years ago (Benson 1978). Located in the rain shadow of the Sierra Nevada and Cascade ranges to the west and the Rocky Mountains to the east, evaporation rates in this area commonly exceed precipitation rates at lower elevations and are subjected to large annual and diel air temperature shifts (Hammer 1986).

Terminal lakes in semi arid regions are typically sensitive to changes in freshwater flow (Beutel 2001; Beutel et al. 2001). Many saline lakes are currently in decline due to reduction of inflow (Hammer 1986) and anthropogenic desiccation has occurred in numerous saline lakes worldwide (Hammer 1986; Williams 1993). Anthropogenic desiccation on Walker Lake, between 1882 and 1996, has decreased the lake volume by almost 75% and between 1979 and 2005 there has been a 99.9% reduction in river flow reaching the lake for agricultural uses. As a result of these anthropogenic influences salinity has increased from 2.6 to 12.4 g/l (Beutel et al. 2001).

Although species diversity is low in the lake it did at one time support a robust fisheries. Prior to desiccation, Walker Lake supported a large population of Lahontan Cutthroat trout (*Oncorhynchus clarki henshawi*) and the forage fish, tui chub (*Gila bicolor*). However dam construction on the Walker River stopped spawning runs and in conjunction with other environmental factors the Walker Lake cutthroat trout strain is now extinct and is maintained by an intensive stocking program with non-Walker strains of Lahontan Cutthroat Trout (Elliot 1995). The benefits of increasing river flow will depend upon water quantity and quality, and timing of release. Fish are limited by high salinity and ion concentrations and if there is not an increase in flow to Walker Lake over the next ten years it may be unable to support a fishery in the future as the lake increases in salinity (Beutel et al. 2001). Increase to annual flow could off set the desiccation and increased levels of salinity in Walker Lake.

The goal of this study was to characterize the contemporary ecological condition in Walker Lake focusing on: i) documentation of seasonal changes in water quality and physical conditions ii) secondary consumers (zooplankton and benthic invertebrates) and iii) determine the predatory-prey interactions and food web structure.

MATERIALS AND METHODS

Study Area

Walker Lake is located in the desert region of west-central Nevada southeast of Reno, Nevada (N38 42.012, W118 42.948). With a surface elevation of 1234 m, it has an approximate area of 140 km^2 with a mean depth of 19.3 m. The Walker River discharge into the lake occurs on the north end and has two major branches, the East and West forks. The forks flow north roughly 200 km originating in the central southeastern Sierra's before turning south and towards the lake. Both forks contain reservoirs, Bridgeport on the upper East fork and Topaz on the West fork. Weber Reservoir is located on the main-stem 40 km north of the lake.

Water Quality

We sampled from six locations at regular intervals (4-6 weeks) between March 2007 and June 2008 in order to capture annual variability of water quality, zooplankton, and physical conditions affecting lower food web production. There are three main sampling locations running south to north and three more sampling locations near the inlet. Samples were collected at discrete depths (surface to depth at 3 m intervals) at the three main sampling locations, with surface grabs at the three inlet locations, to capture chemical processes during stratified and nonstratified periods along with fine scale physical processes.

A high precision, continuous water quality sampler (Seabird Technologies, model SBE 19) was calibrated for conditions at Walker Lake and used to measure temperature and dissolved oxygen at each of the six locations. Water quality constituents (total and dissolved phosphorus, soluble reactive phosphorus, ammonium, and nitrate) were analyzed from each discrete depth. Due to their saline nature, methods developed as part of the Clean Lakes Granting process for U.S. EPA for Nevada lakes were used to determine the different water quality constituents (Solórzano 1969; Liddicoat et al. 1975; Jones 1984; Reuter & Goldman 1990).

Primary and Secondary Consumers

Zooplankton was collected from three pelagic sampling stations during the same time as the limnological sampling. Zooplankton was collected using a vertical, zooplankton tow (153 μm mesh), from the bottom to the surface and preserved with sucrose–Lugol's solution. In order to determine the current feeding behavior and energetics of zooplankton in Walker Lake a second zooplankton tow was taken at the same three sampling locations mentioned above. Live zooplankton from each of the dominant species (*Moina hutchinsoni*, *Leptodiaptomus sicilis*, and *Hexarthra*) at the time of sampling, were pooled (10 samples; 50-100 individuals or each species) for stable isotope (carbon and nitrogen) analysis. Due to the patchy nature of zooplankton composition (Newton 2007) with the lake we assumed that zooplankton samples collected from our three locations were sufficient to determine biomass and abundance throughout the lake.

