## AN ABSTRACT OF THE THESIS OF

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Abstract approved:


Ten high mountain ponds in Mount Rainier National Park, Washington State, were studied from June through September 1992 to investigate the influences of fluctuating pond volumes on zooplankton communities. A temporary pond of short wet phase duration was inhabited by zooplankton taxa with short generation times and a crustacean taxa with the ability to encyst as drought-resistant resting bodies at immature stages of development. Relative to permanent ponds, rotifer densities typically were low in temporary ponds, although Brachionus urceolaris was abundant shortly before the ponds dried. High volume loss was associated with declining populations of crustaceans. Daphnia rosea was not present in the crustacean communities of temporary ponds after fall recharge. Deep-permanent ponds had slower copepod development and two additional large bodied crustacean taxa relative to shallow-permanent ponds. Because of their small sizes and sensitivity to environmental change, ponds such as these may provide an early signal of changes in aquatic systems from global warming.

# EFFECTS OF HYDROLOGY ON ZOOPLANKTON COMMUNITIES IN HIGH MOUNTAIN PONDS, MOUNT RAINIER NATIONAL PARK 

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# EFFECTS OF HYDROLOGY ON ZOOPLANKTON COMMUNITIES IN HIGH MOUNTAIN PONDS, MOUNT RAINIER NATIONAL PARK 

## INTRODUCTION

High mountain ponds in temperate regions are subjected to extreme fluctuations in physical and chemical conditions because the ponds are small in size, susceptible to water loss, and located where the climate is severe (Nedler and Pennack, 1955; Schmitz, 1959). High mountain ponds in the Pacific Northwest are covered or filled with snow and ice during winter. The ponds become free of snow and ice (ice-out) in early summer and are flushed with snow-melt runoff. During summer and early fall when air temperatures are relatively high and precipitation levels low, ponds without surface or ground-water inflow decrease in volume, with small ponds often drying. The ponds typically refill to capacity by precipitation before becoming capped or filled with snow and ice in early winter.

Temporary and permanent ponds are inhabited by a wide variety of zooplankton species (Stout, 1964; Morton and Bayly, 1977; Wiggins et al., 1980; Fryer, 1985; Williams, 1987; Jeffries, 1989). Several factors appear to be important in structuring zooplankton communities in ponds, including pond size and habitat diversity (Schmitz, 1959; Sprules, 1972; Anderson, 1974; Crosetti \& Margaritora, 1987; Mahoney et al., 1990), water chemistry (Carter, 1971; Jeffries, 1989), competition (Hammer and Sawchyn, 1968; Sprules, 1972) and invertebrate predation (Sprules, 1972; Dodson, 1974; Hebert \& Loaring, 1980; Maly et al., 1980; Arts et al., 1981). Wiggins et al. (1980) contended that temporary waters constitute a discrete type of freshwater habitat where structural, behavioral and physiological adaptations of invertebrates are required in order for invertebrates to survive during periods of drying. However, few researchers have evaluated differences in zooplankton communities between temporary and permanent waters of similar size and habitat complexity. Cole (1966) observed that some species of
calanoid copepods were found in ephemeral and permanent ponds in Arizona, whereas other species were limited either to ephemeral or permanents. In a study of high mountain ponds in Colorado, Sprules (1972) observed differences in the structure of zooplankton communities between deep, permanent ponds and shallow, ephemeral ponds. However, the presence of large crustacean zooplankton species in the shallow ponds was mostly attributed to the absence of invertebrate and vertebrate predation. A combination of drying during summer and freezing to the bottom during winter appeared to eliminate salamanders (Ambystoma tigrinum) and Chaoborus larvae from the ponds. In contrast, Barclay (1966) observed neither quantitative nor qualitative differences in crustacean zooplankton taxa between temporary and permanent ponds of similar size within a small geographical area in New Zealand. Maly et al. (1980) suggested that declines in pond volume due to evaporation can increase zooplankton density and inter- or intraspecific competitive interactions. Furthermore, decreasing pond volume results in increased ratios of surface area to volume, which may lead to increased predation on the zooplankton from benthic macroinvertebrates (Maly et al., 1980).

Several studies have provided evidence that the number of cladoceran species in ephemeral ponds decreased as the duration of wet phases shorten (Crosetti \& Margaritora, 1987; Ebert \& Balko, 1987; Mahoney et al., 1990). Although it is not clear why this reduction in the number of species occurred, some species may not have been able to reproduce in ponds where the wet phases were shorter than their generation times. In general, the relationship between length of wet phase and generation time of zooplankton species inhabiting particular ponds remains poorly defined and questions remain unanswered. First, are there significant differences in the species assemblages and densities of the zooplankton inhabiting similar-sized temporary and permanent ponds? Second, are the zooplankton communities in temporary ponds with short wet phases dominated by zooplankton species with short generation times? Third, does the annual amount of water volume loss affect the characteristics of zooplankton communities in
permanent ponds? These questions were investigated by studying zooplankton communities in ten subalpine ponds in a small geographical area of Mount Rainier National Park (Fig. 1). Based on field observations made between 1989 and 1991, four of the ten study ponds dry (referred to as type I ponds) during summer and six ponds retain surface water. Three of the permanent ponds lose significant percentages of their volumes (type II), but do not become dry. The other ponds (type III) lose only a small percentage of their volumes (G. Larson, personal observations). At maximum volume, type I and type II ponds are relatively shallow ( $0.5-0.8 \mathrm{~m}$ ), whereas type III ponds are between 1.5 and 2.1 meters deep. Summer rain events partially refill the ponds for short periods in some years. In fall, the ponds refill from rain events prior to being capped or filled with ice and snow. The objectives of this study were to compare the species assemblages and temporal changes of the zooplankton communities in type I, II and III ponds relative to: (1) duration of the wet phase; (2) rate of volume loss; and (3) percentage of volume loss.


Figure 1. Location of type I (shaded), type II (hashed) and type III (open) study ponds in Mount Rainier National Park. ( 6.1 m contour intervals).

Mount Rainier National Park is located in the south central portion of Washington State on the western slope of the Cascade Mountain Range. The topography of the park is dominated by Mount Rainier, a dormant volcano $4,363 \mathrm{~m}$ in height. The 10 study ponds were located within a $0.35 \mathrm{~km}^{2}$ area of Mazama Ridge in the southern part of the park (Fig. 1). A large mudflow is believed to have formed the Mazama Ridge ponds between 5,800 and 6,600 years ago (Tom Sisson, USGS, pers. comm.; Crandell, 1969). The set of ponds ranged between 1578 m and 1672 m in elevation, $75 \mathrm{~m}^{2}$ to $1959 \mathrm{~m}^{2}$ in surface area at full volume, 48 cm to 210 cm in maximum depth and $16 \mathrm{~m}^{3}$ to $1566 \mathrm{~m}^{3}$ in maximum volume (Table 1). Catchment areas of the ponds were subalpine parkland and meadow dominated by subalpine fir (Abies lasiocarpa), avalanche fawnlily (Erythronium mantanum), ovalleaf hucklebery (Vaccinium ovatum) and various subalpine herbs. Elk (Cervus elaphus) frequented the ponds during summer, apparently to drink and wallow.

Warm moist air from the Pacific Ocean provides an annual precipitation of approximately 2450 mm at Paradise, which is less than 2 km from the location of the study area. More than 75 percent of the precipitation falls as snow from October through March, typically reaching depths of 5 m to 7 m by March or April (Richardson, 1972; Franklin et al., 1988). The snow-free season is relatively short, normally beginning in July (Paradise mean snow-melt date 17 July $\pm 16$ days, 1970-1991) and lasting through September or October. On average, less than 15 percent of the annual precipitation occurs during June September ( $\mathrm{N}=62$ ).

During the period of snow-melt runoff and fall recharge, the study ponds had outlets, with the exception of MI10. Three of the ponds were interconnected by streams during the periods of snow-melt runoff and fall recharge; LZ16 received outflow from M16, LZ17 received outflow from Noname, and LZ15 received outflow from LZ14 (Fig. 1). At the conclusion of snow-melt runoff, the ponds began to shrink in volume and

Table 1. Elevation, maximum surface area, maximum depth, maximum volume, catchment area, approximate date of ice out, minimum volume, percent of total volume lost, rate of volume lost, wet phase length, date of drying, and approximate number of days dry for Mazama Ridge ponds, June - September, 1992.

| Variable | Type I |  |  |  | Type II |  |  | Type III |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | MI10 | Noname | LZ16 | LZ18 | M16 | LZ14 | LZ12 | LZ15 | LZ17 | LZ19 |
| Elevation (m) | 1672 | 1588 | 1604 | 1604 | 1605 | 1623 | 1652 | 1622 | 1578 | 1590 |
| Maximum surface area ( $\mathrm{m}^{2}$ ) | 75 | 189 | 180 | 294 | 522 | 522 | 385 | 1775 | 1959 | 1329 |
| Maximum depth (cm) | 49 | 48 | 59 | 77 | 73 | 65 | 68 | 150 | 210 | 203 |
| Maximum volume ( $\mathrm{m}^{3}$ ) | 16 | 39 | 42 | 63 | 108 | 153 | 133 | 1446 | 1566 | 1427 |
| Catchment area ( $\left.\mathrm{m}^{2}\right)^{\text {a }}$ | 1560 | 8793 | 13,321 | 4333 | 10,339 | 5177 | 17,152 | 13,909 | 16,224 | 2849 |
| Approximate date of ice out | 20 Jun | 15 Jun | 18 Jun | 15 Jun | 11 Jun | 11 Jun | 13 Jun | 11 Jun | 11 Jun | 2 Jun |
| Minimum volume ( $\mathrm{m}^{3}$ ) | 0.0 | 0.0 | 0.0 | 0.0 | 7.7 | 8.5 | 41.9 | 1008 | 1201 | 1068 |
| Percent of total volume lost | 100 | 100 | 100 | 100 | 92.8 | 94.4 | 68.5 | 30.3 | 23.3 | 25.2 |
| Rate of volume loss ( $\mathrm{m}^{3} /$ day ) | 0.5 | 0.7 | 0.5 | 0.9 | 1.5 | 1.8 | 1.4 | 5.5 | 7.0 | 3.6 |
| Wet phase length (days) | 44 | 75 | 77 | 80 | 98 C | 98 c | $98{ }^{\text {c }}$ | $98{ }^{\text {c }}$ | $98{ }^{\text {c }}$ | 98 C |
| Date of drying | 3 Aug, 17 Aug | 29 Aug | 2 Sep | 3 Sep | NA ${ }^{\text {d }}$ | NA ${ }^{\text {d }}$ | $N A^{\text {d }}$ | NAd | NA ${ }^{\text {d }}$ | $\mathrm{NA}^{\text {d }}$ |
| Number of days dry | $\begin{gathered} 5 \\ 16^{\mathrm{b}} \\ \hline \end{gathered}$ | 6 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |

[^0]then outlets become dry. LZ18, LZ16, Noname, and MI10 were type I ponds, LZ12, LZ14, and M16 were type II ponds and LZ15, LZ17 and LZ19 were type III ponds. Type III ponds were considerably larger in surface area, volume, and depth than type I and type II ponds (Table 1). Macrophytes (Carex lenticularis Michx. var. lenticulais, Juncus filiformis L. and Callitriche verna L.) were not abundant and were limited mostly to the periphery of the ponds. Isotes echinospora Dur., a quillwort, occasionally inhabited the bottoms of type II and III ponds.

## MATERIALS AND METHODS

## Sampling schedule

The ten ponds were sampled every two weeks starting just after ice-out in the middle of June and lasting through September, 1992 (Table 2). Each pond was visited eight times (sample weeks $1,3,5,7,9,11,13,15$ ), except pond MI10, which was sampled five times. All ponds were sampled within a three-day period during each sampling week once the ponds had iced-out, except LZ16 during week 1. LZ16 was sampled five days after the first pond was sampled in week 1 because it iced-out later than the others. MI10 iced-out during week 3 but was not sampled until week 5 .

Table 2. Dates of sampling (month-day) in Mazama Ridge ponds, June - September, 1992.

| Week | Type I |  |  |  | Type II |  |  | Type III |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | MI10 | NN | LZ16 | LZ18 | M16 | LZ14 | LZ12 | LZ15 | LZ17 | LZ19 |
| 1 | NA | 6-17 | 6-22 | 6-18 | 6-19 | 6-18 | 6-19 | 6-18 | 6-17 | 6-17 |
| 3 | NA | 6-30 | 6-30 | 6-30 | 6-30 | 7-2 | 7-2 | 7-1 | 7-1 | 7-1 |
| 5 | 7-16 | 7-15 | 7-15 | 7-15 | 7-15 | 7-16 | 7-16 | 7-14 | 7-14 | 7-14 |
| 7 | 7-29 | 7-27 | 7-27 | 7-27 | 7-27 | 7-29 | 7-29 | 7-28 | 7-28 | 7-28 |
| 9 | 8-11 | 8-10 | 8-10 | 8-10 | 8-10 | 8-11 | 8-11 | 8-12 | 8-12 | 8-12 |
| 11 | NA | 8-24 | 8-24 | 8-24 | 8-24 | 8-25 | 8-24 | 8-25 | 8-25 | 8-25 |
| 13 | 9-8 | 9-8 | $9-8$ | 9-8 | 9-8 | 9-9 | 9-9 | 9.9 | 9.9 | 9-9 |
| 15 | 9-23 | 9-21 | 9-21 | 9-21 | 9-23 | 9-22 | 9-23 | 9-22 | 9-22 | 9-22 |

## Physical and chemical variables

Because of the shallow depths in type I and type II ponds, water samples for chemical analysis were collected from shore using a modified two-liter high density polyethylene Nalgene bottle connected to the end of a telescoping pole (maximum length was 4.6 m ). The inverted bottle was placed mid-depth in the water column and slowly turned to allow the bottle to fill. In type III ponds, water was collected with a LaMotte water sampler at one meter in depth, with the person collecting the sample in a rubber raft positioned over the deepest area of each pond. Water samples were transferred to one liter Nalgene bottles. Samples were transported on ice in a cooler to the park's Resource Laboratory in Longmire for analysis.

Concentrations of dissolved oxygen were estimated using the Azide modification of the Winkler method. Samples were fixed with reagents (Hach powder pillows) shortly after collection and were later titrated with $2.0-\mathrm{N}$ sodium thiosulfate. Percent saturation was calculated according to Wetzel and Likens (1991).

