Canyon Ferry Reservoir zooplankton population dynamics
by Chadwick Lee Martin

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Abstract:
A limnological study involving four stations on Canyon Ferry Reservoir was conducted during 1971 and 1972. This thesis was primarily concerned with zooplankton population analysis. Part of the study involved comparisons of physical, chemical, and biological aspects with a study conducted on the same reservoir during 1956, 1957, and 1958 by Wright (1958, 1959, 1960, 1961, 1965).

Zooplankton production in 1971 and 1972 was less than that of 1957 and 1958.

A difference in production between the summers of 1971 and 1972 was found. This difference was attributed to a 1971 reservoir draw down and reflooding, which released nutrients from the sediments causing increased phytoplankton production, increased zooplankton production and increased predator (Leptodora kindtii) production. These effects were observed to be most pronounced at the upper end of the reservoir near the nutrient release source.

Overall zooplankton concentrations were similar among the four stations. Zooplankton production was greatest at the upper end of the reservoir, where the greatest phytoplankton production was found.

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Salinity tolerance of diapausing eggs of freshwater zooplankton

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SUMMARY

1. Many freshwater zooplankton produce diapausing eggs capable of withstanding periods of adverse environmental conditions, such as anoxia, drought and extreme temperature. These eggs may also allow oligostenohaline species to survive increased salinity during periods of tidal flux or evaporation, and here we test the ability of diapause eggs to withstand such conditions.

2. Salinity tolerance may also enable organisms to invade new environments. The increased rate of introduction of non-indigenous species to the Laurentian Great Lakes since 1989, when ballast water exchange regulations (to replace fresh/brackish water at sea with full seawater) were first implemented for transoceanic vessels, has stimulated studies that explore mechanisms of introduction, other than of active animals, in ballast water. One hypothesis proposes that freshwater organisms transported in ballast tanks as diapausing eggs may be partially responsible for the increased rate of species introduction, as these eggs may tolerate a wide array of adverse environmental conditions, including exposure to saline water.

3. We collected ballast sediments from transoceanic vessels entering the Great Lakes, isolated diapausing eggs of three species (*Bosmina liederi, Daphnia longiremis* and *Brachionus calyciflorus*), and measured the effect of salinity on hatching rate. In general, exposure to salinity significantly reduced the hatching rate of diapausing eggs. However, as non-indigenous species can establish from a small founding population, it is unclear whether salinity exposure will be effective as a management tool.

Keywords: ballast water exchange, biological invasion, hatching rates, resting eggs, salinity tolerance

Introduction

The introduction of non-indigenous species is a potent agent of biodiversity change, particularly for lake ecosystems (Sala *et al.*, 2000) and measures are urgently needed to identify and eliminate the vectors that transport them. Ballast water is recognised as the single most important vector for species introduction to aquatic habitats. Approximately 10 billion tonnes of ballast water (and its associated biota) are transferred annually between global ports, providing the primary means of transport and introduction of non-indigenous aquatic biota to ecosystems, including bacteria, dinoflagellates, phytoplankton, zooplankton and fish (Rigby, Hallegraeff & Sutton, 1999; Ruiz *et al.*, 2000). Transoceanic shipping accounts for 77% of the species introduced to the Laurentian Great Lakes since 1970 (Ricciardi, 2001). To reduce this threat, voluntary regulations were enacted in 1989, and mandated in 1993, that effectively require inbound vessels to exchange fresh or brackish ballast water with open-ocean saltwater if that water is to be discharged in the

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Great Lakes (United States Coast Guard, 1993). Despite these regulations, the rate at which new species have been recorded in the Great Lakes tripled between 1989 and 1999 compared with the preceding 40 years (Grigorovich *et al.*, 2003). Increased sampling effort and time lags between establishment and discovery of non-indigenous species may partially account for this pattern (Costello & Solow, 2003; Grigorovich *et al.*, 2003), although modelling exercises indicated that ballast water exchange offers only incomplete protection and is least successful for species with benthic or dormant stages contained within ballast sediments (MacIsaac, Robbins & Lewis, 2002). Alternatively, the recent surge in non-indigenous species may be because of the presence of live or dormant organisms contained in the residual ballast of ships declaring 'no ballast on board', which are exempt from the regulations (MacIsaac *et al.*, 2002; Bailey *et al.*, 2003). These vessels carry tonnes of residual sediment and ballast water, and dominate trade inbound to the Great Lakes (Colautti *et al.*, 2003).

Many freshwater zooplankton, including copepods, cladocerans and rotifers, produce diapausing or 'resting' eggs during annual population cycles. These dormant stages probably evolved as an adaptation to periods of adverse environmental conditions, including anoxia, drought and extremely low or high temperature (Gilbert, 1974; Hairston, 1996; Hairston & Cáceres, 1996; Williams, 1998). These eggs could also provide temporal escape from unfavourable salinity, facilitating the intercontinental transfer of freshwater species in sediments of ballast tanks, even those subjected to ballast water exchange. Some of the species recently recorded in the Great Lakes are euryhaline endemics of the Ponto-Caspian region of southeast Europe, which may have been transported as resting stages in ballast water and/or sediments (Ricciardi & MacIsaac, 2000; Reid & Orlova, 2002). While the salinity tolerance of some juvenile and adult freshwater cladocerans and rotifers has been examined (e.g. Miracle & Serra, 1989; Teschner, 1995; Hall & Burns, 2002), very little is known of the salinity tolerance of the diapausing eggs of freshwater taxa. Consequently, it is difficult to infer whether invertebrates capable of producing diapausing eggs could circumvent the salinity 'filter' imposed on potential Great Lakes invaders by ballast water exchange.

In this study, we examine the effect of salinity on the hatching rate of diapausing eggs of the cladocerans *Bosmina liederi* De Melo & Hebert and *Daphnia longiremis* Sars, and the rotifer *Brachionus calyciflorus* Pallas, common inhabitants of ballast sediments of transoceanic vessels entering the Great Lakes. While these three species are native to the Great Lakes, their presence in residual ballast sediments suggests that they are representative of the types of organisms that pose a potential risk of invasion. Bailey *et al.* (2003) tested the viability of diapausing eggs recovered from ballast sediments and noted a tendency for reduced viability with high pore water salinity, although this relationship was not tested directly. Here, we test the hypothesis that diapausing eggs of freshwater zooplankton will be destroyed by exposure to saline water.

Methods

Sample collection

Residual sediments were collected from five transoceanic vessels entering the Great Lakes in 'no ballast on board' status in December 2000, May, August and December 2001, and in June 2002. Ships were sampled at the ports of Hamilton, Thorold and Toronto, Ontario, Canada, and Cleveland, OH, U.S.A. Residual sediment was collected from at least one ballast tank per ship, with additional tanks sampled depending upon availability and the ease and safety of access. Sediments were collected along longitudinal shell frames that trapped sediment in areas away from drainage flows. Approximately 4 kg of sediment (in total) were collected from at least five areas within each tank and placed in a single container. These composite samples were stored in the dark at 4 °C until experimentation. The salinity of residual sediment pore water, separated from sediment by centrifugation at approximately 3300 *g* (approximately 32 360 m s^{-2}) for 15 min, was measured using an optical refractometer (F. Dobbs, Old Dominion University, Norfolk, VA, U.S.A.).

Egg density counts

After thorough mixing, four 40-g subsamples (wet weight) were taken from each sample and preserved in 95% ethanol. Subsamples were each washed

through a 45 μm sieve to remove fine sediment. Diapausing eggs were subsequently separated from the coarse sediment using the colloidal silica Ludox® HS 40 (Burgess, 2001) and counted under a dissecting microscope.

Hatching experiments

Sediments were stored in plastic containers in the dark at 4 °C for at least 4 weeks to allow a refractory period before hatching experiments commenced (see Grice & Marcus, 1981; Schwartz & Hebert, 1987). After this time, diapausing eggs were removed from sediment using a sugar flotation method (Bailey *et al.*, 2003). Briefly, sediment was processed through a 45 μm sieve and washed into centrifuge tubes using a 1 : 1 (w : v) mixture of sucrose and water. After centrifugation (5 min at approximately ~27 *g*) the supernatant was decanted and rinsed thoroughly with water through 45 μm mesh before being transferred to a counting dish. Diapausing eggs were immediately recovered from the supernatant and sorted by size and gross morphology under a dissecting microscope, selecting only fully intact, apparently healthy eggs. A single, replicated experiment was conducted on the most abundant egg type (*Brachionus* or *Daphnia* species) for each of five tanks. For sediment from ship 1, in which *Brachionus budapestinensis* Daday eggs dominated (see Table 1), experiments were attempted using *B. budapestinensis*, but were abandoned owing to loss of eggs over time because of their extremely small size. Experiments were therefore conducted on a subdominant species, *B. liederi*. All other eggs were incubated at 0‰ (parts per thousand salinity) for identification purposes only. Occasionally, two or three species hatched during a single trial (see Table 1). These secondary species always contributed <1% of the total number of hatchlings. In total, 11 species hatched, although only three were used in the replicated experiments. Four trials were conducted with the rotifer *B. calyciflorus* and one trial each for the cladocerans *D. longiremis* and *B. liederi*.

