



Re-appearance of rotifers in hypersaline Mono Lake, California, during a period of rising lake levels and decreasing salinity

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Abstract

The surface elevation of Mono Lake, California, rose ~ 2 m and mixed-layer salinities declined about 5 g kg^{-1} during the 3 years (1995–1997) following the decision to restrict water diversions out of the Mono Basin. Abundant ($18\,000 \text{ m}^{-2}$) *Hexarthra jenkiniae* de Beauchamp were noted in pelagic samples in October 1997 after three decades of absence or very low abundance. Abundance subsequently increased to $100\,000 \text{ m}^{-2}$ in December 1997 before declining to low numbers through 1998 and 1999. The re-appearance of *Brachionus plicatilis* Müller in pelagic samples occurred in September 1998. *B. plicatilis* areal abundance increased to $\sim 15\,000 \text{ m}^{-2}$ in October–December of both 1998 and 1999 but was low throughout the rest of the year. Both rotifers were noted in nearshore ponds, but were only abundant in those with salinities below 53 g kg^{-1} . During 1998–1999 when the salinities of the upper water column were $73\text{--}75 \text{ g kg}^{-1}$, less saline shoreline habitats may have been seeding the offshore rotifer populations.

Introduction

Zooplankton species diversity is severely reduced in hypersaline ($>50 \text{ g kg}^{-1}$) lakes compared to less saline and freshwater lakes (Hammer, 1986). Mono Lake, California, U.S.A., is a large, hypersaline saline, lying in a hydrologically closed high-desert basin just east of the Sierra Nevada within the North American Great Basin. Throughout much of the 20th century, the surface elevation of Mono Lake declined and salinity increased, first due to extended drought early in the century and then due to diversion of streams out of the basin beginning in 1941. Over the next 40 years, the lake's salinity doubled as its volume was halved. During limnological surveys of Mono Lake in 1959, 1963 and 1964, when the salinity was $60\text{--}70 \text{ g kg}^{-1}$, Mason (1967), noted the presence of several species of protozoans; the two rotifers, *Hexarthra jenkiniae* and *Brachionus plicatilis*; and the endemic brine shrimp, *Artemia monica*. Subsequent to these observations, the

lake continued to shrink and the salinity increased to $\sim 82 \text{ g kg}^{-1}$ in 1976, by which time, rotifers were not reported in plankton samples (Winkler, 1977). During the next 16 years, the surface elevation of the lake continued to decline reaching its historic low of 1942 m during winter 1981–1982, at which time, the salinity was $\sim 92 \text{ g kg}^{-1}$ (Jellison & Melack, 1993b).

In 1994, the California State Water Resources Control Board decided to raise the surface elevation of Mono Lake to 1948 m as part of a general restoration plan (Decision #1631) by restricting water diversion by the City of Los Angeles. By October 1997, the lake had risen ~ 2 m to 1945.2 m and the mixolimnetic salinity decreased by 5 g kg^{-1} to 76 g kg^{-1} when the re-appearance of rotifers in plankton samples was first noted. Here, we describe the pelagic abundance of *Hexarthra jenkiniae* and *Brachionus plicatilis* during late 1997 through 1999. We also sampled nearshore less saline ponds, some of which contained abundant rotifers.

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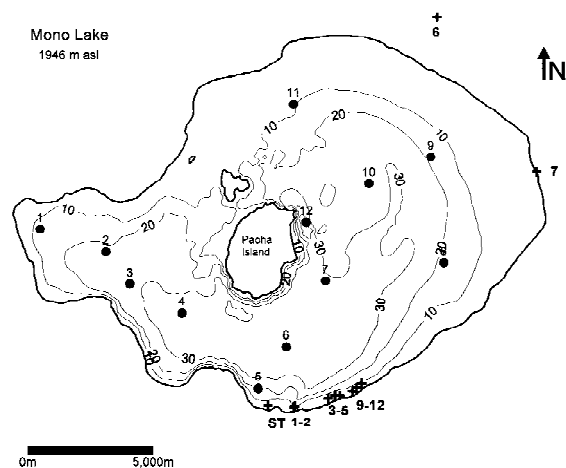


Figure 1. Pelagic sampling stations on Mono Lake (solid circles) and locations of adjacent nearshore ponds (crosses; ST is the South Tufa pond). All ponds were immediately adjacent to the lake except for pond #6.