Immediately upon returning to the Longmire Resource Laboratory after field sampling, an Orion meter with Orion Sureflow combination or Orion combination electrodes was used for pH determination. A modified protocol for pH determination in waters of low ionic strength was used (Metcalf, 1984). Acid-neutralizing capacity ( $\mu \mathrm{eq} / \mathrm{I}$ ), a measure of pH buffering capacity, was determined by Gran Titration (Gran, 1952) using $0.16-\mathrm{N}$ sulfuric acid (endpoint $\approx 3.5 \mathrm{pH}$ ). Turbidity (NTU) was measured with a Hach turbidity meter, model 2100A. Conductivity ( $\mu \mathrm{mhos} / \mathrm{cm}$; corrected to $25^{\circ} \mathrm{C}$ ) was measured with a Beckman conductivity bridge, model RG-16D.

Samples for nutrient and ion analyses were collected from each pond during week 11 (August 24 and 25), except for MI10 which was dry during this period. Samples were filtered through pre-washed $45-\mu \mathrm{m}$ glass filters and refrigerated until the following day when they were shipped in coolers with ice packs to the Cooperative Chemical Analytical Laboratory at Oregon State University, Corvallis, Oregon. Samples arrived at
the laboratory within approximately 48 hours of collection and were analyzed following standard procedures (Table 3 ).

A digital thermometer with 3 m submersible sensor (VWR brand) was used to measure mid-depth water temperature $\left({ }^{\circ} \mathrm{C}\right)$ at the time of sampling. Daily water temperatures were recorded using standard Taylor maximum-minimum thermometers, typically over three consecutive days during each sampling week. The thermometers were positioned in the deepest region of each pond. A small float kept the thermometer upright in the water column with the bulb approximately 20 cm off the sediments. The thermometers were recovered each morning using a telescoping pole and hook to record daily maximum and minimum temperatures and reset the instruments.

General pond shapes were determined from enlarged aerial photographs. Bathymetry was estimated from multi-transect depth measurements taken at snow melt when ponds were at or near maximum volume. Constructed depth contours $(10 \mathrm{~cm})$ were digitized for surface area using the park's Geographical Information System. Maximum volumes were estimated assuming the depth strata represented a series of truncated irregular cones, the sum of which approximated total volume (Wetzel and Likens, 1991). Pond volumes were then estimated at any depth during the sample season using a relationship (5th-order polynomial) between a pond's total volume at each successive contour line and the depth at that contour.

Rate of volume loss ( $\mathrm{m}^{3} /$ day) was calculated as total volume lost divided by number of days from the day the outlet stopped flowing to day of minimal volume. Multiple regression analysis was used to compare relationships between physical variables. A test for physical and chemical differences between the three sets of ponds during each sampling week was made using a Least-Squared-Means ANOVA.

Table 3. Laboratory analytical procedures used by Cooperative Chemical Analytical Laboratory, Corvallis, Oregon (Cameron Jones, pers. comm).

| Variable | Method |
| :--- | :--- |
| Kjeldahl-N | Nessler's Reagent finish |
| Nitrate-N + Nitrite-N | Technicon Autoanalyzer, automated cadmium reduction |
| Ammonia-N | Technicon Autoanalyzer, colormetric automated phenate |
| Total phosphorus | Persulfate digestion, ascorbic acid finish |
| Orthophosphate-P | Reactive phosphate, ascorbic acid finish |
| Silica | Technicon Autoanalyzer, method 105-71W/B |
| Sodium | Flame atomic absorption |
| Calcium | Flame atomic absorption |
| Magnesium | Flame atomic absorption |
| Potassium | Flame atomic absorption |

## Biological variables

Samples for chlorophyll analysis were filtered through $0.45-\mu \mathrm{m}$ Millipore filters and buffered with a solution of magnesium carbonate. Filters were immediately frozen and kept in the dark, transported to Oregon State University, and analyzed for concentrations of chlorophyll-a using a Turner Fluorometer (APHA, 1985).

Salamanders were enumerated in type III ponds as the researcher rowed around each pond once in an inflatable raft, recording the number of salamanders visible. This effectively covered the entire pond basin including the deepest areas. Salamanders were enumerated in the shallow type I and II ponds by walking the shorelines. These ponds were small and shallow enough that the entire pond could be easily surveyed from shore.

Zooplankton were collected with a 12 -cm-diameter conical net ( $64-\mu \mathrm{m}$ mesh, 1:4 ratio of mouth diameter to length of net). In type I and type II ponds, horizontal tows (3 replicates per pond) were collected by throwing the net from shore along the long axis of a pond and towing the net back by hand with the aid of a calibrated rope. The net was buoyant enough that a tow speed of approximately $0.5 \mathrm{~m} / \mathrm{sec}$ could be maintained without significantly disturbing the bottom sediments and while still keeping the net below the water surface. In type III ponds, vertical tows from a rubber raft were made at the deepest portion of the pond. Tow lengths ( $1-6 \mathrm{~m}$ ) were estimated using the calibrated line connected to the net. Volume filtered was estimated assuming $100 \%$ net-filtration efficiency. After addition of a small amount of sodium bicarbonate, all zooplankton samples were immediately preserved with $95 \%$ ethyl alcohol, giving a final alcohol concentration of about $70 \%$. During week 11 , some pond volumes were so small that horizontal tows were impractical without severe disturbance of the sediments. Therefore, all zooplankton samples in type I and II ponds during week 11 were collected by pouring two liters of pond water through the net. Zooplankton samples from MI10 during week 9 were collected in this manner because of reduced volume of the pond at that time.

Each of three replicate zooplankton samples was processed separately for species identification and enumeration for type I and type II ponds. Only one sample was analyzed from type III ponds due to time constraints. A total of 140 samples were processed from sampling weeks $1,7,9,11,13$, and 15 . A processing error, which resulted in growths of fungus within sample containers, destroyed all samples from weeks 3 and 5. The fungus limited identification and enumeration of small zooplankters, especially rotifers, although the samples were still analyzed for presence and absence of crustacean taxa. For zooplankton processing, replicate zooplankton samples were split separately using a Folsom plankton splitter. Half of each split sample was used for zooplankter identification, length measurements, and fecundity determination, the other half was used for enumeration. To make counting practical, the enumeration subsample was often split
additional times to give a target count of about 200 organisms. Zooplankton were counted in settling chambers using an inverted microscope (70X), and counts of taxa were arithmetically extrapolated to estimate the number of organisms per liter (No./Liter). Life stages of copepods (naupli, copepodid, adult male, adult female) and Daphnia (female, egg carrying female, male) were counted separately. Dissecting (40X) and compound (32-1000X) microscopes were used for taxonomic identification utilizing several keys (Balcer et al., 1984; Stemberger, 1979; Ward and Whipple, 1959).

Seasonal patterns in structure and abundance of rotifer and crustacean zooplankton communities were expressed as relative abundance and total density (No./Liter) over time. Because zooplankton in the ponds were concentrated and diluted during the study due to large decreases and increases in pond volumes, total populations of rotifers and crustaceans were estimated for each pond by multiplying density (No./Liter) by the estimated pond volume.

Qualitative samples for benthic macro-invertebrates were collected from shore during week 11 using a dip net and were preserved in 70 percent alcohol.

## RESULTS

## Physical and chemical variables

The ponds became free of ice and snow between June 2 and June 20. At that time, all ponds were filled to capacity with snow-melt runoff (Figs. 2-11). Thereafter, pond volumes declined, and four ponds eventually became dry. MI10 was dry on August 3. However, MI10 partially refilled after a precipitation event in early August, only to dry again by August 17. Noname, LZ16, and LZ18 were dry on August 29, September 2, and September 3, respectively. LZ12, LZ14, and M16 did not go dry, but each pond lost a considerable percentage of their volume by early September (Table 1). In contrast, LZ15, LZ17, and LZ19 lost comparatively little volume by early September (Table 1). Large precipitation events in September (Fig. 12) refilled all ponds to capacity (Figs. 2-11), and all had surface outlets by the end of September.

Water temperatures of the ponds increased rapidly after ice-out (Figs. 2-11). Water temperatures were highest between the middle of July (week 3 ) and the middle of August (week 11). Mean daily water temperatures did not differ markedly among ponds of greatly differing volume (Fig. 13), and mean water temperatures were not significantly different between the three different types of ponds except during weeks 1 and 3 when some ponds were still influenced by localized snow-melt run-off (Table 4). However, daily range in water temperatures in ponds with small volumes often were greater than in ponds of large volume, especially between the middle of July and late August (Fig. 14). Therefore, daily water temperature ranges were significantly higher in type I and II ponds than in type III ponds during weeks 5-11 (Table 4). Pond volume and daily mean air temperature accounted for 65 percent of the variation in daily water temperature ranges based on multiple regression analysis ( $\mathrm{p}<0.05, \mathrm{~N}=146, \log$ transformed). Air and water temperatures were lower following fall volume recharge in early September (weeks 13 and 15).


Figure 2. Volume $\square$, mean daily water temperature and range (bars), turbidity $\bigcirc$, conductivity $\bullet$, dissolved oxygen $\diamond, \mathrm{pH} \Delta$, and acid neutralizing capacity $\Delta$ in MI10, June - September, 1992.


Figure 3. Volume $\square$, mean daily water temperature and range (bars), turbidity $\bigcirc$, conductivity $\bullet$, dissolved oxygen $\diamond, \mathrm{pH} \boldsymbol{\wedge}$, and acid neutralizing capacity $\Delta$ in Noname pond, June - September, 1992.


Figure 4. Volume $\square$, mean daily water temperature and range (bars), turbidity $\bigcirc$, conductivity $\bullet$, dissolved oxygen $\diamond, \mathrm{pH} \Delta$, and acid neutralizing capacity $\Delta$ in LZ16, June - September, 1992.


Figure 5. Volume $\square$, mean daily water temperature $\bullet$ and range (bars), turbidity $O$, conductivity $\bullet$, dissolved oxygen $\diamond, \mathrm{pH} \boldsymbol{\wedge}$, and acid neutralizing capacity $\Delta$ in LZ18, June - September, 1992.


Figure 6. Volume $\square$, mean daily water temperature $\bullet$ and range (bars), turbidity O , conductivity $\bullet$, dissolved oxygen $\diamond, \mathrm{pH} \Delta$, and acid neutralizing capacity $\Delta$ in M16, June - September, 1992.


Figure 7. Volume $\square$, mean daily water temperature and range (bars), turbidity $\bigcirc$, conductivity $\bullet$, dissolved oxygen $\diamond, \mathrm{pH} \uparrow$, and acid neutralizing capacity $\Delta$ in LZ14, June - September, 1992.


Figure 8. Volume $\square$, mean daily water temperature $\bullet$ and range (bars), turbidity $\bigcirc$, conductivity $\bullet$, dissolved oxygen $\diamond, \mathrm{pH} \Delta$, and acid neutralizing capacity $\Delta$ in LZ12, June - September, 1992.


Figure 9. Volume $\square$, mean daily water temperature and range (bars), turbidity O , conductivity $\uparrow$, dissolved oxygen $\diamond, \mathrm{pH} \star$, and acid neutralizing capacity $\Delta$ in LZ15, June - September, 1992.


Figure 10. Volume $\square$, mean daily water temperature $\bullet$ and range (bars), turbidity $O$, conductivity $\uparrow$, dissolved oxygen $\diamond, \mathrm{pH} \Delta$, and acid neutralizing capacity $\Delta$ in LZ17, June - September, 1992.


Figure 11. Volume $\square$, mean daily water temperature - and range (bars), turbidity $O$, conductivity $\diamond$, dissolved oxygen $\diamond, \mathrm{pH} \Delta$, and acid neutralizing capacity $\Delta$ in LZ19, June - September, 1992.


Figure 12. Daily precipitation (solid line) and mean daily air temperature (dashed line) at Paradise weather station, June - September, 1992 (Source: National Park service).r


Figure 13. Relationship between volume and mean sampling week temperature for Mazama Ridge study ponds, June - September, 1992.

Table 4. Difference in weekly means between type I, II, and III ponds for mean water temperature, water temperature range, maximum water temperature, pH (tested on hydrogen ion concentration), and conductivity. P-value based on a Least Squared Means ANNOVA (* $\leq 0.05, \dagger \leq 0.01$ ).

|  | Sample Week |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1 | 3 | 5 | 7 | 9 | 11 | 13 | 15 |
| Mean temp |  |  |  |  |  |  |  |  |
| I versus II | $-3.1^{*}$ | 2.4 | -0.9 | -1.7 | 0.4 | -0.4 | -1.5 | 0.2 |
| I versus III | $-4.9 \dagger$ | -1.7 | 0.5 | 0.2 | 2.6 | 1.4 | -0.9 | 1.1 |
| II versus III | -2.8 | $-4.1 \dagger$ | 1.4 | 1.9 | 2.2 | 1.8 | 0.6 | 0.9 |

## Temp range

| I versus II | -2.9 | -2.3 | 1.6 | 2.4 | $4.6 \dagger$ | $4.8 \dagger$ | -1.2 | -1.3 |
| :---: | :---: | :---: | :---: | :---: | ---: | ---: | ---: | :--- |
| I versus III | 2.4 | 3.0 | $9.2 \dagger$ | $11.1 \dagger$ | $10.0 \dagger$ | $14.2 \dagger$ | 2.6 | 3.0 |
| II versus III | $5.3 \dagger$ | $5.3 \dagger$ | $7.6 \dagger$ | $8.7 \dagger$ | $5.4 \dagger$ | $9.4 \dagger$ | $3.8^{*}$ | $4.3^{*}$ |

Max temp

| I versus II | $-4.7 *$ | 1.3 | 3.3 | -0.5 | 2.6 | 2.0 | -2.1 | -0.4 |
| :---: | :---: | ---: | :--- | :---: | :--- | :--- | ---: | ---: |
| I versus III | -3.7 | -0.2 | $5.1 \dagger$ | $5.8 \dagger$ | $7.5 \dagger$ | $8.5 \dagger$ | 0.3 | 2.7 |
| II versus III | 1.0 | -1.5 | 1.8 | $6.3 \dagger$ | $4.9 \dagger$ | $6.5 \dagger$ | 2.4 | 3.1 |

pH

| I versus II | -0.15 | -0.11 | -0.10 | -0.15 | -0.01 | 0.07 | -0.19 | -0.13 |
| :---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| I versus III | -0.09 | -0.01 | -0.16 | -0.23 | $0.29 \dagger$ | 0.02 | -0.10 | -0.07 |
| II versus III | 0.06 | 0.10 | 0.06 | -0.08 | $0.30 \dagger$ | -0.05 | 0.09 | 0.06 |

## Conductivity

| I versus II | NA | -0.1 | 0.0 | 1.4 | $5.7 \dagger$ | $3.3^{*}$ | $5.0 \dagger$ | 2.7 |
| :--- | :--- | ---: | :--- | :--- | :--- | :--- | ---: | :--- |
| I versus III | NA | 1.5 | 1.6 | $2.9 *$ | $7.9 \dagger$ | $6.4 \dagger$ | $10.5 \dagger$ | $6.9 \dagger$ |
| II versus III | NA | 1.6 | 1.6 | 1.5 | 2.2 | $3.1^{*}$ | $5.5 \dagger$ | $4.2 \dagger$ |

* p-value $\leq 0.05$
$\dagger$ p-value $\leq 0.01$


Figure 14. Relationship between volume and mean sampling week temperature range for Mazama Ridge study ponds, June - September, 1992.