Eggs used in the experiments were separated into 20 replicates of 20 eggs each, and placed into vials containing 15 mL of sterile medium (0, 8, 16, or 32‰) representing incremental efficiencies of ballast exchange. Five replicates were placed into each

Table 1 List of species hatched from ballast sediments through quantitative and qualitative hatching studies

Ship	No. of replicates	Species	No. eggs per 40 g	Pore water salinity (‰)
1 (FP)	N/A	*Brachionus budapestinensis*	92	2
	5	*Bosmina liederi*	56	
	N/A	*Brachionus calyciflorus*	52	
	N/A	*Daphnia longiremis*	6.3	
	N/A	*Daphnia ambigua* Scourfield*		
2 (DB)	5	*Daphnia longiremis*	391	10
	N/A	*Daphnia ambigua**		
3 (DB)	5	*Brachionus calyciflorus*	100	35
	N/A	*Brachionus quadridentatus* f. *rhenanus* (Lauterborn)*		
	N/A	*Brachionus urceolaris* Müller*		
	N/A	*Brachionus budapestinensis*	56.5	
	N/A	*Brachionus angularis* Gosse*		
4 (DB)	5	*Brachionus calyciflorus*	57.8	4
	N/A	*Daphnia magna* Straus	1.5	
	N/A	*Diaphanosoma* sp.	<1	
4 (FP)	5	*Brachionus calyciflorus*	119.5	20
5 (DB)	5	*Brachionus calyciflorus*	187.8	10
	N/A	*Asplanchna brightwelli* Gosse	1.5	

Species with N/A replicates were not used during experimentation, and were hatched only for identification purposes. Ship tanks are identified by type: FP, forepeak tank; DB, double-bottom tank.

*Denotes secondary species hatched from single morphological egg type listed immediately above.

salinity treatment at 20 °C (photoperiod 16 h light : 8 h dark), resulting in an experimental design using 400 eggs per trial. The 0‰ treatment was considered a control to assess maximum viability for these freshwater species. Synthetic pond water (Hebert & Crease, 1980) or diluted, filtered, natural seawater (collected from a vessel transiting the Great Lakes loaded with ocean water ballast, filtered through 0.2 μm Whatman number 5 paper filter) were used as hatching media. Vials were checked for emergence every 24 h for 10 days, with all hatched individuals removed daily. Media were refreshed on day 5. On day 10 all remaining eggs were transferred to synthetic freshwater media by pipette to examine hatching rates after salinity exposure. Again, the number of hatchlings was recorded daily. Negative controls containing only treatment media were kept in each treatment group to detect any introductions of organisms from the environment. We chose the 10 day hatching period after exposure for two reasons. First, previous experiments indicated that 96% of hatching occurs within the first 10 days of trials run for 20 or 30 days in the manner described above (Bailey *et al.*, 2003; unpublished data). Secondly, the typical transit time of a 'no ballast on board' vessel carrying Great Lakes water within the lake system is 7–10 days. If the uptake of Great Lakes water does induce diapausing eggs contained in ballast sediments to hatch (as suggested by Bailey *et al.*, 2003), this is the period of greatest risk.

Variation in the cumulative proportion of diapausing eggs hatched between treatments was analysed using a one-way ANOVA with repeated measures using Systat 8.0 (SPSS, 1998; SPSS, Chicago, IL, U.S.A.). Tukey's multiple comparison test was performed on the total proportion of eggs hatched to determine the impact of salinity on hatching rate. As emergence was inhibited at higher salinities, analyses were conducted on the 10-day hatching segment for each treatment, depending on the timing of emergence (i.e. days 0–10 for 0 and 8‰ treatments were compared with days 10–20 for 16 and 32‰; if no hatching occurred during days 0–10 for the 8‰ treatment, then days 10–20 were used). Only days when hatching occurred in at least one of the replicates were analysed. The proportion of eggs hatched was normalised using an arcsine square root transformation before analysis.

Results

Hatching experiments were conducted on zooplankton diapausing eggs isolated from residual ballast sediment collected from six tanks on five vessels. Salinity of sediment pore water varied from 2 to 35‰ (Table 1). Diapausing egg densities of dominant taxa were high (>50 eggs per 40 g sediment, Table 1). Eggs were induced to hatch in all experiments, with hatching rates ranging from 16 to 89% in the 0‰ treatment (Fig. 1). In each experiment the proportion hatching declined with increasing salinity. No organisms were recorded in the negative control vials. *Brachionus calyciflorus* generally began to hatch within 24 h of incubation at 0‰, while for the cladocerans *B. liederi* and *D. longiremis* emergence began at day 3 (Fig. 1). Development also began promptly in the 8‰ treatments, with *B. calyciflorus* hatching in three out of four trials by day 5. In addition, development of eye-stage embryos was recorded by day 5 in the 8‰ treatments for 50 and 90% of *Daphnia* and *Bosmina* eggs, respectively (see Fig. 2a). Apparently, these species could not tolerate emergence into brackish water, as development always stopped before emergence from eggs was complete. None of the eye-stage embryos recorded in 8‰ treatment continued development after the medium was replaced with 0‰ water on day 10. Conversely, no organisms hatched or completed significant development during the 10 days of exposure at either of the two higher salinities (i.e. 16 and 32‰, Fig. 2b,c), although some lipid accumulation was noted in the 16‰ treatment. Rather, emergence occurred in these treatments only after brackish or saltwater media were exchanged for 0‰ water (Fig. 1). After exchange, hatching rates among experiments varied between 0–31 and 0–78% for the 16 and 32‰ treatments, respectively. *Bosmina liederi* was the only species tested for which no hatching occurred after exposure to any of the salinity (>0‰) treatments.

The difference in hatching rate between treatments was highly significant for all trials ($P < 0.05$, ANOVA, Table 2). All trials exhibited divergence of hatching rates over time, as time × treatment interaction terms were significant ($P < 0.0001$, ANOVA, Table 2). The proportion of eggs hatched was higher in the 0‰ treatment for eggs recovered from ships 1–4 (Fig. 1a-e; $P < 0.05$, Tukey *post hoc* test). The hatching rates of *B. calyciflorus* for the 0 and 32‰ treatments for ship 5

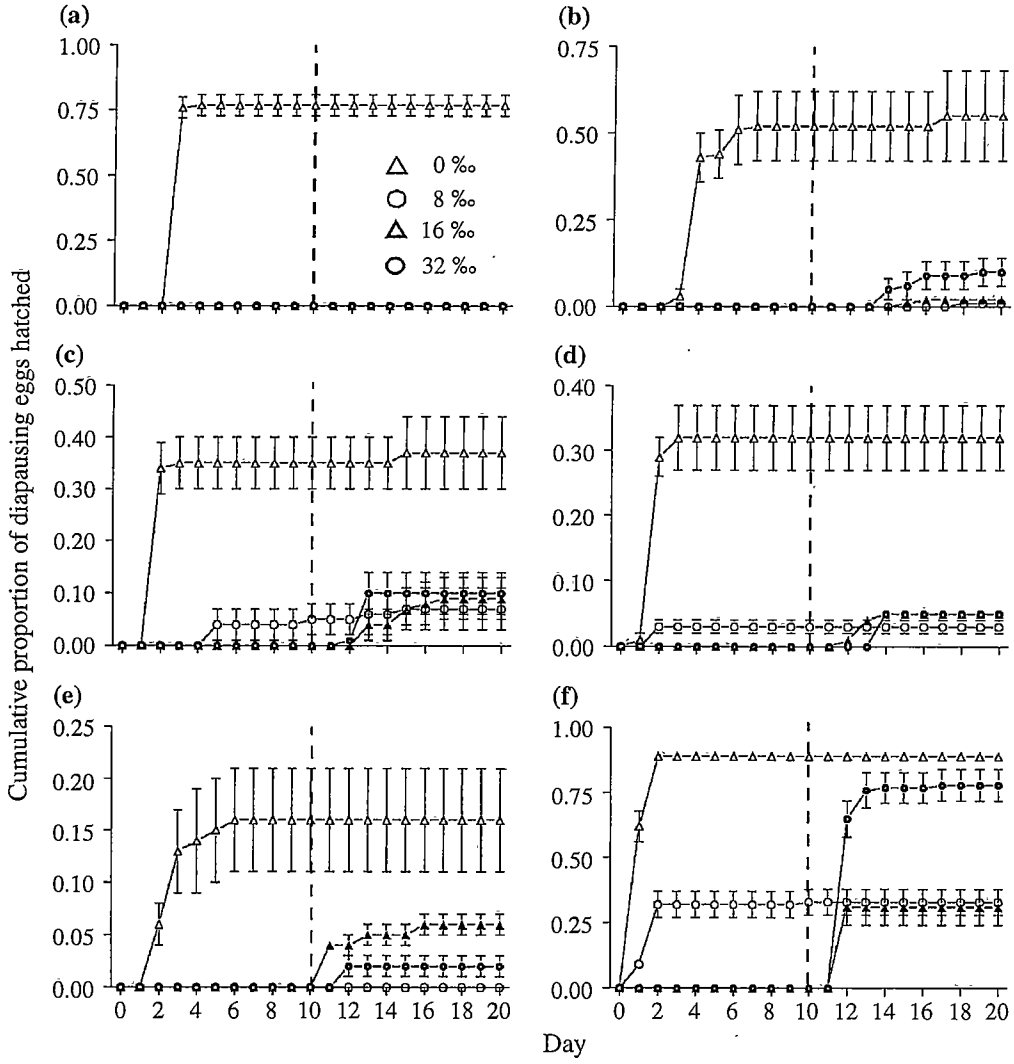

Fig. 1 Mean (±SE) cumulative proportion of diapausing eggs hatched under salinity treatments, by species. (a) *Bosmina liederi* (ship 1), (b) *Daphnia longiremis* (ship 2), (c) *Brachionus calyciflorus* (ship 3), (d) *B. calyciflorus* (ship 4-DB), (e) *B. calyciflorus* (ship 4-FP) and (f) *B. calyciflorus* (ship 5). After 10 days (dotted vertical line) all unhatched eggs in each treatment group were transferred to 0‰ media. Note scale difference for each ordinate. Error bars <0.03 are hidden by graph symbol.

were significantly higher than for the other two treatments (Fig. 1f; $P < 0.001$, Tukey *post hoc* test).