Research from other lakes suggests temporal and spatial changes of invertebrates by depth and over time due to temporal changes in water quality and algae production in pelagic and benthic habitats (Chandra et al. 2005; Vander Zanden et al. 2006). Recently, studies have suggested that benthic invertebrate production is very important for fisheries energetics in Walker Lake (Chandra & Lawrence 2006). In order to capture changes across depth and inflow, benthic invertebrates were collected in the spring, summer, and fall using multiple (3 to 5) Petite Ponar grabs at 5 m intervals from the inlet of Walker Lake (1-5 m) to 30 m (deepest part of the lake). All samples were screened through a 500 μm mesh bucket for each location. Samples were immediately stored in 70% ethanol and identified to the lowest taxonomy possible. Invertebrates were measured for biomass and analyzed for carbon analysis to determine the source of energy uptake (benthic or pelagic algae).

Previous research suggests that alterations to water quality/lower food web production can alter ecosystem structure and fish growth (Vander Zanden et al. 2003; Chandra 2003; Chandra et al. 2005; Allen et al. 2006). In order to assess the contemporary food web structure in the lake prior to its restoration we measured stable isotope (carbon and nitrogen) from different fish species. Fish of different size classes were collected through coordination with state (Nevada Department of Wildlife) and federal (U.S. Fish and Wildlife service) biologists currently sampling the lake using 4 monofilament experimental gill nets (38 m x 1.8 m with mesh size starting at 1.27 cm and increasing by 0.64 cm until reaching 15.24 cm) set on the west side of the lake and creel census. Tui chub were identified for morphotype (benthic or pelagic) by counting gill rakers. Fish dorsal muscle tissues were collected from each fish for stable isotope analysis. Five Lahontan cutthroat trout were collected for analysis during creel surveys, while 48 tui chub were collected and utilized for stable isotope samples collected from gill netting. Tissue samples were dried at 70°C for 24 hours and ground to fine powder using a mortar and pestle. Samples were packed into tin capsules (8 x 5 mm), then carbon and nitrogen were analyzed using a continuous flow isotope ratio mass spectrometer (IRMS) (20-20, PDZ, Europa Science, Sandbach, United Kingdom). Samples were combusted to CO_2 and N_2 occurring at 1000°C in an inline elemental analyzer (PDZEurope Science, ANCA-GSL). A Carbosieve G column (Supelco, Bellefonte, PA, USA) separated the gas before introduction to the IRMS. Standard gases (Pee Dee Belemnite for $\delta^{13}C$ and N_2 gas for $\delta^{15}N$) were injected directly into the IRMS before and after the sample peaks. Every twenty samples a replicate and standard was added to the analysis sequence to determine reproducibility and method variability.

Isotopic ratios were expressed as per mil (‰) notation. Mean $\delta^{15}N$ and $\delta^{13}C$ values (±1 standard error, SE) for major taxonomic groups of the Walker Lake food web were calculated.

RESULTS

Water Quality

Temperature measurements indicated Walker Lake stratification periods during the summer starting in May and continuing through September with mixed conditions during other seasons. During December the lake becomes isothermic with an average temperature range in the winter between 6 and 11˚C. Dissolved oxygen ranged from 5.3 mg/l at the surface in February to 9.5 mg/l in March (note: DO was not taken in July due to absence of the Seabird sampler during the sampling period). The hypolimnion became devoid of oxygen by the end of May (4 to 6˚C bottom to surface) and remained anoxic throughout the summer and into early October (14 to 17˚C bottom to surface).

Only the water quality data taken from our index site (deepest part of the lake) is presented here. Total phosphorus levels were generally very high ranging from 600 ppb in May around, 20 m, to 950 ppb in August. Phosphorus varied by depth during each sampling period indicating patchiness within the lake. Nitrogen concentrations were highly variable (ammonium 0-30 ppb, nitrate-nitrite 0-12 ppb) over time. During July nitrate levels increased to over 120 ppb at 20 m. August also showed an increase in nitrate levels between 18 m and 20 m. Average values for phosphorus and nitrogen are given in Table 1.