The ponds were low in conductivity, low in alkalinity, and were moderately acidic (Figs. 2-11). Conductivity generally increased after ice-out in all ponds, although conductivity increased faster in ponds which lost more volume. Refilling in fall had little affect on conductivity values. Consequently, conductivities during weeks 11-15 were significantly higher in type I ponds followed by type II ponds and were lowest in type III ponds (Table 4).

In general, alkalinity in type II and III ponds decreased from ice-out through week 13 (Figs. 6-11). In Noname, alkalinity was fairly stable through week 9, whereas alkalinity in MI10 was variable. Most type I ponds increased in alkalinity shortly before going dry (Figs. 2-5). Type I and II ponds exhibited an increase in alkalinity in fall following volume recharge, whereas alkalinity in type III ponds remained low. Pond pH remained fairly stable throughout the sampling season, and there were no significant differences in pH between type I, II or III ponds except during week 9 when type III ponds were on average 0.30 pH units lower (Table 4).

Pond turbidity was lowest when volumes were high (Figs 2-11). In general, water was more turbid either when pond volumes were low or just after storm events. The turbidity of LZ14 was extremely high on August 25 because elk (Cervus elaphus) waded in the pond in the morning before sampling. Turbidity in type III ponds tended to be lower than in type I or II ponds.

Concentrations of dissolved oxygen (DO), expressed as percent saturation, ranged between 45 and 85 (Figs. 2-11). Dissolved oxygen was significantly higher in type III ponds than in type I ( $\mathrm{p}<0.01$ ) and type II ( $\mathrm{p}<0.01$ ) ponds. Although dissolved oxygen concentrations were not significantly different between type I and II ponds based on samples throughout the period of study ( $p>0.5$ ), concentrations of dissolved oxygen were lower in type I ponds just prior to drying (week 11) than in type II ponds. Concentrations of dissolved oxygen increased in all ponds during week 13 but decreased thereafter.

Concentrations of nutrients and cations were measured in the ponds during week 11
(Table 5). These data suggested that ponds that lost the most water were highest in Kjeldahl-nitrogen, ammonia, and orthophosphate. Concentrations of cations were not associated with amount of volume loss and were variable among ponds.

## Biological variables

Chlorophyll-a was low in concentration in all ponds immediately after ice-out (Fig. 15). Large peaks in chlorophyll were generally observed when ponds were low in volume. Concentrations in LZ18, LZ16, LZ12, LZ19, LZ17 and LZ15 remained low throughout the study with only small increases during weeks 11 and 15. Large peaks in chlorophyll-a occurred in Noname, MI10 and LZ14 during weeks 11 and 15. The large peak in LZ14 during week 11 coincided with a large bloom of Peridinium sp. M16 had a high concentration of chlorophyll-a in week 15; however, unlike the other ponds, M16 had a substantial rise in chlorophyll-a during weeks 7 and 9 as well.

Several predacious macro-invertebrate taxa were present in the study ponds, including predacious diving beetles (Dytiscidae), back swimmers (Notonectidae), water boatmen (Corixidae), water striders (Gerridae), and dragon fly nymphs (Aeshnidae and Corduliidae). Each pond, except for possibly MI10, had between two and five of these various taxa present during week 11. MI10 was not sampled for benthic invertebrates because it was dry during this time. Additional macro-invertebrate taxa present include cased caddis flies (Limniphilidae), horse flies (Tabanidae), and midges (Chironomidae).

Neotenic salamanders (Ambystoma gracile) were abundant in type III ponds but were rare or absent in type I and II ponds. Mean abundance (number per pond) and range of larvae (exclusive of newly hatched larvae) observed in LZ19, LZ17, and LZ15 were 30 (10-70), $10(0-30)$, and $33(15-42)$, respectively. Two larvae were observed in LZ14 during week 5. However, these adult neotenic salamanders may have originated in LZ15, which is immediately adjacent to LZ14, and used LZ14's outlet during snow-melt to

Table 5. Nutrient, silica, cation concentrations, and percent of total volume remaining in type I, II, and III ponds during week 11 (24-25 August, 1992).

| $\begin{aligned} & \mathbf{T} \\ & \mathbf{Y} \\ & \mathbf{P} \\ & \mathbf{E} \end{aligned}$ | Pond | Percent of total volume | Total Kjeldahl $N$ ( $\mathrm{mg} / \mathrm{L}$ ) | $\begin{gathered} \mathrm{NO}_{3}-\mathrm{N} \\ + \\ \mathrm{NO}_{2}-\mathrm{N} \\ (\mathrm{mg} / \mathrm{L}) \end{gathered}$ | $\mathrm{NH}_{3}-\mathrm{N}$ <br> (mg/L) | Total dissolved $\mathbf{P}$ ( $\mathrm{mg} / \mathrm{L}$ ) | Orthophosphate P ( $\mathrm{mg} / \mathrm{L}$ ) | Dissolved silica (mg/L) | Dissolved Sodium (mg/L) | Dissolved Potassium (mg/L) | Dissolved Calcium (mg/L) | Dissolved Magnesium (mg/L) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| I | Noname | e 0.1 | 1.21 | *0.000 | 0.021 | 0.195 | 0.020 | 1.65 | 0.75 | 0.70 | 0.42 | 0.187 |
|  | LZ16 | 2.9 | 0.71 | *0.000 | 0.042 | 0.113 | 0.027 | 0.23 | 0.57 | 0.66 | 0.40 | 0.222 |
|  | LZ18 | 1.3 | 0.78 | *0.001 | 0.058 | 0.102 | 0.025 | *0.07 | 0.35 | 1.06 | 0.32 | 0.220 |
| II | M16 | 10.3 | 0.76 | *0.000 | 0.005 | 0.099 | 0.018 | 0.26 | 0.28 | 0.10 | 0.30 | 0.157 |
|  | LZ14 | 16.3 | 0.51 | *0.001 | 0.004 | 0.044 | 0.003 | 0.67 | 0.27 | 0.09 | 0.36 | 0.146 |
|  | LZ12 | 47.4 | 0.48 | 0.003 | 0.032 | 0.048 | 0.005 | 0.32 | 0.60 | 0.52 | 0.33 | 0.136 |
| III | LZ15 | 77.2 | 0.20 | 0.003 | 0.012 | 0.013 | *0.001 | 0.28 | 0.20 | 0.19 | 0.13 | 0.056 |
|  | LZ17 | 82.2 | 0.18 | *0.001 | *0.001 | 0.016 | *0.001 | 0.35 | 0.19 | 0.11 | 0.13 | 0.059 |
|  | LZ19 | 77.3 | 0.19 | *0.001 | 0.004 | 0.010 | *0.001 | 0.29 | 0.21 | 0.06 | 0.15 | 0.065 |

* below detection level.


Figure 15. Chlorophyll-a concentrations in Mazama Ridge study ponds, June September, 1992.
migrate the short distance between ponds (approximately 3 m ). No egg masses or newly hatched larvae were observed in LZ14. Several newly hatched salamanders were observed in Noname (3) and LZ16 (6) immediately before the ponds dryed. These salamanders probably resulted from reproduction of terrestrial adults because neotenic adults would have been easily observed in these small ponds. It is doubtful these larvae survived drying because they had difficulty burrowing into the sediments and still had gills when only a few centimeters of water remained in the ponds.

Collectively, zooplankton communities included 16 rotifer taxa in the ten ponds (Table 6). Rotifers were low in density in all ponds during week 1 (Table 7). In general, rotifer densities in type I ponds were lower than those in type II or type III ponds during weeks 7-15, with the exception of high densities in MI10 during week 7 and in Noname during week 11 (Table 7). During week 13, densities of rotifers were lower in type I and II ponds than in type III ponds. Rotifer densities in type I and II ponds generally increased by week 15 .

Seasonal patterns in the total populations of rotifers (total number of individuals per pond) were highly variable among the ten ponds (Fig. 16). In general, changes in total populations in type III ponds closely paralleled seasonal changes in patterns of rotifer density. However, changes in the total rotifer populations in type I ponds did not correspond closely with changes in rotifer densities, while type II ponds were intermediate.

Composition of rotifer communities varied through the sampling season and varied between pond types. Three genera of rotifers, Encentrum, Notholca and Polyarthra were present in the study ponds immediately after ice-out but were not present during weeks 7-15 (Table 6). The rotifer communities in type III ponds were dominated almost exclusively by Keratella spp. throughout the season (Fig. 17). In type II ponds, the rotifer communities were dominated mostly by Keratella during weeks 7-15 (Fig. 18), with the exception of LZ12 during week 11-13 when Asplanchna brightwelli and Bdelloid rotifers

Table 6. Presence of zooplankton taxa collected during week 1 (A), weeks 7-11 (B) and weeks 13-15 (C) in Mazama Ridge ponds, June - September, 1992. Parentheses show taxa acronyms.

| Taxa | Type I |  |  |  | Type II |  |  | Type III |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | MI10 | NN | LZ16 | LZ18 | M16 | LZ14 | LZ12 | LZ15 | LZ17 | LZ19 |
| Rotifera |  |  |  |  |  |  |  |  |  |  |
| Keratella sp. (KERA) | BC | ABC | ABC | ABC | ABC | ABC | ABC | ABC | ABC | ABC |
| Monostyla lunaris (MOLU) | C | BC | BC | BC | ABC | BC | C |  | BC | C |
| Bdelloidea | BC | BC | ABC | ABC | ABC | ABC | ABC | B |  |  |
| Brachionus urceolaris (BRUR) | BC | BC | BC | ABC | BC |  | C |  |  | B |
| Lecane sp. (LECA) | B | C | C |  | BC | C | C |  |  |  |
| Asplanchna brightwelli (ASBR) | B |  |  | B | B | BC | B |  |  | BC |
| Notholca sp. (NOTH) |  | A | A | A | A | A | A | A |  |  |
| Encentrum sp. (ENCE) |  | A | A | A | A |  | A | A |  |  |
| Polyarthra sp. (POLY) |  | A | A |  |  |  | A |  |  |  |
| Cephalodella sp. (CEPH) | C |  |  |  | BC |  | C | C |  |  |
| Conochilus unicornis (COUN) |  |  |  |  | B | B |  |  |  | AB |
| Trichocerca sp. (TRIC) |  |  |  |  | BC | B |  |  |  |  |
| Notommata sp. (NOTO) |  |  |  |  | BC | C |  |  |  |  |
| Monommata sp. (MONO) |  |  |  |  | B |  |  |  |  |  |
| Lepadella sp. (LEPA) | BC |  |  | C |  |  |  |  |  |  |
| Ascomorpha ecaudis (ASEC) |  |  | B |  |  |  |  |  |  |  |
| Crustacea |  |  |  |  |  |  |  |  |  |  |
| Daphnia rosea (DAP) |  | B | B | B | ABC | ABC | BC | BC | ABC | ABC |
| Chydorus sphaericus (CHSP) |  |  | B | BC | BC | C | BC | C |  | ABC |
| Ceriodaphnia reticulata (CERE) |  |  | B |  |  | C | BC |  |  |  |
| Scapholeberis kingi (SCKI) | . | B | B |  | B |  |  |  |  |  |
| Holopedium gibberum (HOGI) |  |  |  |  |  |  |  | B* | B* | B* |
| Diaptomus signicauda (SIG) |  | AB | ABC | ABC | ABC | ABC | ABC | ABC | ABC | ABC |
| Diaptomus kenai (KENI) |  |  |  |  |  |  |  | B* | BC* | AB |
| Diaptomus franciscanus (FRA) |  |  | B |  |  |  |  |  |  |  |
| Eucyclops agilis (AGI) | B*C | BC | C | BC | BC | B | BC |  |  | B |
| Harpacticoida (HARP) |  | A | A | A |  | A |  |  |  |  |
| Insecta |  |  |  |  |  |  |  |  |  |  |
| Chaoborus sp. (CHAO) |  |  |  |  |  |  | B |  |  |  |
| Total speices | $9^{\text {a }}$ | 13 | 17 | 13 | 18 | 15 | 15 | $10^{\text {b }}$ | $6^{\text {b }}$ | $11^{\text {b }}$ |

a week 1 not available
b only 1 replicate sample analyzed

* not observed in quantitative sub-samples but present in samples overall

Table 7. Mean densities (No./Liter) and total population of rotifers in Mazama Ridge ponds, June-September, 1992. N = number of replicates.