Discussion

To date, investigations of the salinity tolerance of freshwater zooplankton have been limited to measuring direct effects on growth and survival (e.g. Miracle & Serra, 1989; Teschner, 1995; Hall & Burns, 2002), or examining species richness and composition in waterbodies of varying salinity (Frey, 1993; Brain, Fourie & Shiel, 1995). These approaches have not considered diapausing egg stages, probably resulting in an underestimate of the range of salinities a particular taxon can tolerate, particularly in instances where salinity varies temporally. In this study, we have demonstrated that the hatching rate of diapausing eggs is reduced by exposure to saline conditions. The ability of diapausing eggs to tolerate fluctuations in salinity may stem from an evolutionary history in temporary habitats, which generally fluctuate more in their physical and chemical environment than adjacent, permanent ones (Williams, 1998).

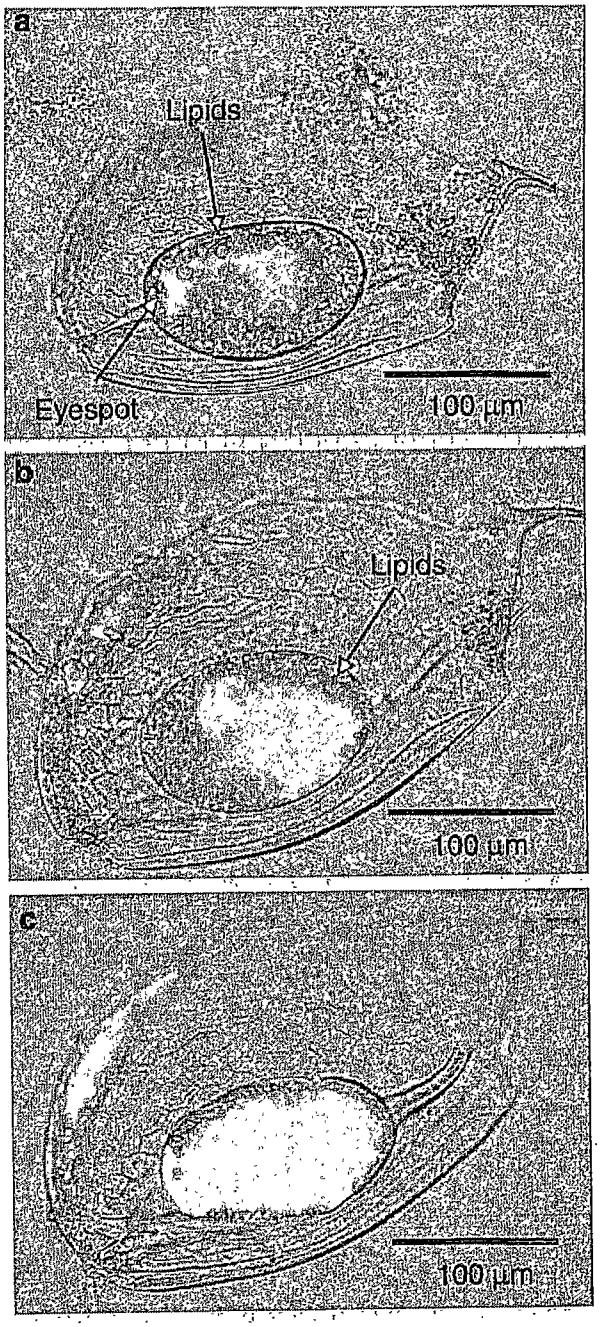

Fig. 2 Condition of diapausing eggs of *Bosmina liederi* after 10 days at each treatment. (a) 8‰, aborted eyed-embryo, (b) 16‰, little differentiation and (c) 32‰, no change. Scale bars (100 µm) are included on each image.

Of the species examined here, diapausing eggs of *B. liederi* appear to exhibit the lowest salinity tolerance with no hatching after exposure to saltwater. *Daphnia longiremis* exhibited a modest degree of salinity tolerance, as a small proportion of diapausing eggs hatched following saltwater exposure. *Brachionus calyciflorus* demonstrated the widest tolerance, with up to 78% eggs hatching after saltwater exposure. Interestingly, *B. calyciflorus* also displayed a wider salinity tolerance as adults than either *B. liederi* or *D. longiremis*. Although typically considered to 'prefer' freshwater, *B. calyciflorus* is frequently observed in brackish waters (e.g. Brain *et al.*, 1995; Park & Marshall, 2000). It is also the only species in these trials that successfully hatched into 8‰ salinity during days 0–10, albeit at rates significantly lower than in freshwater. This finding is consistent with observations of Snell *et al.* (1991), who reported an approximately 40% reduction in the hatching rate of *B. calyciflorus* at 8‰ as compared with 2‰ growth media.

The 'maximum' hatching rates observed at 0‰ ranged from 16–89%. Bailey *et al.* (2003) suggested that pore water salinity might be negatively correlated with hatching success. Our study also found a low hatching rate for eggs recovered from sediments with a pore water salinity of 20‰ or higher (16 and 37%). However, lower pore water salinity (≤10‰) did not guarantee a high hatching rate (i.e. 32% hatch for 4‰), so other factors (such as age of eggs, duration of diapause or hatching cues) are probably involved. In addition, the effects seen in both studies may be impacted by the wide salinity tolerance of *B. calyciflorus* (i.e. 10‰ is only slightly above the natural range for this species, resulting in a high hatching rate at intermediate salinity). Alternatively, pore water salinity measured at the time of collection may not be a good indicator of egg history; eggs may have been retained in ballast sediments for years, experiencing widely varying salinity, of which only the most recent may be reflected by pore water salinity. Nevertheless, while it is possible that the 'maximum' hatching rate (and subsequent reductions in hatching rate) measured in this study may be affected by previous exposures, our results do indicate the effectiveness of ballast water exchange because the sediments carried in transoceanic vessels originate from ports of varying salinity.

Hatching during days 10–20, following transfer to 0‰ medium, occurred mainly in the 16 and 32‰ treatments. Very little hatching occurred during this period in either the 0 or 8‰ treatments, with individuals emerging only from eggs that had not visibly developed during the first 10 days. This suggests that

Table 2 Analysis of variance with repeated measures demonstrating the effect of salinity treatment on the hatching rate of diapausing eggs

Ship	Organism	ANOVA effects [*F* value (d.f.)]		
		Treatment	Time	Time × treatment
1 (FP)	*Bosmina liederi*	32.56 (3,16)***	43.48 (3,48)***	16.98 (9,48)***
2 (DB)	*Daphnia longiremis*	368.97 (3,16)***	353.05 (9,144)***	350.90 (27,144)***
3 (DB)	*Brachionus calyciflorus*	19.78 (3,17)***	41.08 (7,119)***	10.39 (21,119)***
4 (DB)	*Brachionus calyciflorus*	36.60 (3,16)***	47.26 (4,64)***	15.10 (12,64)***
4 (FP)	*Brachionus calyciflorus*	6.15 (3,16)*	14.97 (6,96)***	6.54 (18,96)***
5 (DB)	*Brachionus calyciflorus*	35.25 (3,16)***	322.04 (4,64)***	22.47 (12,64)***

Data were arcsine square root transformed prior to analysis. Significance levels for *F*-values: *$P < 0.05$; ***$P < 0.0001$. Ship tanks are identified by type: FP, forepeak tank; DB, double-bottom tank.

the *Bosmina* and *Daphnia* eye-stage embryos that developed by day 5 at 8‰ were no longer viable. It is possible that a salinity of 8‰ is sufficiently low for the initiation of egg development in freshwater species, but too high for complete development and emergence to occur. In contrast, no development in these genera was apparent in eggs exposed to 32‰ water, thus there remained a 'bank' of viable embryos left to emerge following transfer to freshwater media. Although both *B. liederi* and *D. longiremis* displayed this trend, we cannot explain why only *Daphnia* eggs hatched after exposure to 32‰. However, this trend was also observed for *B. calyciflorus*, with a higher emergence rate after exposure to higher rather than to lower salinity during the latter half of the experiment, particularly for eggs from ship 5. A similar phenomenon was observed by Lutz, Marcus & Chanton (1994), who exposed copepod resting eggs to variable oxygen conditions. They noted that low oxygen concentrations were more detrimental to egg viability than total anoxia because metabolism was completely shut down during anoxia but not under low oxygen conditions. Thus, there appears to be greater interaction between the embryo and the environment under nearly favourable conditions than under extreme conditions. However, it is also possible that the transfer of eggs from 32 to 0‰ acted as a stronger hatching cue than the transfer of eggs from 8 or 16 to 0‰. If this is the case, then subjecting diapause eggs to ballast water of 32‰ may actually promote mass hatching once the eggs are returned to freshwater conditions.

Charmantier & Charmantier-Daures (2001) suggested that rehydrated *Artemia* embryos are protected from high salinity by the cyst envelope that is permeable to water but impermeable to ions. However, salinity and temperature are known to interact in their effects on tolerance, with temperature affecting metabolic rate, ion uptake rate, and membrane permeability (Lee & Bell, 1999). Our experiments explored salinity tolerance at 20 °C, arguably a more challenging environment than exposure at a lower temperature for temperate species. It will be necessary to conduct future trials at a variety of temperatures to deduce the interaction between temperature and salinity on diapausing egg viability.