Primary and Secondary Consumers

The number of zooplankton was highly variable in space with the highest abundance occurring in the late spring and fall. The highest abundance of *Leptodiaptomus* occurred in June (0.09 organisms/m^3), at the northern end of the lake while *Moina* abundance was greatest in October (0.08 organisms/m^3) at our southern sampling station (furthest from inflow). *Hexarthra* only occurred at two of the three locations in smaller numbers (< 0.01 organisms/m^3 at each location) from the center of the lake in June to the southern end of the lake in July.

The major taxonomic groups identified from the benthic invertebrate sampling were oligochaeta, diptera, and odonata. Biomass and diversity was highest during June in the littoral zone (52 mg dry weight/m^2), then gradually decreasing throughout the summer. Oligochaeta were only found during the June sampling period at 3 m of (12.9 mg dry weight/m^2). Two odonata were identified in our samples, *Coenagrion* and *Coniagron*. *Coenagrion* was only found in the littoral zone and in our June (13.3 mg dry weight m^2) and August (12.7 mg dry weight/m^2) sampling periods. *Zoniagron* was only found at out 30 m sampling depth in June (9.5 mg dry weight/m^2). However in our last sampling period in October *Zoniagron* was found in the littoral and profundal zones at each depth sampled up to 18 m (12.9 mg dry weight/m^2). The chironomidae, tanypodinae had the highest overall abundance during each sampling period and were also present at each depth. The highest abundance of tanypodinae was found in August at 4 m (13.5 mg dry weight/m^2) and in October at 13 m (12.9 mg dry weight/m^2).

Only two periphyton samples have been analyzed to date. Mean isotope values of δ^{13}C and δ^{15}N were -22.0‰ and 4.4.0‰, respectively. Mean zooplankton isotope values of δ^{13}C and δ^{15}N were -22.8‰ and 11.0‰, respectively. Mean benthic primary consumers isotopes for δ^{13}C and δ^{15}N were -19.9‰ and 9.4‰, respectively. However, there was a difference in the benthic invertebrate δ^{15}N signature in the littoral (8.3‰) and profundal zones (10.0‰) indicating an energy reliance difference. The only fish caught in the lake were tui chub (pelagic morphotype) and the top predator Lahontan cutthroat trout. Pelagic tui chub δ^{13}C and δ^{15}N concentrations were -20.5‰ and 12.6‰, respectively. Cutthroat trout δ^{13}C and δ^{15}N concentrations were -19.8‰ and 15.7‰, respectively (Figure 1).

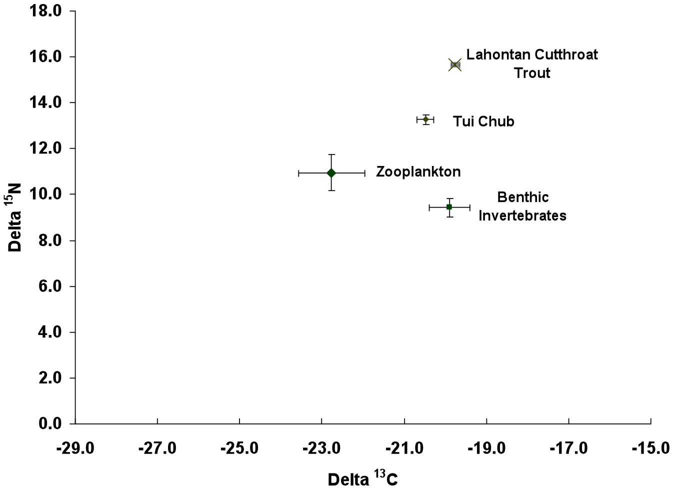

Figure 1–Stable isotope (δ^{15}N and δ^{13}C) food web diagram for the major taxa of Walker Lake, Nevada.

Table 1–Water quality constituents collected in 2007. All numbers are presented in ppb.