| Pond | Week | N | Keratell cochlearis |  | Brachionus urceolaris |  | Other rotifers |  | Total rotifers |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | No./L | Total | No./L | Total | No./L | Total | No./L | Total |
| MI10 | 1 | 3 | NA |  | NA |  | NA |  | NA |  |
|  | 7 | 3 | 260.0 | 6.6E5 | 555.0 | 1.4E6 |  | 2.3E5 | 906.1 | 2.3E6 |
|  | 9 | 3 | 20.3 | 6.8E4 | 5.0 | 1.7E4 | 17.7 | 5.9E4 | 43.0 | 1.4 E 5 |
|  | 11 | 3 | NA |  | NA |  | NA |  | NA |  |
|  | 13 | 3 | 0.3 | 4.4E3 |  |  | 3.1 | 4.7E4 | 3.4 | 5.1E4 |
|  | 15 | 3 | 0.7 | 6.8 E 3 | 11.4 | 1.1 E 5 | 19.9 | 1.9E5 | 32.0 | 3.0E5 |
| NN | 1 | 1 | 0.2 | 9.4E3 |  |  | 2.8 | 1.1E5 | 3.1 | 1.2E5 |
|  | 7 | 3 | 0.5 | 6.8 E 3 | 0.1 | 1.7E3 |  |  | 0.6 | 8.6E3 |
|  | 9 | 3 | 1.3 | 1.1E4 |  |  | 1.1 | 9.7E3 | 2.4 | 2.1E4 |
|  | 11 | 3 | 16.0 | 1.6E2 | 399.0 | 4.0E3 |  |  | 415.0 | 4.2E3 |
|  | 13 | 3 | 0.1 | 2.0E3 | <0.05 | 1.7E3 | 1.4 | 4.5E4 | 1.4 | 4.7E4 |
|  | 15 | 3 | 0.4 | 7.3 E 3 | 3.4 | 6.5E4 | 1.3 | 2.4E4 | 5.0 | 9.6E4 |
| LZ16 | 1 | 3 | 0.7 | 2.7E4 |  |  | 9.8 | 4.0E5 | 10.5 | 4.3E5 |
|  | 7 | 3 | 4.0 | 8.3E4 | 0.2 | 3.9E3 | 2.4 | 5.0E4 | 6.6 | 1.4 E 5 |
|  | 9 | 3 | 18.7 | 3.7E5 |  |  | 0.6 | 1.1E4 | 19.3 | 3.8E5 |
|  | 11 | 3 | 169.0 | 3.4E5 |  |  | 5.3 | 1.1E4 | 174.3 | 3.5E5 |
|  | 13 | 3 | 0.4 | 1.1E4 |  |  | 0.9 | 2.7E4 | 1.3 | 3.8E4 |
|  | 15 | 3 | 9.2 | 2.3E5 | 0.1 | 2.3E3 | 3.4 | 8.6E4 | 12.7 | 3.2 E 5 |
| LZ18 | 1 | 3 | 1.2 | 7.6E4 | 0.1 | 4.4E3 | 4.3 | 2.7E5 | 5.6 | 3.5E5 |
|  | 7 | 3 | 9.9 | 1.7E5 | 24.5 | 4.1E5 | 0.5 | 7.9E3 | 34.9 | 5.9E5 |
|  | 9 | 3 | 5.3 | 6.8E4 |  |  | 1.1 | 1.6E4 | 6.6 | 8.4E4 |
|  | 11 | 2 | 26.0 | 3.1E4 | 4.0 | 4.8E3 | 3.3 | 4.0E3 | 33.3 | 4.0E4 |
|  | 13 | 3 |  |  |  |  | 0.6 | 2.4E4 | 0.6 | 2.4E4 |
|  | 15 | 3 | 0.7 | 2.1E4 | 27.3 | 9.0E5 | 0.2 | 6.9 E 3 | 28.2 | 9.3E5 |
| M16 | 1 | 3 | 1.0 | 1.0E5 |  |  | 1.0 | 1.0E5 | 2.0 | 2.1E5 |
|  | 7 | 3 | 980.0 | 7.8E7 |  |  | 2.7 | 2.4E5 | 983.0 | 7.8E7 |
|  | 9 | 3 | 317.0 | 1.9E7 | 0.2 | 1.4 E 4 | 9.0 | 7.4E5 | 329.5 | 2.0E7 |
|  | 11 | 3 | 722.0 | 2.2E7 |  |  | 20.7 | 1.1E6 | 759.4 | 2.3E7 |
|  | 13 | 3 | 10.6 | 1.1E6 |  |  | 3.3 | 3.4E5 | 13.9 | 1.4 E 6 |
|  | 15 | 3 | 54.5 | 3.5E6 | 0.5 | 3.1 E4 | 2.1 | 1.4E5 | 57.1 | 3.7E6 |
| LZ14 | 1 | 3 | 0.7 | 1.0E5 |  |  | 1.2 | 1.9E5 | 1.9 | 2.9E5 |
|  | 7 | 3 | 426.0 | 4.1E7 |  |  | 0.8 | 7.3E4 | 426.8 | 4.2E7 |
|  | 9 | 3 | 524.0 | 3.7E7 |  |  | 0.4 | 3.9E4 | 524.6 | 3.7E7 |
|  | 11 | 3 | 834.0 | 2.1E7 |  |  | 6.7 | 1.7E5 | 840.7 | 2.1E7 |
|  | 13 | 3 | 79.9 | 6.6E6 |  |  | 1.9 | 1.6E5 | 81.9 | 6.7E6 |
|  | 15 | 3 | 871.0 | 6.4 E 7 |  |  | 2.2 | 1.7E5 | 873.3 | 6.4 E 7 |
| LZ12 | 1 | 3 | 0.1 | 1.6E4 |  |  | 1.7 | 2.3E5 | 1.9 | 2.5E5 |
|  | 7 | 2 | 1618.0 | 1.6E8 |  |  | 6.6 | 6.4 E 5 | 1624.6 | 1.6 E 8 |
|  | 9 | 3 | 175.0 | 1.6 E 7 |  |  | 10.1 | 9.5E5 | 185.1 | 1.7E7 |
|  | 11 | 3 | 86.7 | 5.5E6 |  |  | 98.7 | 6.2E6 | 185.4 | 1.2 E 7 |
|  | 13 | 3 | 1.4 | 1.7E5 |  |  | 1.2 | 1.4E5 | 2.6 | 3.1E5 |
|  | 15 | 3 | 13.0 | 1.6 E 6 | 1.2 | 1.5E5 | 2.1 | 2.6E5 | 16.3 | 2.0E6 |

Table 7. (cont.)

| Pond | Week | N | Keratell cochlearis |  | Brachionus urceolaris |  | Other rotifers |  | Total rotifers |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | No./L | Total | No./L | Total | No./L | Total | No./L | Total |
| LZ15 | 1 | 1 | 0.9 | 1.3E6 |  |  | 1.2 | 1.7E6 | 2.1 | 3.0E6 |
|  | 7 | 1 | 105.8 | 1.3E8 |  |  | 0.4 | 4.8E5 | 106.2 | 1.3E8 |
|  | 9 | 1 | 737.1 | 8.2E8 |  |  | 0.0 |  | 737.1 | 8.2E8 |
|  | 11 | 1 | 277.3 | 2.9E8 |  |  | 0.0 |  | 277.3 | 2.9E8 |
|  | 13 | 1 | 87.7 | 9.8E7 |  |  | 0.0 |  | 87.7 | 9.8E7 |
|  | 15 | 1 | 65.1 | 7.3E7 |  |  | 0.7 | 7.8E5 | 65.8 | 7.4E7 |
| LZ17 | 1 | 1 | 1.3 | 2.0E6 |  |  | 0.0 |  | 1.3 | 2.0E6 |
|  | 7 | 1 | 210.7 | 3.0E8 |  |  | 0.0 |  | 210.7 | 3.0E8 |
|  | 9 | 1 | 408.4 | 5.4E8 |  |  | 0.2 | 2.7E5 | 408.6 | 5.4E8 |
|  | 11 | 1 | 1065.8 | 1.4E9 |  |  | 0.9 | 1.2E6 | 1066.7 | 1.4E9 |
|  | 13 | 1 | 1311.4 | 1.8E9 |  |  | 1.9 | 2.6E6 | 1313.3 | 1.8E9 |
|  | 15 | 1 | 1309.1 | 1.8E9 |  |  | 0.0 |  | 1309.1 | 1.8E9 |
| LZ19 | 1 | 1 | 56.6 | 7.8 E 7 |  |  | 1.1 | 1.5E6 | 57.7 | 8.0E7 |
|  | 7 | 1 | 971.7 | 1.2E9 |  |  | 10.4 | 1.4 E 7 | 983.3 | 1.2E9 |
|  | 9 | 1 | 255.6 | 2.9E8 | 0.5 | 5.8E5 | 5.7 | 8.8E6 | 263.7 | 3.0E8 |
|  | 11 | 1 | 325.4 | 3.6E8 | 0.9 | 9.9E5 | 0.0 | 2.1E6 | 328.2 | 3.6E8 |
|  | 13 | 1 | 100.3 | 1.1E8 |  |  | 1.2 | 3.4 E 6 | 103.3 | 1.2E8 |
|  | 15 | 1 | 377.7 | 4.3E8 |  |  | 0.7 | 4.7E6 | 381.9 | 4.3E8 |



Figure 16. Mean rotifer density $(\uparrow)$ and percent of maximum total rotifer population (O) in Mazama Ridge ponds, June - September, 1992. $\mathrm{N}=3$. ( ${ }^{\mathrm{a}} \mathrm{N}=2$, ${ }^{\mathrm{b}} \mathrm{N}=1, \mathrm{~N}=1$ in type III ponds).


Figure 17. Dominant and subdominant rotifer taxa ( $>10 \%$ proportional abundance)in Mazama Ridge ponds, June -
September, 1992. A ">" separates dominant and subdominant taxa (difference $>10 \%$ ), whereas equal dominance (within $10 \%$ ) is indicated by a " $/$ ". Acronyms correspond to table 6.


Figure 18. Proportional abundance of rotifer taxa in Mazama Ridge ponds, June September, 1992. Arrows indicate drying.
were abundant (Fig. 17). Composition of rotifer communities in type I ponds were more variable. Keratella dominated Noname during week 7 and LZ18 and LZ16 during weeks 9 and 11. B. urceolaris dominated MI10 and LZ18 during week 7 and Noname during week 11. Ascomorpha ecaudis was sub-dominant in LZ16 during week 7, whereas during week 9, Monostyla lunaris and Bdelloidea were sub-dominant in Noname and MI10, respectively. During week 13 after fall recharge, IBdelloidea dominated all type I ponds but were low in density. Keratella dominated in LZ16 during week 15, whereas $B$. urceolaris or, B. urceolaris and Cephalodella, dominated the other three type I ponds during the final sampling week.

Ten crustacean taxa were collected in the study ponds (Table 6). Diaptomus kenai and Holopedium gibberum were observed in type III ponds only, whereas Diaptomus franciscanus was only found in LZ16. Densities of crustaceans were low during week 1 (Table 8) and highest during weeks 9-11 (Fig. 19). With the exception of MI10, densities were similar between type I and II ponds prior to fall recharge (Fig. 19). Densities were extremely low in MI10 throughout the study period and were not represented in the quantitative subsamples until week 15. Crustacean densities in type I and II ponds decreased greatly between weeks 11 and 13 after the ponds refilled in volume. Densities in type III ponds also decreased during this period, although not as much as in type I and II ponds. Crustacean densities in type I ponds remained low during the final sampling week, but increased in type $\Pi$ ponds.

Although densities of crustacean taxa were high during week 11 in type I ponds (except MI10), total population abundance (number per pond) was low (Fig. 19).

Likewise, total population abundance in type II ponds was generally lower during week 11 than during week 7, with the exception of LZ12. In contrast, total population abundance in type III ponds was higher during week 11 than during week 7. After fall recharge

Table 8. Mean density (No./Liter) and total population of crustaceans in Mazama Ridge ponds, June-September, 1992. $\mathrm{N}=$ number of replicates.

| Pond | Week | N | Daphia rosea |  | Diaptomus signicauda |  | Othercrustaceans |  | Total crustaceans |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | No./L | Total | No./L | Total | No./L | Total | No./L | Total |
| MI10 | 1 | 3 | NA |  | NA |  | NA |  | NA |  |
|  | 7 | 3 | 2.7 | 6.9 E 3 |  |  |  |  | 2.7 | 6.9E3 |
|  | 9 | 3 |  |  |  |  |  |  | 0.0 |  |
|  | 11 | 3 | NA |  | NA |  | NA |  | NA |  |
|  | 13 | 3 |  |  |  |  |  |  | 0.0 |  |
|  | 15 | 3 |  |  |  |  | 0.2 | 1.9 E 3 | 0.2 | 1.9 E 3 |
| NN | 1 | 1 |  |  |  |  |  |  | 0.0 |  |
|  | 7 | 3 | 86.0 | 1.2E6 | 27.2 | 3.9 E 5 | 0.4 | 5.8E3 | 113.6 | 1.6 E 6 |
|  | 9 | 3 | 42.9 | 3.8E5 | 27.7 | 2.4E5 |  |  | 70.6 | 6.2 E 5 |
|  | 11 | 3 | 154.0 | 1.5 E 3 | 81.7 | 8.2E2 | 6.6 | 6.6E1 | 242.3 | 2.4 E 3 |
|  | 13 | 3 |  |  |  |  | 0.2 | 6.6E3 | 0.2 | 6.6E3 |
|  | 15 | 3 |  |  |  |  | $<0.1$ | 9.6 E 2 | <0.1 | 9.6E2 |
| LZ16 | 1 | 3 |  |  |  |  | 0.8 | 3.3E4 | 0.8 | 3.3E4 |
|  | 7 | 3 | 16.0 | 3.3E5 | 3.8 | 7.9E4 | 2.4 | 5.0E4 | 22.2 | 4.6 E 5 |
|  | 9 | 3 | 158.0 | 3.1E6 | 6.2 | 1.2 E 5 | 0.8 | 1.6 E 4 | 165.0 | 3.2E6 |
|  | 11 | 3 | 78.0 | 1.6 E 5 | 6.0 | 1.2E4 | 10.7 | 2.2E4 | 94.7 | 1.9 E 5 |
|  | 13 | 3 |  |  | <0.1 | 1.4 E 3 | 1.5 | 4.3E4 | 1.5 | 4.3E4 |
|  | 15 | 3 |  |  | 4.1 | 1.0E5 | 0.3 | 7.5E3 | 4.4 | 1.1 E 5 |
| LZ18 | 1 | 3 |  |  |  |  | 0.4 | 2.5E4 | 0.4 | 2.5E4 |
|  | 7 | 3 | 5.6 | 9.5E4 | 102.1 | 1.7E6 | 12.0 | 2.0E5 | 119.7 | 2.0E6 |
|  | 9 | 3 | 9.7 | 1.2 E 5 | 76.0 | 9.7E5 | 9.1 | 1.2E5 | 94.8 | 1.2 E 6 |
|  | 11 | 2 | 18.0 | 2.2E4 | 258.0 | 3.1E5 | 24.0 | 2.9E4 | 300.0 | 3.6 E 5 |
|  | 13 | 3 |  |  |  |  | 2.2 | 8.6E4 | 2.2 | 8.6E4 |
|  | 15 | 3 |  |  |  |  | 0.2 | 6.6E3 | 0.2 | 6.6E3 |
| M16 | 1 | 3 | 0.6 | 6.2E4 |  |  |  |  | 0.6 | 6.2E4 |
|  | 7 | 3 | 75.0 | 5.9E6 | 50.5 | 4.0E6 | 8.4 | 6.7E5 | 133.9 | 1.1 E 7 |
|  | 9 | 3 | 64.2 | 3.9E6 | 31.9 | 1.9E6 | 3.8 | 2.3E5 | 99.9 | 6.0E6 |
|  | 11 | 3 | 99.0 | 3.0E6 | 70.0 | 2.1E6 | 13.0 | 4.0E5 | 182.0 | 5.6E6 |
|  | 13 | 3 | 0.2 | 2.1E4 | 1.4 | 1.4 E 5 | 4.4 | 4.5E5 | 6.0 | 6.2E5 |
|  | 15 | 3 | 6.8 | 4.4 E 5 | 39.4 | 2.6E6 | 0.9 | 5.8E4 | 47.1 | 3.1E6 |
| LZ14 | 1 | 3 | 0.1 | 1.5E4 |  |  |  |  | 0.1 | 1.5E4 |
|  | 7 | 3 | 46.5 | 4.5E6 | 74.0 | 7.2E6 | 1.0 | 9.7E4 | 121.5 | 1.2 E 7 |
|  | 9 | 3 | 25.0 | 1.7E6 | 36.0 | 2.5E6 | 0.2 | 1.4 E 4 | 61.2 | 4.3E6 |
|  | 11 | 3 | 184.0 | 4.6E6 | 41.7 | 1.0E6 |  |  | 225.7 | 5.6E6 |
|  | 13 | 3 | 0.2 | 1.6E4 | 3.0 | 2.5E5 | 0.1 | 8.2E3 | 3.3 | 2.7E5 |
|  | 15 | 3 | 6.8 | 5.0E5 | 7.8 | 5.8E5 | 0.1 | 7.4 E 3 | 14.7 | 1.1 E 6 |
| LZ12 | 1 | 3 |  |  |  |  |  |  | 0.0 |  |
|  | 7 | 2 | 48.1 | 4.7E6 | 83.0 | 8.1E6 | 1.4 | 1.4 E 5 | 132.5 | 1.3 E 7 |
|  | 9 | 3 | 57.2 | 5.4E6 | 60.0 | 5.6E6 | 0.2 | 1.9E4 | 117.4 | 1.1 E 7 |
|  | 11 | 3 | 467.0 | 2.9E7 | 67.0 | 4.2E6 | 4.0 | 2.5E5 | 538.0 | 3.4 E 7 |
|  | 13 | 3 | 4.1 | 4.8E5 | 3.1 | 3.7E5 | 1.4 | 1.7E5 | 8.6 | 1.0E6 |
|  | 15 | 3 | 30.8 | 3.8E6 | 21.9 | 2.7E6 | 15.6 | 1.9E6 | 68.3 | 8.4E6 |