The variation in hatching rate seen among *B. calyciflorus* trials after exposure (day 10–20) may have resulted from the disparate histories of the populations tested, as indicated by pore water salinity of ballast sediments. Of particular interest was the hatching rate of *B. calyciflorus* collected from ship 5, as 78% eggs hatched successfully after exposure to salinities up to open-ocean levels (i.e. 32‰). In contrast, hatching rates of the other three *B. calyciflorus* populations were significantly reduced after similar exposure (<10%). It is possible that salinity experienced during diapause egg formation may influence the range of salinities eggs can survive while dormant, much like it affects the optimal salinity for the initiation of hatching for the euryhaline rotifer *Brachionus plicatilis* Müller (Gilbert, 1974). We were unable to explore this hypothesis, as the origins of the diapausing eggs in this study are unknown. Future studies using clonal populations from both permanent and temporary habitats may help clarify this possibility.

In general, <10% of *Daphnia* and *Brachionus* eggs hatched after salinity exposure in our experiments. Nevertheless, considering the high egg density in ballast sediments (10^4–10^5 eggs m^{-2} using 1.6 g cm^{-3}

conversion factor for wet sediment), large populations of viable zooplankton eggs may remain after salinity exposure. While it is possible that a longer exposure may have reduced egg viability further, the length of transoceanic crossings will generally not permit longer exposure regimes. As only a small 'seed population' is necessary to establish a cohort of reproductive individuals, and given that the maximum density of diapausing eggs in natural populations ranges between 10^3 and 10^6 eggs m^{-2} (Hairston, 1996), new populations could establish when salinity returns to favourable values (i.e. when the vessel subsequently loads freshwater, or if the eggs get flushed into a freshwater environment). Hall & Burns (2001) suggest that resting eggs of *Boeckella hamata* Brehm, a freshwater copepod, are responsible for the recolonisation of the tidally-influenced Lake Waihola, New Zealand, after seasonal salinisation up to 4.8‰. The average hatching rate for resting eggs of *B. hamata* was only 2.3% under optimal conditions in the laboratory. Therefore, while ballast water exchange may reduce the viability of diapausing eggs by as much as 90% for some taxa, it apparently does not offer complete protection against non-indigenous species entering the Great Lakes by this mechanism. Interestingly, our study indicates that ballast water exchange using brackish water (e.g. 8‰) may have a larger impact on diapausing egg viability than 32‰; however, this effect would have to be weighed against the possibility of introducing live euryhaline species in water of lower salinity, for which ballast water exchange of 32‰ is decidedly more effective (Locke *et al.*, 1993; MacIsaac *et al.*, 2002).

Furthermore, most transoceanic vessels currently trading on the Great Lakes declare 'no ballast on board' status (Colautti *et al.*, 2003), and thus are exempt from ballast water exchange regulations (United States Coast Guard, 1993). MacIsaac *et al.* (2002) suggested that these vessels, collectively, may pose a higher invasion risk than vessels entering the system with saline ballast water owing to the abundance of viable diapausing eggs contained within residual sediments. Our results suggest that the risk posed by diapausing eggs present in sediments of these vessels could be reduced, but not eliminated, by introducing a lens of saltwater into the 'empty' ballast tanks similar to ballast exchange.

Sala *et al.* (2000) suggested that lakes will experience very steep declines in biodiversity this century owing to biotic exchange, land use change and climate change. The salinity of endorheic freshwater habitats is likely to increase during summer months as water inputs decline and evaporation increases (Schindler, 1997, 2001). In addition, coastal lakes and freshwater habitats upstream from tidal estuaries may suffer periodic salinisation as pulsing surges of saltwater seep inland owing to evaporation and anthropogenic diversion of freshwater (Jones, 1994; Hall & Burns, 2003). The persistence of populations through salinity fluctuations by means of diapausing eggs could have profound implications on the extent of biodiversity loss during habitat change. Species incapable of tolerating changing salinity could be replaced by taxa tolerant of brackish or saline conditions (Schindler, 1997); however, this study demonstrates that some populations may be capable of tolerating enhanced fluctuations in habitat salinity, providing a mechanism for enriching biodiversity if the habitat returns to freshwater conditions.

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CANYON FERRY RESERVOIR ZOOPLANKTON POPULATION DYNAMICS

by

CHADWICK LEE MARTIN

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Botany

Approved:

John C. Wright
Chairman, Examining Committee

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Head, Major Department

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Vita

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In August 1972 he was married to Christine Lee Neff.

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Evening near the river side -

A scene for a painter,

Throwing on his straw raincoat,

The fisherman returns home.

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ABSTRACT

A limnological study involving four stations on Canyon Ferry Reservoir was conducted during 1971 and 1972. This thesis was primarily concerned with zooplankton population analysis. Part of the study involved comparisons of physical, chemical, and biological aspects with a study conducted on the same reservoir during 1956, 1957, and 1958 by Wright (1958, 1959, 1960, 1961, 1965).

Zooplankton production in 1971 and 1972 was less than that of 1957 and 1958.

A difference in production between the summers of 1971 and 1972 was found. This difference was attributed to a 1971 reservoir draw down and reflooding, which released nutrients from the sediments causing increased phytoplankton production, increased zooplankton production and increased predator (Leptodora kindtii) production. These effects were observed to be most pronounced at the upper end of the reservoir near the nutrient release source.

Overall zooplankton concentrations were similar among the four stations. Zooplankton production was greatest at the upper end of the reservoir, where the greatest phytoplankton production was found.

INTRODUCTION

Canyon Ferry is a main-stem impoundment on the Missouri River between Helena and Townsend, Montana. The dam was constructed during 1949 - 1954 and storage began in March of 1953. The reservoir was filled for the first time during 1955. Since that time the reservoir has become an increasingly popular recreational site and a large number of summer and permanent homes have been built along its shores.

A major objective of the study was to compare 1971 and 1972 production to that of 1957 and 1958 (Wright 1958, 1959, 1960, 1961, 1965; Kaiser, 1971).

Dr. Ron Rada, in partial fulfillment of a Doctor of Philosophy degree, analyzed physical, chemical, and phytoplankton paramaters.

Hall, Cooper, and Warner (1970) said, "Food chain dynamics and the role of zooplankton have been neglected except for the fundamental work done on ponds in Czecheslovakia and Poland". Thus, comparison of various zooplankton related parameters between the summers and among the stations were made.

DESCRIPTION OF THE STUDY AREA

Canyon Ferry Dam is located 24 kilometers east of Helena, Montana (Fig. 1, Rada, 1974). Its major uses are for irrigation, power generation, flood control and recreation. The reservoir receives water from a 41, 191 square kilometer drainage area. The reservoir is approximately 40 kilometers long with a mean width of 3.5 kilometers. At maximum operating pool level (1157 meters m.s.l.) the reservoir has a capacity of 24.01×10^8 meters^3, a surface area of 13,936 hectares, a maximum depth of 49.2 meters and a mean depth of 18.0 meters.

Samples were taken at four stations 8 kilometers apart. Stations one, two, three, and four were approximately 50, 35, 25, and 20 meters deep, respectively (Fig. 1).

Stations one and two became thermally stratified by July 1. Station three rarely became stratified. Station four never became stratified because of its shallow depth. Wind and wave action increased from station one through four as a result of the prevailing westerly winds. Turbidity increased from station one through four (Fig. 2, Rada, 1974).

Figure 1. Map of the study area, Canyon Ferry Reservoir, Montana (Rada, 1974).