Constituents	March	May	June	August
Total Phosphorus	848.1 ± 17.2	822.9 ± 100.3	868.3 ± 51.9	901.6 ± 22.9
Dissolved Phosphorus	867.2 ± 14.4	688.8 ± 68.5	851.9 ± 42.4	747.9 ± 38.2
Soluble Reactive Phosphorus	469.6 ± 10.0	419.1 ± 26.1	434.0 ± 18.1	424.6 ± 29.0
Ammonium	12.3 ± 2.9	10.1 ± 11.8	22.4 ± 21.3	29.3 ± 52.2
Nitrate	5.3 ± 1.8	6.8 ± 1.7	27.1 ± 37.7	14.5 ± 17.0

DISCUSSION

Despite low water conditions and increased in salinity, Walker Lake exhibited monomictic conditions, stratifying during summer period. Typical of other lakes and similar to previous studies of Walker Lake more than a decade earlier, nutrient concentrations varied over time and depth. The lake continued to undergo anoxic conditions in the hypolimnion during summer resulting in the accumulation of ammonia. Internal loading processes do to sediment microbial activity and redox changes continue to be a strong contributor to the nitrogen budget of the lake. Similar finding have been shown for neighboring Pyramid Lake. Nitrogen loading also occurs from blue-green algae blooms (Beutel 2001). Phosphorus levels remained high throughout the study, similar to the findings of Beutel et al. (2001). The combination of nutrient data continued to suggest the lake is strongly N-limited even as water levels have declines in the lake.

Zooplankton varied spatially and temporally, typical for lake systems. Zooplankton species had different seasonal patterns and were found in highest abundances in shallow sites. The patchy nature of zooplankton composition within the lake is likely due to both biotic and abiotic factors. Biotic factors contributing to patchiness within Walker Lake may include diel vertical migration, competition, predation, and reproduction (Pinel-Alloul et al. 1988). It is well documented that zooplankton change positions in the water column on a daily bases for predator avoidance and to reduce competition and for reproduction (Horne & Goldman 1994; Wetzel 2001). Resource limitation in terms of food availability and quality in the seston likely played a large role in contributing to patchiness (Newton 2007). Furthermore, Walker Lake exhibits strong physical mixing and internal processes due to wind and weather changes throughout the season resulting in patchiness of both zooplankton and phytoplankton across the lake (Laurie Newton, unpublished data).

Benthic invertebrate's diversity was highest in June and decreased throughout the rest of the summer as the hypolimnetic water stratified and underwent periods of oxygen reduction. The littoral zone, 0 to 10 m, had the highest biomass found during late spring and fall. Odonata were almost entirely found in the littoral habitat, among macrovegetation and burrowing in surficial sediments. Odonata have high respiratory demands (Wetzel 2001) which would also explain why their biomass was highest in the spring and fall when oxygen levels were highest. Diptera are among the most important groups of aquatic insects and are commonly dominant components of benthic invertebrate communities. Because tanypodinae possess hemoglobin in their blood that functions at low levels of oxygen, they were found at all depths and throughout the seasons.

Only 2 fish species were caught in Walker Lake compared to 5 native fish taxa in neighboring Pyramid Lake. Only one tui chub (pelagic morphotype) was identified from the lake despite a large netting effort to collect fishes. It is believed that other fish species common to this region (Tahoe sucker, Lahontan redside shinners, speckled dace, tui chub-benthic morphotype) would exist in the lake given more freshwater circumstances. Stable isotope information suggests cutthroat trout, while maintained through hatchery processes is the top predator feeding on tui chubs and primary consumers. Pelagic tui chubs are the second dominant consumer feeding mostly on primary consumers. A continuous monitoring program by the state of Nevada's Department of Wildlife suggests limited recruitment of young of the year tui chub due to increasing saline condition and low freshwater flows entering the lake (Solberger, personal communication). It is unclear if this recruitment impacts cutthroat energetics and maintenance of their population however these fish comprise a significant amount of diet for cutthroat trout in neighboring Pyramid Lake (Chandra & Lawrence 2006).

Stable isotope carbon information also strongly suggests the Walker lakes fishery is supported by benthic production (Figure 1). Pelagic zooplankton is highly patchy in the lake environment and may not be available for fish consumption. Stomach analysis suggest both tui chub and cutthroat trout contain benthic invertebrate during all sampling periods (Umek & Chandra, unpublished data) with a dominance of Odonata in the stomachs during the early spring and fall creel surveys.

Walker Lake is currently under high saline and ion conditions. If there is not an increase in flow to Walker Lake over the next ten years it may be unable to support a trout fishery in the future as the lake increases in salinity (Beutel et al. 2001). An increase in annual flow could off set the desiccation and increased levels of salinity in Walker Lake. Furthermore changes in lake structure and food production in different habitat should be monitored simultaneously to determine impacts on fish production. These data should provide baseline data for a comparison study, if in the future, inflow from Walker River increases.

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