Methods

Zooplankton samples have been collected at approximately monthly intervals throughout the year at 12–20 stations distributed around the lake (Fig. 1) from 1982 to the present. Samples were taken with a plankton net (1×0.30 m diameter, 120- μ m Nitex mesh) towed vertically through the water column at approximately 0.5 m s⁻¹. Samples were preserved with 5% formalin in lakewater, and counted under a stereo microscope (×6 power). While samples were not explicitly examined for the presence of rotifers, abundant rotifers were first noted in October 1997 samples. Therefore, beginning in October 1997 samples were saved following enumeration of *Artemia* and examined for the presence of rotifers. *Artemia* were removed and samples concentrated to 25–70 ml depending on the abundance of rotifers by filtering through a fine sieve and then rinsing individuals into a sample container. Samples were thoroughly mixed and then three or four 1-ml subsamples removed for counting under an inverted microscope (Olympus BX40) with an attached video camera and monitor. In October and December 1997 samples, individual lengths were measured using Optimus 5.2 software specifically designed for the microscope and camera.

Beginning in May 1998, a 50- μ m net lowered to a depth of 5 m was used to collect a separate sample for rotifer enumeration. Low abundances during May and June, prompted a change in sampling protocol. Beginning in July and continuing through mid-1999,

rotifer samples were collected with both 120- and 50- μ m nets. Both vertical tows extended to 20 m depth, but the 50- μ m net was raised at approximately 10 cm s⁻¹.

The efficiency of vertical net tows varies as a function of mesh size, shape, ascent rates and the plankton community. Data reported here assume a 70% net efficiency derived from previous comparisons of *Artemia* abundance collected by vertical net tows and a Schindler–Patalas trap (Lenz, 1980).

Results

Re-appearance, individual size and net efficiency

The re-appearance of the rotifer, *H. jenkinsae*, in vertical net tow samples from Mono Lake was first noted on 27 October 1997 when their mean abundance at three pelagic stations (Stations 1, 6, 8; Fig. 1) was 18 000 m⁻². The mean lengths of 187 individuals from October and 343 individuals from December were nearly identical on the two sampling dates, 233 and 229 μ m, respectively. The frequency distribution of individual lengths indicated 90% of the individuals collected were larger than 180 μ m, and thus, we assume samples collected with the 120- μ m net capture nearly all individuals. As rotifer sampling is often conducted with a 50- μ m net, we sampled with both 50- and 120- μ m mesh nets from July 1998 through 1999. *H. jenkinsae* abundance was too low throughout this period to assess the different net efficiencies, but *B. plicatilis* appeared in plankton samples in September 1998. A comparison of *B. plicatilis* abundance in paired samples indicated the 120- μ m net hauled vertically as ~ 0.5 m s⁻¹ collected significantly more (Wilcoxon signed rank test with $n=18$; $P<0.05$) individuals than the 50- μ m net hauled vertically at ~ 0.1 m s⁻¹. For this reason, the 50- μ m net tows were discontinued.

Pelagic abundance 1997–1999

Following the discovery of *H. jenkinsae* in plankton tows from October 1997, lakewide abundance (mean of stations 1, 6, 8) increased from 18 000 to 100 500 m⁻² on 3 December before declining to 670 m⁻² on 18 March 1998 (Fig. 2). Numbers of *H. jenkinsae* remained low throughout the rest of the year never exceeding 1700 m⁻². Assuming they are distributed throughout the oxic portion of the water column, the 1998 areal estimates translate to <1 l⁻¹. In 1999,

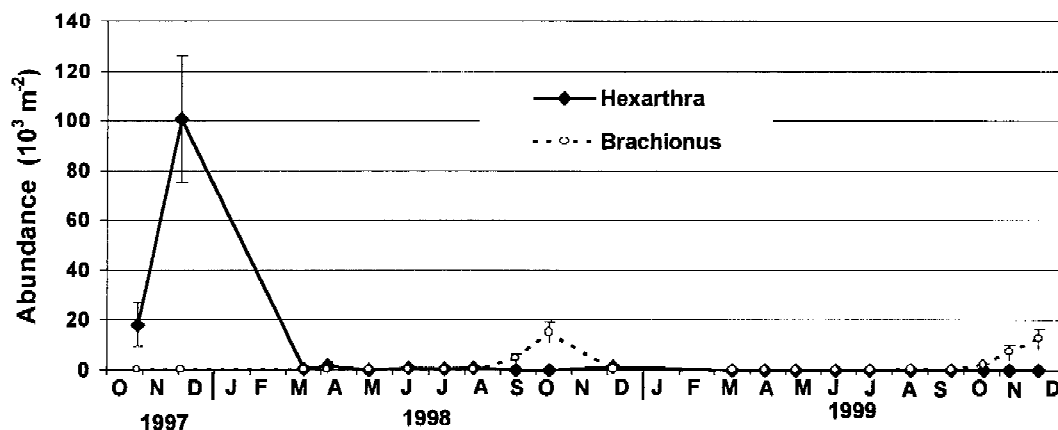


Figure 2. Abundance of *H. jenkinsae* and *B. plicatilis* in Mono Lake, October 1997–1999; error bars indicate plus or minus one standard error.