Table 8. (cont.)

| Pond | Week | N | Daphiarosea |  | Diaptomus signicauda |  | Other crustaceans |  | Total crustaceans |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | No./L | Total | No./L | Total | No./L | Total | No./L | Total |
| LZ15 | 1 | 1 |  |  |  |  |  |  | 0.0 |  |
|  | 7 | 1 | 4.1 | 4.9E6 | 12.9 | 1.5E7 | <0.1 | <1.2E6 | 17.0 | 2.0E7 |
|  | 9 | 1 | 26.9 | 3.0 E 7 | 26.8 | 3.0 E 7 |  |  | 53.7 | 6.0E7 |
|  | 11 | 1 | 79.4 | 8.3E7 | 14.2 | 1.5 E 7 |  |  | 93.6 | 9.8E7 |
|  | 13 | 1 | 31.8 | 3.6E7 | 7.7 | 8.6E6 | 1.4 | 1.6 E 6 | 40.9 | 4.6E7 |
|  | 15 | 1 | 19.8 | 2.2E7 | 14.2 | 1.6 E 7 |  |  | 34.0 | 3.8E7 |
| LZ17 | 1 | 1 | 0.1 | 1.6 E 5 |  |  |  |  | 0.1 | 1.6E5 |
|  | 7 | 1 | 22.0 | 3.2 E 7 | 17.9 | 2.6E7 | 2.3 | 3.3 E 6 | 42.2 | 6.1 E7 |
|  | 9 | 1 | 8.0 | 1.1 E 7 | 19.8 | 2.6E7 | 1.8 | 2.4 E 6 | 29.6 | 3.9E7 |
|  | 11 | 1 | 29.2 | 3.8 E 7 | 23.6 | 3.0 E 7 |  |  | 52.8 | 6.8E7 |
|  | 13 | 1 | 24.1 | 3.3 E 7 | 14.7 | 2.0E7 | 0.5 | 6.8 E 5 | 39.3 | 5.4E7 |
|  | 15 | 1 | 10.6 | 1.4 E 7 | 11.3 | 1.5E7 |  |  | 21.9 | 3.0E7 |
| LZ19 | 1 | 1 |  |  |  |  | 0.3 | 4.1E5 | 0.3 | 4.1E5 |
|  | 7 | 1 | 10.9 | 1.3E7 | 19.3 | 2.3E7 | 0.5 | 6.1E5 | 30.7 | 3.7E7 |
|  | 9 | 1 | 21.2 | 2.4 E 7 | 18.0 | 2.1E7 | 1.0 | 1.2E6 | 40.2 | 4.6E7 |
|  | 11 | 1 | 61.3 | 6.8 E 7 | 21.7 | 2.4E7 | 1.8 | 2.0E6 | 84.8 | 9.4E7 |
|  | 13 | 1 | 37.1 | 4.2 E 7 | 3.6 | 4.1E6 | 2.4 | 2.7E6 | 43.1 | 4.9E7 |
|  | 15 | 1 | 24.7 | 2.8 E 7 | 4.9 | 5.5E6 | 0.7 | 7.9E5 | 30.3 | 3.4 E 7 |



Figure 19. Mean crustacean density ( $\leftarrow$ ) and percent of total maximum crustacean population ( O ) in Mazama Ridge ponds, June - September, 1992. $\mathrm{N}=3$. ( ${ }^{\mathrm{a}} \mathrm{N}=2,{ }^{\mathrm{b}} \mathrm{N}=1, \mathrm{~N}=1$ in type III ponds).
(weeks 13 and 15), total populations remained low in type I ponds. Total populations in type II ponds were lowest in week 13 and then increased in week 15 . Total populations generally decreased during weeks 13-15 in type III ponds.

Crustacean community composition varied through the sampling season and varied between pond types. Harpacticoid copepods were collected in LZ16, LZ18, and LZ14, and newly hatched Daphnia rosea were present in M16, LZ14, and LZ17 (Fig. 20). Chydorus sphaericus was dominant in LZ19 in week 1. During weeks 7-11, Diaptomus signicauda dominated the crustacean community in LZ18, whereas the other ponds (except MI10) were dominated by D. rosea and D. signicauda or by D. rosea alone (Fig. 21). Diaptomus kenai was present in type III ponds between week 3-13 but absent in type I and II ponds (Table 9). Holopedium gibberum was found in type III ponds, with individuals present between weeks 3-7 (Table 9). Following drying between weeks 11 and 13, type I ponds were dominated by Eucyclops agilis, whereas D. rosea and adult stages of $D$. signicauda were absent (Fig. 20). Type I ponds were dominated either by E. agilis or C. sphaericus during week 15, with the exception of LZ16, which was dominated by newly hatched copepodid stages of $D$. signicauda. During weeks 13-15, type II and III ponds continued to be dominated by $D$. signicauda and $D$. rosea, except for M16, which had increased proportions of $C$. sphaericus during week 13 (Fig. 20).
D. signicauda matured faster in type I and II ponds than in type III ponds. Adult stages of $D$. signicauda were abundant by week 7 in type I and II ponds, whereas significant numbers of adults were not present in type III ponds until week 9 or week 11 (Fig. 22).

Except for in Noname pond, a second generation of D. signicauda was present after fall recharge in type I ponds, as evidenced by the presence of naupli during week 15 (Fig. 22). A second generation also occurred in type II ponds (Fig. 22). Although the proportional abundance of naupli decreased in LZ12 between weeks 13-15, the density of naupli actually increased over 200 percent. A second generation did not occur in type III


Figure 20. Dominant and subdominant crustacean taxa ( $>10 \%$ proportional abundance) in Mazama Ridge ponds, June September, 1992. A $\ggg$ separates dominant and subdominant taxa (difference $>10 \%$ ), whereas equal dominance (within 10\%) is indicated by a " $/$ ". Acronyms correspond to table 6.


Figure 21. Proportional abundance of crustacean taxa in Mazama Ridge ponds, June September, 1992. Arrows indicate drying.

Table 9. Presence (qualitative) of crustacean zooplankton taxa in Mazama Ridge ponds. Values indicate number of ponds within each pond type with a particular species present.

| Type I A |  | Sample week |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 1 | 3 | 5 | 7 | 9 | 11 | 13 | 15 |
| (MI10) | E. agilis | ICE | NA | 1 | - | - | DRY | - | 1 |
| Type I B | D. rosea | - | 3 | 3 | 3 | 3 | 3 | - | - |
| (LZ18) | C. sphaericus | - | - | - | 1 | 2 | 1 | 1 | 1 |
| (LZ16) | C. reticulata | - | - | - | 1 | - | - | - | - |
| (Noname) | S. Kingi | - | - | - | 1 | 1 | 2 | - | - |
|  | D. signicauda naupli* | 3 | 3 | 3 | 3 | 3 | 2 | 2 | 2 |
|  | copepodid | - | 3 | 3 | 3 | 3 | 2 | 1 | 1 |
|  | adult | - | - | 3 | 3 | 3 | 3 | - | - |
|  | D. kenai | - | - | - | - | - | - | - | - |
|  | D. franciscanus | - | - | - | 1 | - | 1 | - | - |
|  | H. gibberum | - | - | - | - | - | - | $\overline{3}$ | 3 |
|  | E. agilis | - | - | - | 2 | 1 | 2 | 3 | 3 |
|  | Harpacticoids | 3 | - | - | - | - | - | - | - |
| TYPE II | D. rosea | 2 | 3 | 3 | 3 | 3 | 3 | 3 | 3 |
| (M16) | C. sphaericus | - | 2 | 1 | 2 | 2 | 2 | 3 | 1 |
| (LZ14) | C. reticulata | - | 1 | - | 1 | - | - | - | 2 |
| (LZ12) | S. Kingi | - | - | - | 1 | 1 | - | - | - |
|  | D. signicauda naupli* | 3 | 3 | 3 | 3 | 3 | 3 | 2 | 3 |
|  | copepodid | - | 2 | 3 | 3 | 3 | 3 | 3 | 2 |
|  | adult | - | 1 | 2 | 3 | 3 | 3 | 3 | 3 |
|  | D. kenai | - | - | - | - | - | - | - | - |
|  | D. franciscanus | - | - | - | - | - | - | - | - |
|  | H. gibberum | - | - | - | - | - | - | - | - |
|  | E. agilis | - | 2 | - | 1 | 2 | 1 | 2 | 2 |
|  | Harpacticoids | 1 | - | - | - | - | - | - | - |
| TYPE III | D. rosea | 2 | 3 | 3 | 3 | 3 | 3 | 3 | 3 |
| (LZ15) | C. sphaericus | 1 | - | - | - | 1 | 1 | 2 | 1 |
| (LZ17) | C. reticulata | - | - | - | - | - | - | - | - |
| (LZ19) | S. Kingi | - | - | - | - | - | - | - | - |
|  | D. signicauda |  | 3 | 3 | 2 | 2 | 2 | 1 | 1 |
|  | naupli* | 3 1 | 3 | 3 | 3 | 3 | 3 | 3 | 3 |
|  | copepodid adult | - | 3 | - | 2 | 3 | 3 | 3 | 3 |
|  | D. kenai | - | 1 | 3 | 3 | 3 | 3 | 1 | - |
|  | D. franciscanus | - | - | - | - |  | - |  | - |
|  | H. gibberum | - | 2 | 2 | 1 |  | - |  | - |
|  | E. agilis | - | - | - | - |  | - |  |  |
|  | Harpacticoids | - | - | - | - |  | - |  |  |

* Includes all calanoid naupli (D. signicauda and $D$. kenai)


Figure 22. Proportion of Diaptomus signicauda life stages in Mazama Ridge ponds, June - September, 1992. Naupli includes all calanoid naupli (D. signicauda and D. kenai).
ponds during the study period. The low densities of naupli in LZ19 did not increase appreciably between weeks 13-15 and were, therefore, not clearly from a second generation.

## DISCUSSION

This study showed that a temporary pond of short wet phase duration (MI10) was inhabited by zooplankton taxa with short generation times and a crustacean taxa with the ability to encyst as drought-resistant resting bodies at immature stages of development. Relative to permanent ponds, rotifer densities typically were low in temporary ponds, although Brachionus urceolaris was abundant shortly before the ponds dried. High volume loss was associated with declining populations of crustaceans. Daphnia rosea was not present in the crustacean communities of temporary ponds after fall recharge. Deeppermanent ponds had slower copepod development and two additional large bodied crustacean taxa relative to shallow-permanent ponds.

Prior to fall recharge, type I ponds had low densities of Keratella, declining populations of crustaceans, and a greater occurrence of Brachionus. Type II ponds had declining crustacean populations (except in LZ12 between week 9 and 11), high Keratella densities and virtually no Brachionus. Type III ponds, which lost little percent volume, had high densities of Keratella, increasing populations of crustaceans, and additional largesized crustacean taxa. Following fall recharge, ponds which had dryed (except MI10) had low densities of crustaceans, a lack of Daphnia and Diaptomus (other than newly hatched stages), and low densities of rotifers dominated mostly by Brachionus. Crustacean communities in type II and III ponds continued to be dominated by Daphnia and Diaptomus signicauda following fall recharge and had high densities of Keratella.

Pond MI10, which had a short wet phase, was inhabited almost exclusively by rotifers. The absence of cladocerans and calanoid copepods in MI10 may have been influenced by the short wet phase of this pond. Rapid loss of pond volume could reduce habitat quantity and the time for growth and maturation. Short wet phases would limit successful completion of life cycles for crustaceans more than for rotifers because crustaceans have longer generation times than rotifers. For example, the time required to first reproduction ranges from 20-24 days at $10^{\circ} \mathrm{C}$ for several Daphnia species, 28 - 32
days for calanoid copepods, but only 5-7 days for rotifers (Allan, 1976). However, the wet phase of MI10 was 44 days, 12-24 days longer than the life cycle of most copepods (Daphnia requires two life cycles for sexual production of resting eggs). This suggests that conditions may not be suitable for crustacean survival during the entire wet phase of MI10. As pond volume decreased prior to drying, water temperatures exceeded $30^{\circ} \mathrm{C}$, the upper limit for survival of most cladocerans (Dodson and Frey, 1991). Therefore, the functional period for crustacean growth and reproduction in MI10 may be even shorter than the length of the wet phase because of extremes in water quality associated with decreasing pond volume.