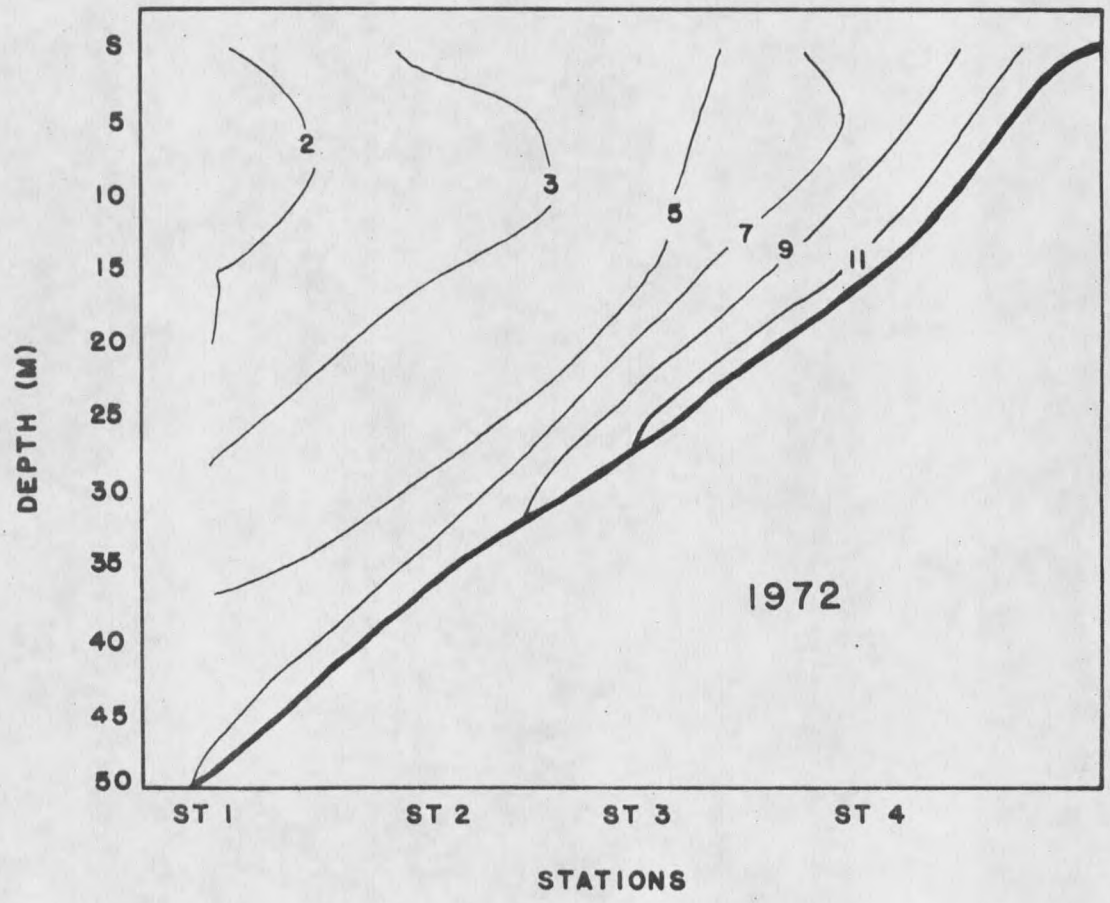

Figure 2. Isoclines of average Jackson Turbidity Units in Canyon Ferry Reservoir during 1972 (Rada, 1974).

MATERIALS AND METHODS

Zooplankton samples were collected during the 38 weekly summer cruises between May and September, 1971 and May and September, 1972. Tows were made in the center of the reservoir at each of the four stations (Fig. 1). Bottom to surface oblique tows were made with a Clarke-Bumpus plankton sampler using a number 20 net and cup (Clarke and Bumpus, 1950). Generally, between 100 and 250 liters were filtered. The number of liters per revolution of the plankton sampler was calculated with the help of Mr. Ted Williams of the Montana State University Civil Engineering Department.

The filtered zooplankters were placed in 100 ml French square bottles, killed with 10 ml 95% ethanol, and then preserved with 10 ml of 95% formalin. Zooplankters were identified to genus and species using a 45 X binocular microscope and Edmondson (1959) as a taxonomic reference. All Leptodora kindtii of the sample were counted. Subsamples were retrieved in a manner recommended by Edmondson (1971). Aliquots of 1 or 2 ml were taken with a Hensen-Stempel pipette and placed in a rotary counting chamber (Ward, 1955). All zooplankters of each aliquot were counted until approximately 100 Daphnia spp. were counted.

Population dynamics of Daphnia spp. were estimated following the methods described by Edmondson (1960), Hall (1964), and Wright (1965) except instantaneous birth rates (b), which were calculated using Caswell's (1972) correction.

The equations for these parameters are:

B = finite birth rate

$= E/DN_o$

where D = egg duration in days

N_o = number of juvenile + adult Daphnia spp. per liter

E = number of eggs per liter,

r = instantaneous growth rate

$= (\ln N_t - \ln N_o)/T$

where T = time interval in days,

b = instantaneous birth rate

$= rB/(e^r-1)$.

Also, instantaneous death rate (d) was calculated as b minus r to give a positive number.

The following counts were made of the Daphnia schodleri and Daphnia galeata mendotae populations: eggs, juveniles, adults and number of eggs per adult. For the copepod species, Cyclops bicuspidatus thomasi and Diaptomus leptopus, counts were made of egg sacs, copepodids, and male and female adults. Nauplii of both species were combined because of inability to determine species differences of nauplii. Only total numbers were counted for Leptodora kindtii, Bosmina sp., Alona sp. and Macrothrix sp. The 1972 data also included size estimation of all zooplankters and number of eggs per egg sac of D. leptopus and C. bicuspidatus.

Relative concentrations of C. bicuspidatus nauplii in 1971 were determined by the following formula:

$$N.CC/(CC+DC) = CN$$

Where CN = estimated number of C. bicuspidatus nauplii

N = total number of nauplii

CC = number of C. bicuspidatus copepodids

DC = number of D. leptopus copepodids.

Relative 1972 C. bicuspidatus nauplii concentrations were determined by the following formula:

$$N.SCC/(SCC+SDC) = CN$$

Where CN = C. bicuspidatus nauplii

SCC = number of stage one + two C. bicuspidatus copepodids

SDC = number of stage one + two D. leptopus copepodids.

Because many eggs were ejected from the carapaces upon preservation the relative number of Daphnia galeata mendotae eggs were determined by the following formula:

$$TN.ND/(ND+NDS) + NDE = TDE$$

Where TDE = total number of D. galeata eggs

NDE = number of enclosed D. galeata eggs

TN = total number of free Daphnia spp. eggs

ND = number of D. galeata juveniles + adults

NDS = number of D. schodleri juveniles + adults.

The remaining free eggs were added to the eggs enclosed in carapaces

of D. schodleri.

Cowell (1967)and Hall, Cooper, and Warner (1970) decided that comparison of stations was more accurate if averages rather than values for individual cruises were used. The author used this method.

Analysis of averages for the second half of the summers often yielded patterns which were not obvious for either the first half or total summer. Therefore, patterns for the first half, second half and total summer were analyzed. Midsummer was defined as July 11.

The probability values (p-values) for the Analysis of Variance (ANØV) program indicate the probability of observing a difference between averages larger than the difference actually observed given that the averages follow a normal distribution.

Nonparametric statistical analysis has some advantages over Analysis of Variance. Nonparametric analysis may be much more meaningful for non-normally distributed averages. Also, nonparametric analysis can often point out the true patterns in a manner much easier to understand than ANØV. A nonparametric test called the sign test was used to compare 1971 averages to 1972 averages and the first half of the summer averages to the second half of the summer averages (Mosteller and Rourke, 1973). This test is based on the statistic of the number of stations for which the 1971 average is larger than the 1972 average. The calculated p-values for this test are the probability of getting a statistic as or more extreme than the one measured, given the

difference in averages is equally likely to be positive or negative. This p-value is based on the number of "exceptions" to the expected pattern.

A special nonparametric statistical analysis was set up by the author to analyze relative increase or decrease of values from station one through four. Basically, possible relative orders of values for the four stations were ordered from increasing from station one through four to decreasing from station one through four (Table 1). Then these were divided into groups (called number of exceptions) indicating the relative increase or decrease.

The p-values for the possibility of getting a value as or more extreme, given actual random occurrence were determined. Table 2 shows the number of combinations of orders, given the number of "exceptions" for each summer. For example, if 1971 averages were 1, 2, 4, 3 and 1972 averages were 1, 2, 3, 4 for stations one through four, this order would be in the 0, 1 group, which has 6 equivalent orders of 0, 1 and 1, 0 "exceptions".

Table 3 shows the number of orders and subsequent probabilities for individual and cumulative number of "exceptions" for the two summers given each order is equally likely to occur. Table 4 gives the cumulative probability values for the nonparametric tests.

Table 1. Possible combinations of four different numbers in groups ranging from increasing to decreasing.

	Number of Exceptions (Relative Group)						
	0	1	2	3	4	5	6
Ordered Values	1	1 2 1	1 2 3 2	1 1 3 3 2 2 4 4	3 3 2 4	3 4 4	4
	2	2 1 3	3 1 1 3	4 4 2 1 3 4 1 1	2 4 4 2	4 2 3	3
	3	4 3 2	4 4 2 1	2 3 1 4 4 1 2 3	4 1 3 1	2 3 1	2
	4	3 4 4	2 3 4 4	3 2 4 2 1 3 3 2	1 2 1 3	1 1 2	1

Table 2. The number of possible ordered values per two groups of "exceptions".

Groups of Exceptions Including Reverse																											
Order	0	0	1	2	2	2	3	3	3	3	4	4	4	4	4	5	5	5	5	5	5	6	6	6	6	6	6	6
	0	1	1	0	1	2	0	1	2	3	0	1	2	3	4	0	1	2	3	4	5	0	1	2	3	4	5	6
Number of Ordered Values	1	6	9	8	24	16	16	48	64	64	8	24	32	64	16	6	18	24	48	24	9	2	6	8	16	8	6	1

Table 3. The possible number of ordered values per total number of exceptions with corresponding individual and cumulative probabilities, assuming each order is equally likely to occur.

Total Number of Exceptions	Number of Ordered Values	Individual probabilities	Cumulative probabilities
0	1 = 1	.0017	.0017
1	6 = 6	.0104	.0121
2	9+8 = 17	.0295	.0417
3	24+16 = 40	.0694	.1111
4	16+48+8 = 72	.1250	.2361
5	64+24+6 = 94	.1632	.3993
6	64+32+18+2=116	.2014	.6007
7	64+24+6 = 94	.1632	.7639
8	16+48+8 = 72	.1250	.8889
9	24+16 = 40	.0694	.9583
10	9+8 = 17	.0295	.9878
11	6 = 6	.0104	.9982
12	1 = 1	.0017	.9999

Table 4. Cumulative probability values for the nonparametric tests.