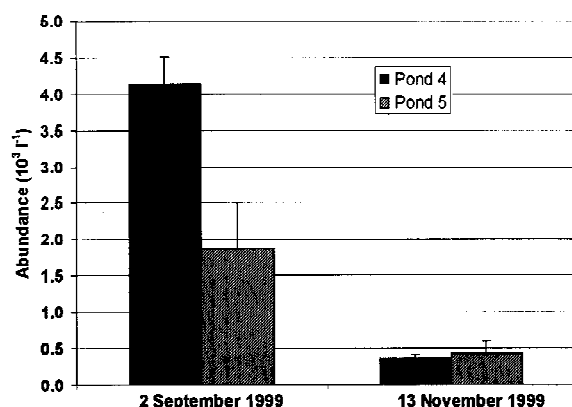


Figure 3. Abundance of *B. plicatilis* in ponds #4 and #5 during autumn 1999; error bars indicate plus or minus one standard error.

no *H. jenkinsae* were observed in plankton samples although a few individuals were observed in ponds adjacent to the lake.

B. plicatilis first appeared in pelagic net tow samples in September 1998 samples when abundance was 4600 m^{-2} . Abundance increased to $15\,100 \text{ m}^{-2}$ in October before declining to 400 m^{-2} by 7 December 1998. In 1999, *B. plicatilis* was absent from samples collected during February through June, but re-appeared at low abundances ($40\text{--}300 \text{ m}^{-2}$) in July through September plankton samples. The population then increased to 2000, 7000 and $12\,000 \text{ m}^{-2}$ in October, November and December, respectively. Assuming the rotifers are distributed over the oxic portion of the water (upper 12–15 m), this abundance is quite low ($\sim 1 \text{ l}^{-1}$) for a viable rotifer population.

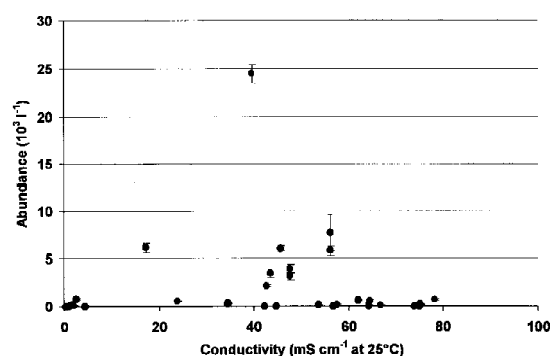


Figure 4. Abundance of *B. plicatilis* in nearshore ponds versus conductivity, autumn 1999; error bars indicate plus or minus one standard error.

Rotifer abundance in nearshore less saline ponds

The low abundance of both these species throughout 1998 and 1999 indicates sub-optimal conditions in the lake and suggests the possibility that the pelagic rotifer population is being ‘seeded’ from less saline nearshore environments where freshwater springs and seeps occur. In summer 1999, the lakeshore was explored for the presence of adjacent less saline ponds. Several areas of less saline ponds, some of which were hydraulically connected to the lake, were identified and sampled (Fig. 1). Rotifers were present in samples from ponds #4–7, 9, 10 and 12. Conductivities of the sampled ponds ranged from 0.5 to 80 ms cm^{-1} at 25°C or assuming a chemical composition similar to Mono Lake water (see Jellison et al., 1999) from nearly fresh to 76 g kg^{-1} . The highest abundance of rotifers ($24\,400 \text{ l}^{-1}$) was observed at pond 4 where conductivity was 40 ms cm^{-1} (corrected to 25°C) (Fig. 3). Although observed across a range of conductivities,

rotifers were never abundant in samples where conductivity was greater than 60 ms cm^{-1} or $\sim 53 \text{ g kg}^{-1}$ (Fig. 4).

Discussion

Rotifers are one of the most characteristic taxa of fresh waters (Pennak, 1989) and often form an important component of the zooplankton in saline lakes. Hammer (1986) reviews the geographic distribution of rotifers in world athalassic water according to salinity. The two rotifers, *H. jenkiniae* and *B. plicatilis*, have broad salinity tolerances and are reported to occur worldwide in saline lakes. Both these species have been reported from other saline lakes in the North American Great Basin at salinities $<50 \text{ g kg}^{-1}$ (Big Soda Lake, Cloern et al., 1983; Pyramid Lake, Galat et al., 1981; L. Winnemucca, Hutchinson, 1937). Also, Mason (1967) noted abundant (170 l^{-1}) *B. plicatilis* in Mono Lake from a single sample collected in mid-December 1959. Based on the surface elevation of 1949.8 m during December 1959, the salinity is estimated to have been 60 g kg^{-1} . Hammer (1986) incorrectly cites Winkler (1977) as noting the presence of rotifers at 90 g kg^{-1} when in fact Winkler was citing their presence at lower salinities reported by Mason (1967). During summer surveys in 1963 and 1964, Mason (1967) observed only a single rotifer on two different occasions in phytoplankton settling chambers when the lake was $\sim 67 \text{ g kg}^{-1}$; he conducted no winter sampling during 1963 or 1964. Subsequent to these early observations, neither species of rotifers were noted in regularly collected plankton samples from 1982 until October 1997. However, the date or salinity at which the rotifers disappeared from the pelagic region of Mono Lake cannot be ascertained with certainty.