The presence of cyclopoid copepods in MI10 might appear to dispute the hypothesis that short duration of the wet phase excludes zooplankton species with long generation times. However, cyclopoids are able to encyst as drought-resistant resting bodies at immature stages of development, sometimes taking several years to complete a single generation (Hutchinson, 1967). Such flexibility apparently allows Eucyclops agilis to survive in MI10 in spite of the pond's short wet phase. Hebert \& Hann (1986) similarly attributed the cyclopoid-dominated copepod communities of the arctic to the encysting abilities of cyclopoids.

Although the composition of crustacean communities was similar between shallow temporary (with the exception of MI10) and shallow permanent ponds prior to fall recharge, community composition of type III ponds was notably different because of the presence of two large species, Holopedium gibberum and Diaptomus kenai. This presence of large-bodied crustacean species in the deep Mazama Ridge ponds (type III) was opposite the findings of Sprules (1972), who observed that large sized crustacean species were restricted to shallow ponds (less than 1.5 m deep) in high mountain ponds in Colorado. Sprules (1972) concluded that the skewed distribution of large-bodied crustacean zooplankton was caused by predation of amphibian and dipteran larvae because neither predator was abundant in the shallow ponds, whereas both were abundant in the deep
ponds. Sprules (1972) suggested that the disjunct distribution of larval amphibian (Ambystoma) and Dipteran (Chaoborus) predators resulted from their inabilities to survive in ponds that dried during summer and froze solid during winter. It is interesting that similar winter conditions and similar predator distributions occurred in the shallow and deep Mazama Ridge ponds, yet the structure of the zooplankton communities did not correspond with the results of the Colorado study. There are several possibilities why this may have occurred.

Large crustacean species may not live in the shallow ponds (type I and II) because of invertebrate predation, chemical limitations, or physical limitations. Maly et al. (1980) suggested that benthic invertebrate predators may have an effect on zooplankton dynamics in shallow ponds because as surface-to-volume ratios increase, predation pressures on zooplankton increase. The influence of benthic invertebrates may be especially important in the shallow Mazama Ridge ponds, which are not only shallow at the time of snow-melt, but also experience dramatic declines in pond volume as the open-water season progresses. Several benthic invertebrate species can influence the densities and size structure of zooplankton taxa in lakes and ponds, e.g., Notonectidae (backswimmers; O'Brien \& Vinyard, 1978; McArdle \& Lawton, 1979; Scott \& Murdoch, 1983), Dytiscidae (predacious diving beetles; Arts et al., 1981), and Odonata (dragon flies; Johnson \& Crowley, 1980). These insect taxa occur in the Mazama Ridge area, with all ponds, except for possibly MI10, inhabited by at least two of the taxa. Therefore, invertebrate predation may have eliminated large bodied crustaceans from type I and type II ponds on Mazama Ridge.

Physical and chemical conditions might also contribute to the lack of large crustaceans in type I and II ponds. Daily water temperature ranges and maximum water temperatures were significantly higher in type I and II ponds compared with type III ponds through most of the study period (Table 4).

The presence of large-bodied crustacean taxa in the type III ponds suggested that size-selective predation by the abundant neotenic salamanders was not so intense as to exclude the large zooplankters. At the same time, the large surface-to-volume ratio of the deep ponds may have lessened the influence of benthic macro-invertebrate predation. Chaoborus did not appear to be abundant in the Mazama Ridge ponds because only one specimen was collected during the study (LZ12).

Diaptomus signicauda matured faster in shallow ponds than in deep ponds. The faster development in type I and type II ponds compared with type III ponds (Fig. 22) might be related to higher overall water temperatures in the shallow ponds. Although mean temperatures were not significantly different between deep and shallow ponds, type I and II ponds had consistently higher maximum water temperatures during weeks 5-11 (Table 4). Higher water temperatures during certain periods of the day may have allowed daily pulses of faster growth of $D$. signicauda in the shallow ponds. It was also possible that delayed development in type III ponds might have had some adaptive significance for the populations, such as avoiding predation by newly hatched salamanders or D. kenai early in the year.

It is unclear why densities of Keratella were higher in type II and III ponds than in type I ponds. It does not appear that the discrepancy in population densities resulted from between-pond differences in water temperatures. Water temperatures were very similar between type I and type II ponds, yet Keratella densities were very different. Likewise, mechanical interference and competition from Daphnia did not appear to influence the low Keratella densities in type I ponds. Although suppression of Keratella populations by mechanical interference and competitive interactions from Daphnia has been documented (Gilbert, 1988; DeMott, 1989) and experimental depletions of $D$. rosea in lake enclosures have resulted in significant increases in rotifer densities (Neill, 1985), D. rosea densities in type I ponds were very similar or lower than densities in type II ponds (Fig. 19). If mechanical interference was responsible for the low Keratella densities in type I ponds,
then one would have expected low Keratella densities in type II ponds which had similar or higher abundances of Daphnia. Furthermore, Keratella densities in type I ponds did not increase greatly in the absence of Daphnia during weeks 13 and 15 following fall recharge. It may be that some aspect of drying in type I ponds had an influence on the low Keratella densities.

Brachionus urceolaris was most abundant in type I ponds (Fig. 18). Although Brachionus has a high reproductive rate for rapid population growth (Hutchinson, 1967), it is highly susceptible to competitive exclusion from Daphnia when food supplies are limited (DeMott, 1989). Consequently, Brachionus usually occurs at high density in association with algal blooms (Pejler, 1964; Stemberger, 1979). Unlike Keratella, Brachionus is not greatly affected by mechanical interference with Daphnia because of it's large size (Gilbert, 1985). However, because of it's high food threshold requirements, Brachionus usually decreases in abundances or disappears as efficient filter feeders, like Daphnia, increase in abundance (Daborn et al., 1978; Hanazato \& Yasuno, 1989). The disappearance of Daphnia and Diaptomus (except newly hatched naupli) after fall recharge in type I ponds may have reduced competitive restrictions on the large rotifer, therefore, allowing Brachionus to dominate in most type I ponds (Fig. 18). Furthermore, the absence of Daphnia and Diaptomus in MI10 apparently allowed B. urceolaris to flourish before and after periods of drying and refilling. However, both Brachionus and Daphnia were abundant in Noname pond the sample week (11) before the pond dryed (Table 7 and 8). In fact, explosion of the Brachionus population in Noname pond between weeks 9 and 11 coincided with a greater than 200 percent increase in the density of Daphnia rosea as a result of pond volume decline (the total abundance of the Daphnia population actually decreased by more than $95 \%$ ). However, algae became so abundant as the pond decreased in volume (as evidenced by the high chlorophyll levels, Fig. 15), that Brachionus was probably no longer food limited, whereas Daphnia may have been inhibited by excessively abundant phytoplankton or by extremes in water quality. Algae can become so abundant
that the grooming required by Daphnia to clean it's thoracic leg filters increases respiration to the point of starvation even though food is not limiting (Dodson \& Frey, 1991). Furthermore, water temperatures in Noname exceeded $30^{\circ} \mathrm{C}$ during week 11 because of the extremely low pond volume. Temperatures above $25^{\circ} \mathrm{C}$ have been shown to reduce the feeding efficiency of D. pulex (Lynch, 1977), whereas $30^{\circ} \mathrm{C}$ is considered the approximate upper limit for most cladocerans survival (Dodson and Frey, 1991). Therefore, type I ponds may open an additional niche in the rotifer community by truncating the seasonal dominance of crustaceans. These changes may occur in the presence of crustaceans prior to loss of all surface water and after fall recharge.

The similarities of the crustacean communities between type I and type II ponds through sample week 11 suggest that the requirements needed to successfully inhabit temporary waters, such as ability to tolerate a broad range of environmental conditions, rapid development, marked seasonality in life cycles, and effective dispersal (Wiggins et al., 1980), are advantageous in small permanent ponds. Furthermore, zooplankton in shallow permanent ponds may be subjected to desiccation in winter if ponds freeze solid (Daborn \& Clifford, 1974). Although freezing is not as extreme physiologically to zooplankton as drying (Wiggins et al., 1980), organisms frozen in ice or buried under deep snow packs in ponds must posses the ability to survive a long dormant period under adverse conditions (Ferrari \& Hebert, 1982; Williams, 1987). Since the environmental conditions in winter are probably very similar for any of the small, shallow Mazama ponds, the effects of volume loss and drying in type I ponds versus volume loss in types II may be overshadowed by the environmental demands imposed by winter.

This study suggest that the rate and amount of volume loss can have a significant influence on the structure and densities of zooplankton communities in Mazama Ridge ponds. However, it remains unclear exactly how pond size, competition, predation, and environmental fluctuations influenced the zooplankton communities.

## Conceptual model

Based on the results of this study, a conceptual model was developed to help explain the apparent influence pond size and rate of water loss have on zooplankton community characteristics in Mazama Ridge ponds. The conceptual model attempts to illustrate how zooplankton communities vary between ponds of different size and hydrology through the snow-free season.

At snow-melt the ponds were essentially all the same except for MI10 (Fig. 23). Densities of zooplankton were very low because taxa had just begun to hatch from eggs. Several rotifer taxa dominated the communities at ice-out with no clear pattern evident between ponds (Fig. 17). Newly hatched stages (naupli) of Diaptomus signicauda were present in all ponds, other than possibly MI10 (Fig. 22). The status of MI10 (type IA) is unclear because it was not sampled at snow-melt. However, the lack of all crustaceans, except $E$. agilis, in MI10 during weeks 5-15 suggests MI10 lacked newly hatched crustaceans, other than E. agilis, at snow-melt. Therefore, MI10 was probably different from the other ponds at the beginning of the open water season. Consequently, MI10 is referred to as "type 1 A " in Fig. 23 and the other type I ponds are "type IB."

Zooplankton communities in each of the pond types quickly became distinct from one another during the summer (Fig. 23). Pond type IA was decisively different from the others throughout the study because it lacked virtually all crustaceans except low densities of E. agilis. Type IB ponds had low densities of Keratella throughout the study period and typically had higher abundances of B. urceolaris, whereas D. rosea and D. signicauda dominated the crustacean communities prior to drying. Type II ponds were dominated by high densities of Keratella and D. rosea and D. signicauda dominated the crustacean communities throughout the entire study period. Type III ponds had high densities of Keratella, similar to type II ponds, and D. rosea and D. signicauda dominated the crustacean communities. However, crustacean communities in the type III ponds had D. kenai and H. gibberum present.


Figure 23. Conceptual model of Mazama Ridge zooplankton communities relative to pond type and degree of volume loss.

After fall recharge Daphnia and adult Diaptomus were absent in ponds that dryed (types IA and IB). However, calanoid copepod eggs, presumably of D. signicauda, hatched in most type IB ponds, thereby initiating an attempted second generation. Naupli of a second generation were also present in most type II ponds after fall recharge. A second generation of Diaptomus was not apparent in type III ponds. D. rosea and adult stages of $D$. signicauda were dominant in type II and type III ponds during the fall recharge phase.

## Speculations on the impact of global climate change

Mazama Ridge ponds are sensitive to environmental changes because of their small sizes. Consequently, changes in climatic conditions could affect ponds by altering rates of volume loss. Based on the results of this study, such changes in hydrologic conditions could have significant impacts on the zooplankton communities in Mazama Ridge ponds. If summertime climatic conditions were to become dryer and warmer, rates of volume loss in Mazama Ridge ponds would increase due to increases in evaporation. Under this scenario type IB ponds might dry sooner following snowmelt. Conceptually, a shorter wet phase would shift type IB ponds into more of a type IA
(Fig. 24). The wet phase length could become so short that successful development of crustacean zooplankton would be inhibited. Continued unsuccessful reproduction of crustaceans could result in major changes in the zooplankton communities. Increased evaporation rates could cause type II ponds to dry during the summer and functionally shift them into type IB ponds (Fig. 24). Drying would require the crustaceans to enter resting stages earlier in the summer and would truncate their seasonal dominance. As a result the rotifer $B$. urceolaris would probably increase in dominance. It is not clear whether the high Keratella densities in type II ponds would be effected by changes in the hydrologic conditions. If changes in climatic patterns were to result in increased precipitation in the area during the summer, zooplankton communities in Mazama Ridge ponds might also be


Figure 24. Conceptual model of pond types relative to pond volumes after ice-out.
affected. Wetter conditions might lengthen the wet phase of the type IA pond to the point that crustaceans dispersed into it could become established through successful development and reproduction of resting eggs. Type IB ponds might functionally become type II ponds. Consequently, crustacean communities would not be truncated by complete surface water loss and, as a result, $B$. urceolaris might be restricted due to increased competition. Ponds such as these on Mazama Ridge might provide an early signal of change in aquatic systems as a result of alterations to regional or global climates.