Test	Number of Exceptions	Cumulative Probability Value	Test	Number of Exceptions	Cumulative Probability Value
Comparison	0	.062		0	.0017
of 1971	1	.312		1	.0121
and 1972	2	.688		2	.0417
	3	.938		3	.1112
	4	1.000	Analysis	4	.2361
Comparison	0	.004	of the	5	.3993
of the	1	.035	Four	6	.6007
first half	2	.145	Stations	7	.7639
of the	3	.363		8	.8889
summers	4	.637		9	.9583
to the	5	.855		10	.9878
second	6	.965		11	.9982
half of the	7	.996		12	1.0000
summers	8	1.000			

RESULTS AND DISCUSSION

The major zooplankton taxa, excluding rotifers, encountered during the study were Daphnia schodleri Sars, Daphnia galeata mendotae Birge, Cyclops bicuspidatus thomasi S. A. Forbes, Diaptomus leptopus S. A. Forbes, and Leptodora kindtii Focke. These were the major species found during 1957 and 1958 (Wright 1965). As found by Wright (1965), Daphnia schodleri was Canyon Ferry's major zooplankton producer. Bozmina sp., Macrothrix sp., and Alona sp. were rarely found.

During June of 1971 the water level of Canyon Ferry was lowered to an elevation below the lowest water level of 1972 (Fig. 3). The 1971 water level was then raised to a level comparable to that of 1972. Thus, during 1971 more reservoir bottom was exposed and then reflooded than during 1972. Apparently, dissolved nutrients, algal populations, and zooplankton populations were affected differently in 1971 than 1972. The effects of the 1971 drawdown on the zooplankton populations were most prominent during the second half of the summer, after July 11.

DAPHNIA SCHODLERI

Daphnia schodleri was the dominant Canyon Ferry zooplankton species. The 1971 and 1972 summer populations were bimodal in appearance (Fig. 4). Stations one and two showed this pattern more clearly than stations three and four. The minimum between the two peaks occurred in early July for both summers.

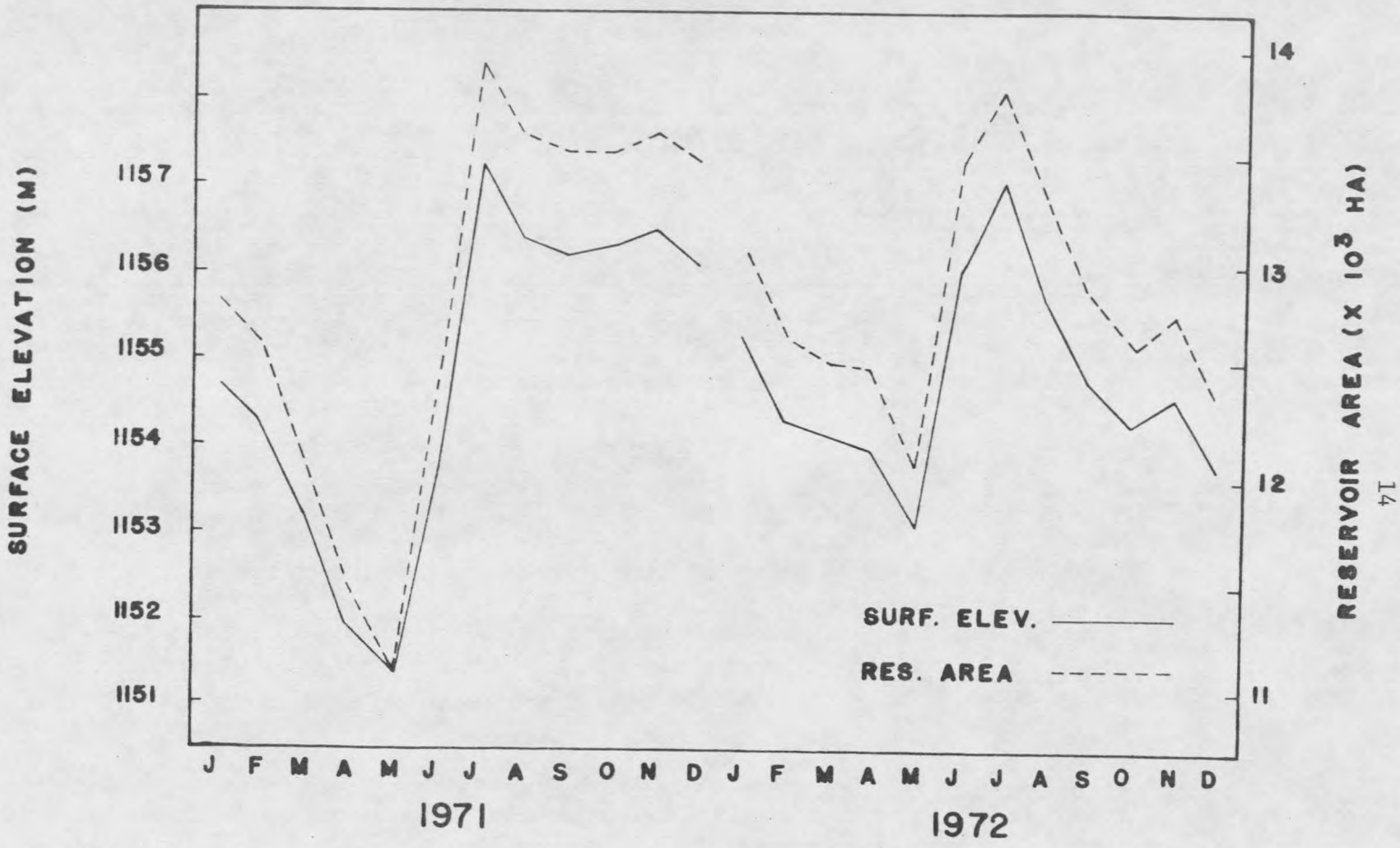

Figure 3. Monthly mean surface elevations and reservoir areas in Canyon Ferry Reservoir during the calendar years 1971 and 1972 (Rada, 1974).

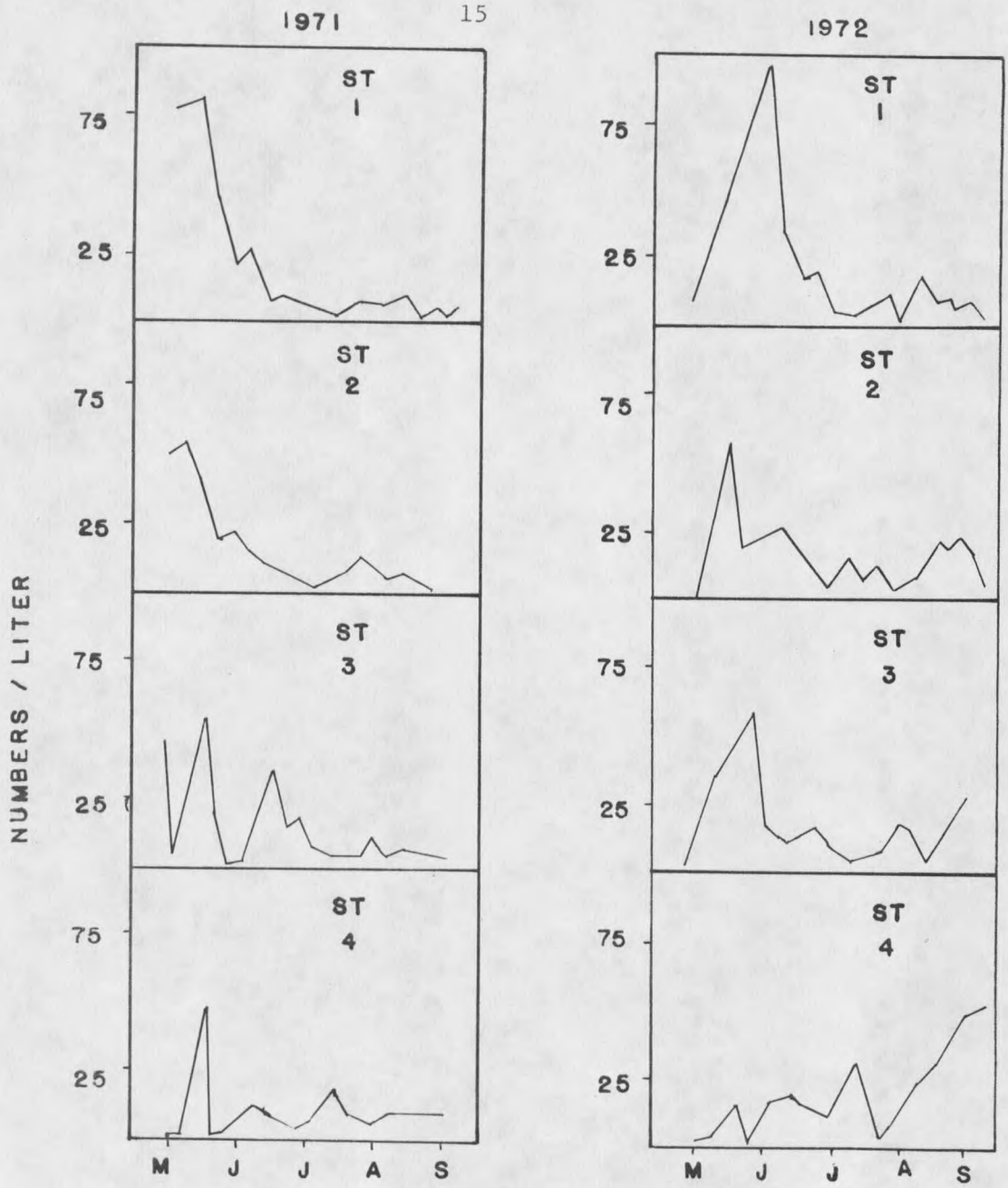

Figure 4. Concentration variations of Daphnia schodleri.