The re-appearance of rotifers in Mono Lake plankton samples was first observed in October 1997 at mixolimnetic salinities of 75 g kg^{-1} . While *H. jenkiniae* abundance subsequently increased to $100\,000 \text{ m}^{-2}$ in the December 1997 survey, it decreased to below 2000 m^{-2} in 1998 and was not observed in any of the plankton samples collected in 1999. *B. plicatilis* first appeared in July 1998 plankton samples. In both 1998 and 1999, *B. plicatilis* abundance increased beginning in September and reached peak abundances of about $15\,000 \text{ m}^{-2}$ late in the year (October–December) while they were virtually absent the rest of the year. Iltis and Riou-Duvat (1971) found an upper salinity

limit of 70 g kg^{-1} for *B. plicatilis* and 50 g kg^{-1} *H. jenkiniae* with maximum populations at salinities from $10\text{--}20 \text{ g kg}^{-1}$ in hypersaline lakes northeast of Lake Chad.

The absence of significant numbers of rotifers in the Mono Lake except during late in the year may reflect seasonal 'seeding' from less saline ponds immediately adjacent to the lake. Both *H. jenkiniae* and *B. plicatilis* were present in these ponds during September and November 1999 and *B. plicatilis* were abundant ($2\text{--}4 \text{ ml}^{-1}$) in two of the sampled ponds with conductivity $<60 \text{ ms cm}^{-1}$ at 25°C (salinity $<53 \text{ g kg}^{-1}$). Adjacent ponds are often hydraulically connected to the lake, but maintained at a lower salinity due to inflows of freshwater. In each of 1997–1999, the surface elevation of the lake has risen during January through July after which it has declined $0.3\text{--}0.5 \text{ m}$ late in the year (see Fig. 1; Jellison & Melack, 2001). During this period of decline, immediately adjacent connected ponds would drain into the lake. In September 1999, Pond 5 had an estimated volume of $20\,000 \text{ m}^3$. The *B. plicatilis* density of 2000 l^{-1} in this pond if emptied into the lake would result in a lakewide areal abundance of several hundred per m^2 . Thus a single flushing of this one pond would supply almost 2% of the observed lake abundance. As there are many smaller ponds along the shores, pond abundance was as high as $25\,000 \text{ l}^{-1}$, and rotifer export from adjacent ponds would more likely be continuous during the period of declining lake level, this source could potentially explain all of the observed planktonic abundance.

An alternative hypothesis would be that the autumn increases in planktonic rotifer abundance result from the release of competition with the much larger and efficient filter feeder, *Artemia monica*. Brine shrimp are very abundant in the lake from April through September and graze the phytoplankton population to very low levels (Jellison & Melack, 1993a). During October the brine shrimp population declines and becomes virtually absent midwinter. Associated with this decline and entrainment of nutrients in autumn, a marked autumn bloom of phytoplankton occurs. Thus, food would become less limiting to rotifers late in the year. However, we judge this to be less likely based on the salinity limits observed from other studies and the lack of rotifers observed in adjacent ponds with salinities exceeding 60 ms cm^{-1} ($\sim 53 \text{ g kg}^{-1}$). Salinities in the upper water column of the lake varied from 72 to 75 g kg^{-1} during the autumns of 1998 and 1999.

The effects of the current rotifer population on energy flow and trophic dynamics is low given their small numbers. Rotifer clearance rates are commonly between 1 and 10 $\mu\text{l h}^{-1}$ (Wallace & Snell, 1991), although rates as high as 50 $\mu\text{l h}^{-1}$ have been reported (Bogdan et al., 1980). Assuming clearance rates of 10 $\mu\text{l h}^{-1}$ for 24 h a day yields 0.24 ml day^{-1} and given 2–10 l^{-1} observed in October and December 1997 gives a population clearance rate of less than 3 ml day^{-1} . The clearance rates of individual *Artemia* are 100–200 ml day^{-1} and typical summer abundances are 2–5 l^{-1} . However, much higher *H. jenkinsae* abundances have been reported in other saline lakes (e.g. 17 000 l^{-1} in Red Rock Tarn; Hammer, 1981). If rotifer abundance in Mono Lake approached these numbers, they would certainly make a major contribution to overall zooplankton grazing rates, especially during winter when *Artemia* are mostly absent. However, if rotifers are not reproducing in the lake and the observed populations are due to seeding from adjacent ponds, much higher lakewide abundances would not be expected.

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