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## APPENDICES

Appendix 1．Mean densities（No．／Liter）of zooplankton in Mazama Ridge ponds． $\mathrm{N}=$ number of replicates，$(\mathrm{F})$－females，$(\mathrm{M})=$ males，$(\mathrm{C})=$ copepodids

| Pond | Week | N | $\begin{aligned} & \dot{8} \\ & \text { 合 } \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ | Conochilus unicornis | Asplanchna brightwelli | Brachionus urceolaris |  | $\begin{aligned} & \dot{0} \\ & \text { 苟 } \\ & \text { 華 } \\ & \text { z } \end{aligned}$ | $\begin{aligned} & \text { 5 } \\ & 0 \\ & 5 \\ & 5 \\ & \frac{3}{0} \\ & 2 \end{aligned}$ |  | $\begin{aligned} & \dot{3} \\ & \text { y } \\ & \text { y } \\ & \text { Z } \\ & \text { y } \end{aligned}$ |  |  | $\begin{aligned} & \dot{8} \\ & \text { 世̀ } \\ & \text { Ư } \\ & \text { y } \end{aligned}$ |  | $\begin{aligned} & \dot{8} \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & \frac{0}{3} \\ & \text { 3 } \end{aligned}$ |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1 | 3 | 0.1 |  |  |  | 0.2 | 1.4 | ＜． 05 |  |  |  |  |  |  |  |  | 0.1 |
|  | 7 | 2 | 1618.0 |  | 3.8 |  |  |  |  |  |  |  |  |  |  |  |  | 2.8 |
| LZ12 | 9 | 3 | 175.0 |  | 10.1 |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 11 | 3 | 86.7 |  | 98.7 |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 13 | 3 | 1.4 |  |  |  |  |  |  |  |  |  |  |  |  | 0.1 |  | 1.1 |
|  | 15 | 3 | 13.0 |  |  | 1.2 |  |  |  | 0.5 |  |  |  | 0.2 |  |  |  | 1.4 |
|  | 1 | 3 | 0.7 |  |  |  |  | 0.3 |  |  |  |  |  |  |  |  |  | 0.9 |
|  | 7 | 3 | 426.0 |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.8 |
| LZ14 | 9 | 3 | 524.0 |  | 0.2 |  |  |  |  | 0.1 |  |  | 0.2 |  |  |  |  | 0.1 |
|  | 11 | 3 | 834.0 | 1.3 |  |  |  |  |  | 5.3 |  |  |  |  |  |  |  |  |
|  | 13 | 3 | 79.9 |  | 0.1 |  |  |  |  | 0.5 |  |  |  |  | 1.5 |  |  |  |
|  | 15 | 3 | 871.0 |  | 0.1 |  |  |  |  | 0.3 |  |  |  | 0.1 | 1.7 |  |  | 0.1 |
|  | 1 | 3 | 1.0 |  |  |  | 0.1 | 0.2 |  |  |  |  |  |  |  |  |  | 0.7 |
|  | 7 | 3 | 980.0 |  | 0.3 |  |  |  |  | 1.9 |  |  |  | 0.3 | 0.3 | 0.3 |  |  |
| M16 | 9 | 3 | 317.0 |  | 3.3 | 0.2 |  |  |  | 4.7 |  | 1.2 | 2.4 |  | 0.2 |  |  | 0.5 |
|  | 11 | 3 | 722.0 | 9.3 | 16.7 |  |  |  |  | 2.7 |  | 0.7 | 7.3 |  |  |  |  | 0.7 |
|  | 13 | 3 | 10.6 |  |  |  |  |  |  | 2.6 |  |  | 0.3 |  | 0.1 | 0.2 |  | 0.2 |
|  | 15 | 3 | 54.5 |  |  | 0.5 |  |  |  | 1.2 |  |  | 0.5 |  | 0.5 |  |  |  |
|  | 1 | 3 | 1.2 |  |  | 0.1 | 3.8 | 0.3 |  |  |  |  |  |  |  |  |  | 0.2 |
|  | 7 | 3 | 9.9 |  |  | 24.5 |  |  |  | 0.5 |  |  |  |  |  |  |  |  |
| LZ18 | 9 | 3 | 5.3 |  | 0.1 |  |  |  |  | 0.9 |  |  |  |  |  |  |  | 0.2 |
|  | 11 | 2 | 26.0 |  |  | 4.0 |  |  |  | 1.3 |  |  |  |  |  |  |  | 2.0 |
|  | 13 | 3 |  |  |  |  |  |  |  | 0.1 |  |  |  |  |  |  |  | 0.5 |
|  | 15 | 3 | 0.7 |  |  | 27.3 |  |  |  |  | ＜． 05 |  |  |  |  |  |  | 0.2 |
|  | 1 | 3 | 0.7 |  |  |  | 3.5 | 4.2 | 0.1 |  |  |  |  |  |  |  |  | 2.0 |
|  | 7 | 3 | 4.0 |  |  | 0.2 |  |  |  |  |  |  |  |  |  |  | 2.3 | 0.1 |
| LZ16 | 9 | 3 | 18.7 |  |  |  |  |  |  | 0.4 |  |  |  |  |  |  |  | 0.2 |
|  | 11 | 3 | 169.0 |  |  |  |  |  |  | 5.3 |  |  |  |  |  |  |  |  |
|  | 13 | 3 | 0.4 |  |  |  |  |  |  | 0.1 |  |  |  | 0.1 |  |  |  | 0.8 |
|  | 15 | 3 | 9.2 |  |  | 0.1 |  |  |  | 1.4 |  |  |  | 0.1 |  |  |  | 1.9 |
|  | 1 | 1 | 0.2 |  |  |  | 0.5 | 1.8 | 0.5 |  |  |  |  |  |  |  |  |  |
|  | 7 | 3 | 0.5 |  |  | 0.1 |  |  |  |  |  |  |  |  |  |  |  |  |
| NN | 9 | 3 | 1.3 |  |  |  |  |  |  | 0.9 |  |  |  |  |  |  |  | 0.2 |
|  | 11 | 3 | 16.0 |  |  | 399.0 |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 13 | 3 | 0.1 |  |  | ＜ 05 |  |  |  | 0.1 |  |  |  | 0.1 |  |  |  | 1.2 |
|  | 15 | 3 | 0.4 |  |  | 3.4 |  |  |  | 0.2 |  |  |  | 0.1 |  |  |  | 0.9 |
|  | 1 | 3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 7 | 3 | 260.0 |  | 91.1 | 555.0 |  |  |  |  |  |  |  |  |  |  |  |  |
| M110 | 9 | 3 | 20.3 |  |  | 5.0 |  |  |  |  | 1.3 |  |  | 1.7 |  |  |  | 14.7 |
|  | 11 | 3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 13 | 3 | 0.3 |  |  |  |  |  |  | 0.1 |  |  |  |  |  |  |  | 3.0 |
|  | 15 | 3 | 0.7 |  |  | 11.4 |  |  |  |  | 1.5 |  |  |  |  | 12.0 |  | 6.4 |

Appendix 1. (cont.)

| Pond | Week | N |  |  |  |  |  |  | $\begin{aligned} & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1 | 1 | 56.6 | 1.1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 7 | 1 | 971.7 | 10.4 | 1.2 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| LZ19 | 9 | 1 | 255.6 | 5.7 | 1.9 | 0.5 |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 11 | 1 | 325.4 |  | 1.9 | 0.9 |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 13 | 1 | 100.3 |  | 1.8 |  |  |  |  | 1.2 |  |  |  |  |  |  |  |  |
|  | 15 | 1 | 377.7 |  | 3.5 |  |  |  |  | 0.7 |  |  |  |  |  |  |  |  |
|  | 1 | 1 | 1.3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 7 | 1 | 210.7 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| LZ17 | 9 | 1 | 408.4 |  |  |  |  |  |  | 0.2 |  |  |  |  |  |  |  |  |
|  | 11 | 1 | 1065.8 |  |  |  |  |  |  | 0.9 |  |  |  |  |  |  |  |  |
|  | 13 | 1 | 1311.4 |  |  |  |  |  |  | 1.9 |  |  |  |  |  |  |  |  |
|  | 15 | 1 | 1309.1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 1 | 1 | 0.9 |  |  |  | 0.1 | 1.1 |  |  |  |  |  |  |  |  |  |  |
|  | 7 | 1 | 105.8 |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.4 |
| LZ15 | 9 | 1 | 737.1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 11 | 1 | 277.3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 13 | 1 | 87.7 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 15 | 1 | 65.1 |  |  |  |  |  |  |  |  |  |  |  |  | 0.7 |  |  |

Appendix 1. (cont.)


Appendix 1. (cont.)

| Pond | Week | N | $\begin{aligned} & \text { IU } \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ |  |  |  | Diaptomus signicauda (F) | D. signicauda ( $M$ ) | $\begin{aligned} & 0 \\ & \text { U } \\ & \text { U } \\ & \text { U } \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ | $\begin{aligned} & \text { E } \\ & \text { E } \\ & \text { I } \\ & \text { o } \\ & 0 \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ | $\begin{aligned} & \underset{y}{E} \\ & \dot{Y} \\ & 0 \\ & 0 \end{aligned}$ | $\begin{aligned} & \underline{U} \\ & 0 \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ | Diaptomus franciscanus |  | $\begin{aligned} & \text { :قㅡㄹ } \\ & \stackrel{\rightharpoonup}{\vec{E}} \end{aligned}$ |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| LZ19 | 1 | 1 |  |  | 0.3 |  |  |  |  |  |  |  |  |  | 17.3 |  |
|  | 7 | 1 | 10.9 |  |  |  | 0.2 |  | 19.1 |  | 0.5 |  |  |  | 0.9 |  |
|  | 9 | 1 | 21.2 |  | 0.5 |  | 3.8 | 5.7 | 8.5 |  | 0.5 |  |  |  | 13.2 |  |
|  | 11 | 1 | 61.3 |  | 0.9 |  | 8.5 | 9.4 | 3.8 | 0.9 |  |  |  |  | 1.9 |  |
|  | 13 | 1 | 37.1 |  | 2.4 |  | 0.6 | 2.4 | 0.6 |  |  |  |  |  | 0.6 |  |
|  | 15 | 1 | 24.7 |  | 0.7 |  | 2.1 | 2.8 |  |  |  |  |  |  | 0.7 |  |
| LZ17 | 1 | 1 | 0.1 |  |  |  |  |  |  |  |  |  |  |  | 0.7 |  |
|  | 7 | 1 | 22.0 |  |  |  |  |  | 17.9 | 1.5 | 0.4 | 0.4 |  |  |  |  |
|  | 9 | 1 | 8.0 |  |  |  | 0.7 |  | 19.1 | 0.9 | 0.7 | 0.2 |  |  |  |  |
|  | 11 | 1 | 29.2 |  |  |  | 1.9 | 2.8 | 18.9 |  |  |  |  |  |  |  |
|  | 13 | 1 | 24.1 |  |  |  | 6.6 | 7.6 | 0.5 |  | 0.5 |  |  |  |  |  |
|  | 15 | 1 | 10.6 |  |  |  | 5.7 | 5.6 |  |  |  |  |  |  |  |  |
| LZ15 | 1 | 1 |  |  |  |  |  |  |  |  |  |  |  |  | 1.6 |  |
|  | 7 | 1 | 4.1 |  |  |  |  | 0.2 | 12.7 |  |  |  |  |  | 0.5 |  |
|  | 9 | 1 | 26.9 |  |  |  | 1.4 | 2.1 | 23.3 |  |  |  |  |  | 1.4 |  |
|  | 11 | 1 | 79.4 |  |  |  |  | 8.5 | 5.7 |  |  |  |  |  | 1.4 |  |
|  | 13 | 1 | 31.8 |  | 1.4 |  | 2.8 | 4.2 | 0.7 |  |  |  |  |  |  |  |
|  | 15 | 1 | 19.8 |  |  |  | 6.4 | 7.1 | 0.7 |  |  |  |  |  |  |  |

Appendix 2. Physical and chemical properties of the Mazama Ridge ponds, June September, 1992.

|  | Week | Date | Maximum depth (cm) | Volume ( $\mathrm{m}^{3}$ ) | Mean temperature ( ${ }^{\circ} \mathrm{C}$ ) | Maximum temperature ( $\left.{ }^{\circ} \mathrm{C}\right)$ | $\qquad$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| LZ12 | 1 | 19-Jun | 68.0 | 133.2 |  |  |  |
|  | 3 | 2-Jul | 65.5 | 123.7 | 13.1 | 15.0 | 11.1 |
|  | 5 | 16-Jul | 62.5 | 112.8 | 21.9 | 29.4 | 14.4 |
|  | 7 | 29-Jul | 58.0 | 97.0 | 22.2 | 29.4 | 15.0 |
|  | 9 | 11-Aug | 57.0 | 93.6 | 20.6 | 26.7 | 14.4 |
|  | 11 | 24-Aug | 47.5 | 63.1 | 13.9 | 20.0 | 7.8 |
|  | 13 | 9-Sep | 64.0 | 118.2 | 10.3 | 13.3 | 7.2 |
|  | 15 | 23-Sep | 65.5 | 123.7 | 6.4 | 11.1 | 1.7 |
| LZ14 | 1 | 18-Jun | 65.0 | 152.8 | 13.9 | 17.8 | 10.0 |
|  | 3 | 2-Jul | 59.5 | 125.4 | 10.9 | 16.1 | 5.6 |
|  | 5 | 16-Jul | 60.0 | 127.8 | 21.7 | 28.9 | 14.4 |
|  | 7 | 29-Jul | 53.5 | 97.3 | 22.0 | 28.9 | 15.0 |
|  | 9 | 11-Aug | 47.0 | 69.8 | 20.9 | 27.8 | 13.9 |
|  | 11 | 25-Aug | 33.0 | 24.9 | 16.1 | 22.2 | 10.0 |
|  | 13 | 9-Sep | 50.0 | 82.0 | 14.4 | 19.4 | 9.4 |
|  | 15 | 22-Sep | 48.0 | 73.7 | 12.2 | 20.0 | 4.4 |
| M16 | 1 | 19-Jun | 72.0 | 102.7 |  |  |  |
|  | 3 | 30-Jun | 71.0 | 98.0 | 15.6 | 20.0 | 11.1 |
|  | 5 | 15-Jul | 66.5 | 79.2 | 20.6 | 28.9 | 12.2 |
|  | 7 | 27-Jul | 65.5 | 79.2 | 23.1 | 30.6 | 15.6 |
|  | 9 | 10-Aug | 61.0 | 60.1 | 20.3 | 26.1 | 14.4 |
|  | 11 | 24-Aug | 49.0 | 30.6 | 16.4 | 27.2 | 5.6 |
|  | 13 | 8-Sep | 72.0 | 102.7 | 10.6 | 13.9 | 7.2 |
|  | 15 | 23-Sep | 62.5 | 64.9 | 7.0 | 12.8 | 1.1 |
| LZ18 | 1 | 18-Jun | 77.0 | 62.9 | 6.1 | 11.1 | 1.1 |
|  | 3 | 30-Jun | 67.5 | 38.9 | 14.8 | 18.9 | 10.6 |
|  | 5 | $15-\mathrm{Jul}$ | 64.5 | 32.1 | 18.7 | 26.7 | 10.6 |
|  | 7 | 27-Jul | 53.5 | 16.9 | 20.3 | 28.3 | 12.2 |
|  | 9 | 10-Aug | 49.5 | 12.8 | 21.7 | 31.7 | 11.7 |
|  | 11 | 24-Aug | 27.5 | 1.2 | 13.9 | 22.8 | 5.0 |
|  | 13 | 8-Sep | 67.5 | 38.9 | 9.2 | 11.7 | 6.7 |
|  | 15 | 21-Sep | 63.5 | 33.0 | 12.8 | 15.6 | 10.0 |
| LZ16 | 1 | 22-Jun | 62.0 | 41.2 | 11.4 | 16.7 | 6.1 |
|  | 3 | 30-Jun | 54.0 | 28.5 | 15.3 | 22.2 | 8.3 |
|  | 5 | 15-Jul | 51.5 | 25.1 | 18.9 | 26.1 | 11.7 |
|  | 7 | 27-Jul | 48.0 | 20.7 | 20.3 | 27.2 | 13.3 |
|  | 9 | 10-Aug | 47.0 | 19.6 | 18.4 | 25.0 | 11.7 |
|  | 11 | 24-Aug | 20.0 | 2.0 | 14.2 | 22.8 | 5.6 |
|  | 13 | 8-Sep | 54.0 | 28.5 | 10.0 | 13.3 | 6.7 |
|  | 15 | 21-Sep | 51.5 | 25.1 | 12.5 | 15.6 | 9.4 |
| Noname | 1 | 17-Jun | 48.0 | 39.2 | 6.1 | 8.9 | 3.3 |
|  | 3 | 30-Jun | 44.5 | 33.1 | 14.7 | 20.0 | 9.4 |
|  | 5 | 15-Jul | 38.0 | 21.6 | 18.9 | 26.1 | 11.7 |
|  | 7 | 27-Jul | 33.5 | 14.5 | 20.3 | 27.8 | 12.8 |
|  | 9 | 10-Aug | 29.0 | 8.8 | 20.0 | 27.8 | 12.2 |
|  | 11 | 24-Aug | 10.5 | 0.1 | 16.2 | 26.7 | 5.6 |
|  | 13 | 8-Sep | 44.5 | 33.1 | 10.0 | 13.3 | 6.7 |
|  | 15 | 21-Sep | 36.5 | 19.1 | 12.5 | 16.1 | 8.9 |
| MIIO | 1 |  |  |  |  |  |  |
|  | 3 |  |  |  |  |  |  |
|  | 5 | 16-Jul | 45.0 | 13.8 | 20.9 | 31.1 | 10.6 |
|  | 7 | 29-Jul | 22.5 | 2.6 | 20.9 | 31.7 | 10.0 |
|  | 9 | 11-Aug | 25.0 | 3.4 | 20.0 | 28.9 | 11.1 |
|  | 11 |  |  |  |  |  |  |
|  | 13 | 8-Sep | 47.5 | 15.3 |  |  |  |
|  | 15 | 23-Sep | 38.0 | 9.5 | 7.2 | 11.1 | 3.3 |