Average and maximum values of numbers per liter, instantaneous rates of change (r), instantaneous birth rates (b) and instantaneous death rates (d) for the summer, first half of the summer, second half of the summer for 1971 and 1972 are presented in Table 5. Average and maximum number of eggs per liter and eggs per clutch are also presented. A statistical analysis of these population parameters is presented in Tables 6 and 7.

Total and first half of the summer concentrations of D. schodleri juveniles + adults were similar in 1971 and 1972. The maxima and second half of the summer values probably were greater in 1972 than 1971. Values for instantaneous rates of change (r) may have been higher in 1971 than 1972.

Average birth (b), death (d) and eggs per liter for both the second half and total summers were definitely higher during 1971 than 1972. Maxima and averages for the first half of the summers were also higher. The number of eggs per clutch for the second half of the summer was definitely higher during 1971 than 1972.

In 1971, turnover time (b^{-1}) was shorter for the total and second half of the summer than 1972. First half of the summer production in 1971 was similar to that in 1972.

Total summer averages for D. schodleri concentrations showed no

Table 5. Daphnia schodleri average values.

Term*	Station	$\bar{X}$ Total of Summers 1971	$\bar{X}$ Total of Summers 1972	$\bar{X}$ First Half of Summers 1971	$\bar{X}$ First Half of Summers 1972	$\bar{X}$ Second Half of Summers 1971	$\bar{X}$ Second Half of Summers 1972	Maximum of Summers 1971	Maximum of Summers 1972
N	1	16.74	13.83	33.62	23.71	3.23	4.93	79.90	90.77
	2	16.69	14.96	26.48	20.81	6.90	9.70	62.01	63.86
	3	13.69	19.11	19.13	23.36	6.71	14.32	46.23	58.66
	4	8.55	19.08	7.42	9.77	9.85	29.73	23.72	58.56
r	1	-.030	-.007	-.065	-.016	.001	.001	.235	.305
	2	-.029	.012	-.048	.028	-.007	-.003	.095	.393
	3	-.015	.019	-.030	.026	.009	.010	.353	.289
	4	.045	.028	.070	.030	.012	.026	.440	.324
b	1	.092	.103	.039	.113	.139	.092	.201	.360
	2	.227	.082	.141	.083	.324	.082	1.213	.308
	3	.359	.105	.086	.089	.770	.126	2.410	.266
	4	.379	.294	.194	.402	.627	.149	2.759	1.176
d	1	.122	.110	.104	.129	.138	.091	.303	.346
	2	.256	.070	.189	.055	.331	.085	1.124	.258
	3	.374	.086	.116	.063	.761	.116	2.395	.271
	4	.334	.266	.124	.372	.615	.123	.551	.688
E/L	1	7.80	6.75	14.98	13.39	2.56	1.44	73.1	44.7
	2	13.24	7.34	20.69	13.04	5.78	2.21	92.7	39.4
	3	10.34	8.98	9.27	13.44	11.72	3.95	46.2	46.4
	4	7.44	7.46	3.58	7.83	12.58	7.04	40.3	14.2
E/C	1	3.55	3.16	3.15	4.09	3.83	2.33	10.8	9.1
	2	2.87	3.44	2.98	5.37	2.77	1.89	6.4	18.4
	3	3.27	3.33	3.51	4.57	3.03	1.94	6.0	10.9
	4	4.17	4.29	5.24	6.05	2.74	2.27	15.2	9.9

* Symbols: N = number of juveniles & adults per liter, r = instantaneous population change rate, b = instantaneous birth rate, d = instantaneous death rate, E/L = number of eggs per liter, E/C = number of eggs per clutch.

Table 6. Daphnia schodleri statistical analysis of station and summer patterns. **

Term	Trend	Nonparametric Analysis (number of Exceptions) $\overline{X}$ for Total of Summer	$\overline{X}$ for First Half of Summer	$\overline{X}$ for Second Half of Summer	Maximum of Summer	Analysis of Variance Probability Values $\overline{X}$ for Total of Summer	$\overline{X}$ for First Half of Summer	$\overline{X}$ for Second Half of Summer
N*	1971	2	2	4	4	.4397	.5505	.1501
r	More	3	3	3	2			
b	Than	1	3	0	1	.1309	.3729	.0732
d	1972	0	2	0	2	.1043	.6707	.0768
E/L		1	2	0	2	.2079	.9458	.0486
E/C		3	4	0	2	.6802	.0366	.0172
N	Values	7	11	1	12	.940	.079	.231
r	Increase	0	1	2	6			
b	From	1	3	2	3	.178	.184	.392
d	Station	3	5	2	4	.336	.631	.411
E/L	One	5	8	0	9	.403	.207	.083
E/C	Through Four	3	2	8	6	.084	.092	.245

Table 7. Daphnia schodleri statistical comparison of the first half to the second half of the summer.

Trend	First half less than second half of the summer.					
Term	N	r	b	d	E/L	E/C
Nonparametric	6	4	3	2	6	7
ANØV*	.1094				.0815	.1714

* Symbols: N = numbers of organisms per liter, r = instantaneous population change rate, b = instantaneous birth rate, d = instantaneous death rate, L = liter, E = number of eggs, C = clutch, ANØV = analysis of variance.

** Nonparametric probability values on page 12.

difference among the four stations (Tables 5 and 6). Maxima and average first half summer populations decreased from stations one through four. This decrease may have been caused by the high flow rate of the spring runoff displacing the zooplankters (Fig. 3). Especially high reservoir turbidities, increasing from station one through four, associated with the spring runoff may have influenced the zooplankton concentration decrease. Cowell (1967) mentioned that high turbidity could markedly reduce zooplankton standing crops. Numbers for the second half of the summer increased from station one through four.

Averages of r for the total and first half of the summers increased from station one through four. Average total b, d, and number of eggs per clutch probably increased from station one through four. Generally, b, d, and number of eggs per liter increased from station one through four the second half of the summer. During this time the number of eggs per clutch probably decreased from station one through four. Since numbers per liter, birth rate, and death rate increased from station one through four, production during the second half of the summer increased from station one through four.

ANØV p-values for differences among the stations generally agreed with non-parametric p-values. Second half of the summer ANØV values for juvenile + adults numbers per liter, b and d were probably too high. The total summer average ANØV value for the number of eggs per clutch was probably too low.

Juvenile + adult number per liter, number of eggs per liter, and number of eggs per clutch were probably greater during the first half of the summers than the second half (Table 7). The first half of the summers b and d were probably less than the second half b and d. ANØV p-values generally agreed with these observations.

Population growth of D. schodleri during the second half of the summers may have been influenced by a variety of factors. Hutchinson (1973) indicated that some blue-green algae, desmids, and dinoflagellates may be inedible due to shape, gellatinous coating, and/or chemical properties. Lund (1969), Schindler (1971), and Tappa (1965) have studied digestibility of various species of algae by several zooplankton species and have found a wide range of algal digestibility among the zooplankton species. Knutson (1970) noticed that zooplankton declines during the second half of the summer coincides with Leptodora kindtii as well as algal declines.

Another factor influencing zooplankton populations during the second half of the summer might have been decreased bacterial food due to inhibitors produced by some blue-green algae (Luferova and Monakov, 1969; Rodina, 1963; Marzolf, 1966).

Gilwiez and Hollbright - Ilkowska (1972) said, "In oligotrophic waters macrofiltrators (mainly Diaphanosoma but to a certain degree also Daphnia and Cyclops) are dominant. They more intensively filter relatively large food particles (up to 10 - 15 microns in diameter)." If these authors are correct, bacterial probably are a minor influence

on Canyon Ferry zooplankton production.

The instantaneous rate of population change (r) indicates little difference between summers, among stations, and between the first half and second half of the summers. Knutson (1970) and Stross, Ness and Kusler (1967) as well as the author found long turnover times (b^{-1}) associated with high Daphnia spp. concentrations (Tables 5 and 8).

DAPHNIA GALEATA MENDOTAE

Daphnia galeata mendotae, a relatively minor species at stations one and two, was more important at stations three and four (Fig. 5). Juvenile + adults number per liter and r values indicated little or no difference between 1971 and 1972 (Tables 8 and 9). Number of eggs per liter, number of eggs per clutch, b, and d were definitely higher in 1971 than 1972 for total summer, second half of the summer, and maximum values. For the first half of the summer there was little difference in all population parameters between 1971 and 1972.

Since juvenile + adults numbers per liter were similar for the two years and b and d were higher during 1971, production of D. galeata was greater during 1971 than 1972. The second half of the summers showed this difference much more clearly than the first half of the summers.

All D. galeata populations definitely increased from station one through four (Tables 8 and 9). Number of eggs per clutch, number of eggs per liter, b, and d generally increased from station one through four. Since juvenile and adult numbers per liter, b, and d increased from station one through four, production also increased.