Appendix 2. (cont.)

|  | Week | Date | pH | Dissolved oxygen (\% saturation) | Conductivity ( $\mu$ mhos) | $\begin{gathered} \text { Acid } \\ \text { neutalizing } \\ \text { capacity }(\mu \mathrm{eq} / \mathrm{L}) \\ \hline \end{gathered}$ | Turbidity (NTU) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| LZ12 | 1 | 19-Jun | 5.51 |  |  | 10.98 |  |
|  | 3 | 2-Jul | 6.15 | 68.1 | 3.9 | 28.32 |  |
|  | 5 | 16-Jul | 5.91 | 65.1 | 4.8 | 11.04 | 1.20 |
|  | 7 | 29-Jul | 6.00 | 59.7 | 5.6 | 10.77 | 1.20 |
|  | 9 | 11-Aug | 5.89 | 58.6 | 7.1 | 22.32 | 1.40 |
|  | 11 | 24-Aug | 5.69 | 63.3 | 10.2 | 4.74 | 1.20 |
|  | 13 | 9-Sep | 6.28 | 74.1 | 8.4 | 5.53 | 1.70 |
|  | 15 | 23-Sep | 6.10 | 58.9 | 8.3 | 15.95 | 0.78 |
| L214 | 1 | 18-Jun | 5.74 | 72.7 |  | 26.70 |  |
|  | 3 | 2-Jul | 6.10 | 62.3 | 4.1 | 14.10 |  |
|  | 5 | 16-Jul | 5.67 | 61.7 | 4.4 | 1.54 | 0.79 |
|  | 7 | 29-Jul | 5.74 | 58.8 | 4.7 | 0.00 | 1.70 |
|  | 9 | 11-Aug | 5.61 | 64.9 | 4.7 | 6.01 | 1.30 |
|  | 11 | 25-Aug | 5.53 | 77.2 | 5.7 | 0.00 | 12.00 |
|  | 13 | 9-Sep | 6.03 | 72.6 | 8.1 | 8.44 | 2.80 |
|  | 15 | 22-Sep | 6.02 | 65.9 | 8.3 | 18.52 | 0.72 |
| M16 | 1 | 19-Jun | 5.72 |  |  | 21.75 |  |
|  | 3 | 30-Jun | 6.05 | 62.3 | 4.2 | 27.03 |  |
|  | 5 | $15-\mathrm{Jul}$ | 5.70 | 65.1 | 4.0 | 6.21 | 0.72 |
|  | 7 | 27-Jul | 5.76 | 63.5 | 4.2 | 21.01 | 0.82 |
|  | 9 | 10-Aug | 5.33 | 73.5 | 4.4 | 4.50 | 1.20 |
|  | 11 | 24-Aug | 5.97 | 59.6 | 4.3 | 6.28 | 1.20 |
|  | 13 | 8-Sep | 6.00 | 81.0 | 12.0 | 14.85 | 1.70 |
|  | 15 | 23-Sep | 5.90 | 49.0 | 9.4 | 24.05 | 0.84 |
| LZ18 | 1 | 18-Jun | 5.42 | 71.0 |  | 2.10 |  |
|  | 3 | 30-Jun | 6.08 | 62.4 | 3.2 | 18.66 |  |
|  | 5 | 15-Jul | 5.37 | 61.6 | 3.9 | 1.05 | 0.74 |
|  | 7 | 27-Jul | 5.53 | 69.3 | 5.5 | 0.00 | 0.68 |
|  | 9 | 10-Aug | 5.57 | 57.0 | 9.7 | 0.44 | 1.20 |
|  | 11 | 24-Aug | 5.65 | 51.0 | 11.5 | 0.00 | 1.40 |
|  | 13 | 8-Sep | 5.90 | 75.4 | 13.6 | 1.66 | 1.50 |
|  | 15 | 21-Sep | 5.85 | 63.2 | 12.3 | 7.87 | 0.60 |
| LZ16 | 1 | 22-Jun | 5.57 | 71.9 | 3.2 | 24.10 |  |
|  | 3 | 30-Jun | 5.73 | 68.2 | 5.1 | 24.41 |  |
|  | 5 | 15-Jul | 5.66 | 71.0 | 4.1 | 10.82 | 0.60 |
|  | 7 | 27-Jul | 5.77 | 76.0 | 4.6 | 9.00 | 0.71 |
|  | 9 | 10-Aug | 5.52 | 63.7 | 9.3 | 1.07 | 1.10 |
|  | 11 | 24-Aug | 5.91 | 63.3 | 8.1 | 8.83 | 1.70 |
|  | 13 | 8-Sep | 5.93 | 79.7 | 12.8 | 1.70 | 1.40 |
|  | 15 | 21-Sep | 5.78 | 68.7 | 11.9 | 13.32 | 0.68 |
| Noname |  | 17-Jun | 5.54 | 66.8 |  | 18.00 |  |
|  | 3 | 30-Jun | 6.16 | 64.2 | 3.7 | 10.91 |  |
|  | 5 | 15-Jul | 5.79 | 53.8 | 4.7 | 13.82 | 0.70 |
|  | 7 | 27-Jul | 5.66 | 54.2 | 5.7 | 13.05 | 0.77 |
|  | 9 | 10-Aug | 5.71 | 47.6 | 8.7 | 12.49 | 1.50 |
|  | 11 | 24-Aug | 5.84 | 44.8 | 10.4 | 22.13 | 3.00 |
|  | 13 | 8-Sep | 6.21 | 77.0 | 10.4 | 0.30 | 1.10 |
|  | 15 | 21-Sep | 6.03 | 66.9 | 10.1 | 19.21 | 0.76 |
| MI10 | 1 3 |  |  |  |  |  |  |
|  | 5 | 16-Jul | 5.82 | 74.8 | 5.0 | 11.51 | 0.90 |
|  | 7 | 29-Jul | 5.76 | 53.6 | 8.8 | 28.30 | 2.70 |
|  | 9 | 11-Aug | 5.61 | 65.4 | 16.7 | 32.11 | 3.70 |
|  | 11 |  |  |  |  |  |  |
|  | 13 | 8-Sep | 5.59 | 85.3 | 21.1 | 10.82 | 1.20 |
|  | 15 | 23-Sep | 5.83 | 59.7 | 11.2 | 19.65 | 0.88 |

Appendix 2. (cont.)

|  | Week | Date | Maximum depth ( cm ) | Volume ( $\mathrm{m}^{3}$ ) | Mean temperature ( ${ }^{\text {C }}$ ) | Maximum temperature ( ${ }^{\circ} \mathrm{C}$ ) | $\qquad$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| LZ19 | 1 | 17-Jun | 200.0 | 1382.0 | 13.7 | 15.6 | 11.7 |
|  | 3 | $1-\mathrm{Jul}$ | 194.5 | 1303.0 | 17.8 | 19.4 | 16.1 |
|  | 5 | 14-Jul | 194.0 | 1296.0 | 17.8 | 20.0 | 15.6 |
|  | 7 | 28-Jul | 188.0 | 1216.0 | 20.0 | 22.8 | 17.2 |
|  | 9 | 12-Aug | 183.0 | 1152.0 | 17.5 | 19.4 | 15.6 |
|  | 11 | 25-Aug | 179.0 | 1103.0 | 15.6 | 17.8 | 13.3 |
|  | 13 | 9-Sep | 182.0 | 1140.0 | 12.5 | 14.4 | 10.6 |
|  | 15 | 22-Sep | 181.0 | 1127.0 | 11.7 | 13.3 | 10.0 |
| LZ17 | 1 | 17-Jun | 210.0 | 1566.0 | 9.5 | 12.2 | 6.7 |
|  | 3 | 1-Jul | 209.0 | 1548.0 | 17.0 | 18.9 | 15.0 |
|  | 5 | 14-Jul | 208.5 | 1539.0 | 17.5 | 20.6 | 14.4 |
|  | 7 | 28-Jul | 203.0 | 1444.0 | 19.2 | 22.2 | 16.1 |
|  | 9 | 12-Aug | 196.0 | 1332.0 | 18.9 | 21.7 | 16.1 |
|  | 11 | 25-Aug | 193.0 | 1287.0 | 13.9 | 18.3 | 9.4 |
|  | 13 | 9-Sep | 198.0 | 1363.0 | 11.1 | 13.3 | 8.9 |
|  | 15 | 22-Sep | 197.0 | 1348.0 | 13.1 | 15.0 | 11.1 |
| LZ15 | 1 | 18-Jun | 150.0 | 1447.0 |  |  |  |
|  | 3 | 1-Jul | 143.5 | 1327.0 | 16.4 | 18.3 | 14.4 |
|  | 5 | 14-Jul | 159.5 | 1643.0 | 20.6 | 26.7 | 14.4 |
|  | 7 | 28-Jul | 135.0 | 1189.0 | 20.9 | 23.9 | 17.8 |
|  | 9 | 12-Aug | 129.5 | 1113.0 | 19.2 | 22.2 | 16.1 |
|  | 11 | 25-Aug | 124.0 | 1045.0 | 15.3 | 18.3 | 12.2 |
|  | 13 | 9-Sep | 130.0 | 1118.0 | 10.6 | 12.8 | 8.3 |
|  | 15 | 22-Sep | 130.0 | 1118.0 | 13.9 | 16.7 | 11.1 |


|  | Week | Date | pH | $\begin{gathered} \text { Dissolved } \\ \text { oxygen } \\ (\% \text { saturation }) \end{gathered}$ | Conductivity ( $\mu$ mhos) | $\begin{gathered} \text { Acid } \\ \text { neutalizing } \\ \text { capacity }(\mu \mathrm{eg} / \mathrm{L}) \\ \hline \end{gathered}$ | Turbidity (NTU) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| LZ19 | 1 | 17-Jun | 5.47 | 73.4 |  | 4.01 |  |
|  | 3 | 1-Jul | 5.76 | 67.0 | 2.6 | 16.72 |  |
|  | 5 | 14-Jul | 5.85 | 72.4 | 3.0 | 1.81 | 0.64 |
|  | 7 | 28-Jul | 5.88 | 68.9 | 3.3 | 0.00 | 0.59 |
|  | 9 | 12-Aug | 5.11 | 72.0 | 3.1 | 0.00 | 0.44 |
|  | 11 | 25-Aug | 5.75 | 73.7 | 3.5 | 0.00 | 0.69 |
|  | 13 | 9-Sep | 5.88 | 84.9 | 3.4 | 0.00 | 0.68 |
|  | 15 | 22-Sep | 6.05 | 77.2 | 4.1 | 0.00 | 0.34 |
| LZ17 | 1 | 17-Jun | 5.67 | 83.7 |  | 22.88 |  |
|  | 3 | 1 -Jul | 6.05 | 71.2 | 2.5 | 32.79 |  |
|  | 5 | 14-Jul | 5.89 | 79.9 | 2.6 | 2.83 | 0.66 |
|  | 7 | 28-Jul | 5.95 | 75.4 | 3.1 | 0.00 | 0.51 |
|  | 9 | 12-Aug | 5.32 | 84.2 | 3.0 | 0.00 | 0.45 |
|  | 11 | 25-Aug | 5.78 | 75.4 | 3.4 | 0.00 | 0.68 |
|  | 13 | 9-Sep | 6.15 | 83.8 | 3.9 | 0.00 | 0.70 |
|  | 15 | 22-Sep | 6.01 | 73.8 | 4.5 | 0.00 | 0.45 |
| LZ15 | 1 | 18-Jun | 5.67 | 78.9 |  | 14.36 |  |
|  | 3 | 1 -Jul | 6.18 | 72.2 | 2.5 | 13.04 |  |
|  | 5 | 14-Jul | 5.72 | 77.7 | 2.9 | 0.66 | 0.50 |
|  | 7 | 28-Jul | 5.90 | 74.3 | 3.4 | 0.00 | 0.43 |
|  | 9 | 12-Aug | 5.50 | 79.2 | 3.5 | 0.00 | 0.32 |
|  | 11 | 25-Aug | 5.80 | 71.7 | 4.0 | 0.00 | 0.50 |
|  | 13 | 9-Sep | 6.00 | 81.9 | 4.8 | 5.52 | 0.48 |
|  | 15 | 22-Sep | 5.77 | 74.4 | 4.8 | 0.00 | 0.36 |


[^0]:    ${ }^{a}$ flat map.
    ${ }^{\text {b }}$ partially refilled during early August, only to dry again.
    c entire study period
    ${ }^{d}$ not applicable