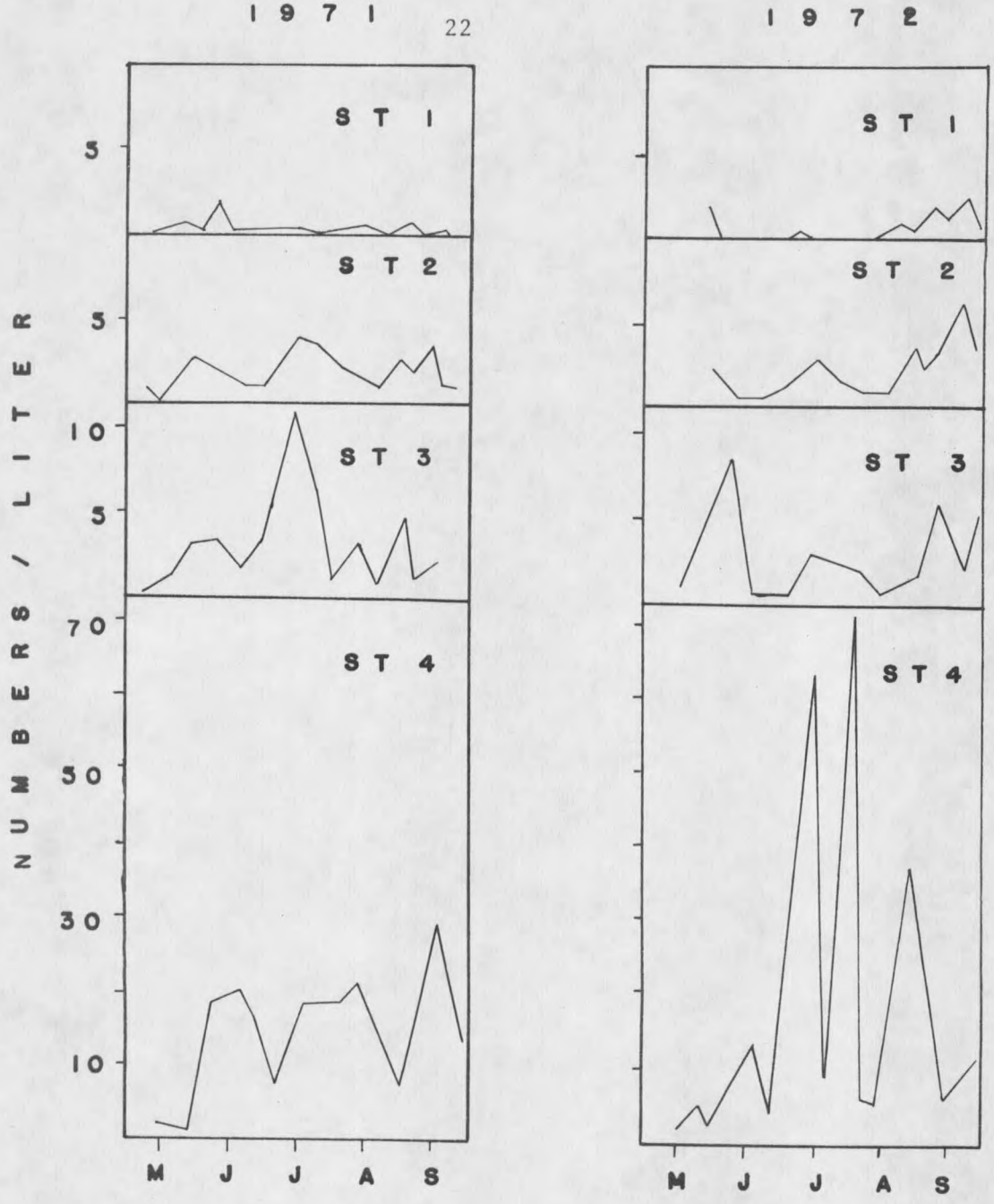

Figure 5. Concentration variations of Daphnia galeata mendotae.

Table 8. *Daphnia galeata* average values.

Term*	Station	$\bar{X}$ Total of Summers 1971	$\bar{X}$ Total of Summers 1972	$\bar{X}$ First Half of Summers 1971	$\bar{X}$ First Half of Summers 1972	$\bar{X}$ Second Half of Summers 1971	$\bar{X}$ Second Half of Summers 1972	Maximum of Summers 1971	Maximum of Summers 1972
N	1	.71	.79	1.04	.628	.47	.87	1.2	2.5
	2	1.92	2.27	2.31	1.67	1.59	2.62	3.9	6.8
	3	3.64	3.42	3.63	3.06	3.65	3.73	11.2	8.4
	4	12.82	14.92	8.89	14.06	17.87	15.78	30.0	63.0
r	1	-.016	.012	-.061	-.063	.015	.045	.596	.323
	2	.003	.000	.011	-.018	-.006	.013	.193	.278
	3	.050	.014	.071	.014	.023	.015	.159	.233
	4	.027	.055	-.007	.109	.078	-.008	.430	.463
b	1	.110	.076	.011	.017	.177	.102	.785	.379
	2	.230	.077	.114	.108	.347	.057	1.400	.408
	3	.327	.078	.095	.056	.676	.100	2.095	.217
	4	.405	.169	.286	.182	.584	.151	2.204	.321
d	1	.126	.064	.072	.080	.162	.057	1.239	.239
	2	.227	.077	.103	.126	.353	.044	1.473	.180
	3	.277	.064	.024	.042	.653	.085	2.001	.383
	4	.378	.114	.293	.073	.506	.159	1.751	.434
E/L	1	.26	.22	.07	.17	.31	.23	.6	.5
	2	1.67	.73	1.58	1.28	1.74	.43	4.9	3.7
	3	3.08	1.31	2.51	1.26	3.65	1.38	12.3	6.8
	4	15.38	9.10	7.28	12.41	25.81	5.24	125.1	13.3
E/C	1	2.51	1.23	1.00	0.00	3.10	1.23	5.5	2.0
	2	2.38	1.59	1.00	2.43	2.73	1.46	4.0	2.4
	3	4.06	2.74	7.90	7.50	2.96	1.50	10.0	7.5
	4	5.35	4.99	7.01	8.26	3.02	1.73	13.7	10.3

* Symbols: N = number of juveniles & adults per liter, r = instantaneous population change rate, b = instantaneous birth rate, d = instantaneous death rate, E/L = number of eggs per liter, E/C = number of eggs per clutch.

Table 9. Daphnia galeata statistical analysis of station and summer patterns. *

Term	Trend	Nonparametric Analysis (number of Exceptions) $\bar{X}$ for Total of Summer	$\bar{X}$ for First Half of Summer	$\bar{X}$ for Second Half of Summer	Maximum of Summer	Analysis of Variance Probability Values $\bar{X}$ for Total of Summer	$\bar{X}$ for First Half of Summer	$\bar{X}$ for Second Half of Summer
N**	1971	3	1	3	3	.3558	.5825	.8378
r	More	2	1	2	3			
b	Than	0	1	0	0			
d	1972	0	3	0	0			
E/L		0	2	0	0		.5076	.3012
E/C		0	2	0	0			
N	Values	0	0	0	0	.001	.038	.001
r	Increase	2	2	6	7			
b	From	0	2	3	4			
d	Station	1	6	2	2			
E/L	One	0	1	0	0	.030	.047	.268
E/C	Through Four	1	1	3	1			

Table 10. Daphnia galeata statistical comparison of the first half to the second half of the summer.

Trend	First half less than second half of the summer.					
Term	N	r	b	d	E/L	E/C
Nonparametric	3	3	2	2	2	5

* Nonparametric probability values for number of exceptions on p 12.

** Symbol definitions on page 23.

Numbers per liter, b, and d were generally less during the first half than the second half of the summer (Table 10). Thus, production was greater the second half than the first half of the summer.

As with D. schodleri, r values of D. galeata indicated little difference between the summers, among the stations, and between the halves of the summer.

CYCLOPS BICUSPIDATUS THOMASI

Cyclops bicuspidatus thomasi was the most abundant and second most productive zooplankton species of Canyon Ferry Reservoir. Its concentration variations were similar to those of Daphnia schodleri (Fig. 6). McQueen (1969) found that the fourth and fifth copepodite stages as well as adult C. bicuspidatus were mainly predators. They fed mostly on their own nauplii, early stage copepodids, Diaptomid nauplii, and rotifers, but ate few Diaptomid copepodids and Cladocerans.

The number per liter of copepodids and adults were lower in 1971 than comparable 1972 concentrations (Table 11 and 12). No difference in nauplii groups was evident between 1971 and 1972. Nauplii values may be poor indicators of true population variation patterns since D. leptopus nauplii could not be discerned from C. bicuspidatus nauplii. Thus, they were artificially divided between the two species. Except for the second half of the summer, number of egg sacs per liter and number of eggs per liter were generally lower in 1971 than 1972.

Populations of C. bicuspidatus, as was the case with D. galeata and D. schodleri, were influenced by the 1971 summer drawdown, sub-

sequent nutrient release, and increased algal production. As shown in Table 11 copepodid and adult concentrations were less in 1971 than 1972 for both halves of the summer, yet egg concentration was higher in 1971 during the second half of the summer. Therefore, production was probably less in 1971 than 1972 for the total and first half of the summer but greater for the second half of the summer. All groups of nauplii decreased in concentration from station one through four (Tables 11 and 12).

Concentrations of copepodid and adult C. bicuspidatus, except for the second half of the summers, decreased from stations one through four. Station four had significantly lower concentrations of adults and copepodids for the first half of the summer. This was probably due to either high silt content inhibiting feeding (Cowell, 1967) or high flushing rate caused by spring runoff. Copepodids and adults definitely increased in concentration from station one through four during the second half of the summers.

There was little or no difference in the number of egg sacs per liter, number of eggs per liter, egg sacs per liter maxima, and eggs per liter maxima for the first half of the summers among the stations. The number of egg sacs per liter and number of eggs per liter definitely increased from station one through four for the total and second half of the summers.

Since number Co + A per liter and number eggs per liter increased from station one through four, production definitely increased from

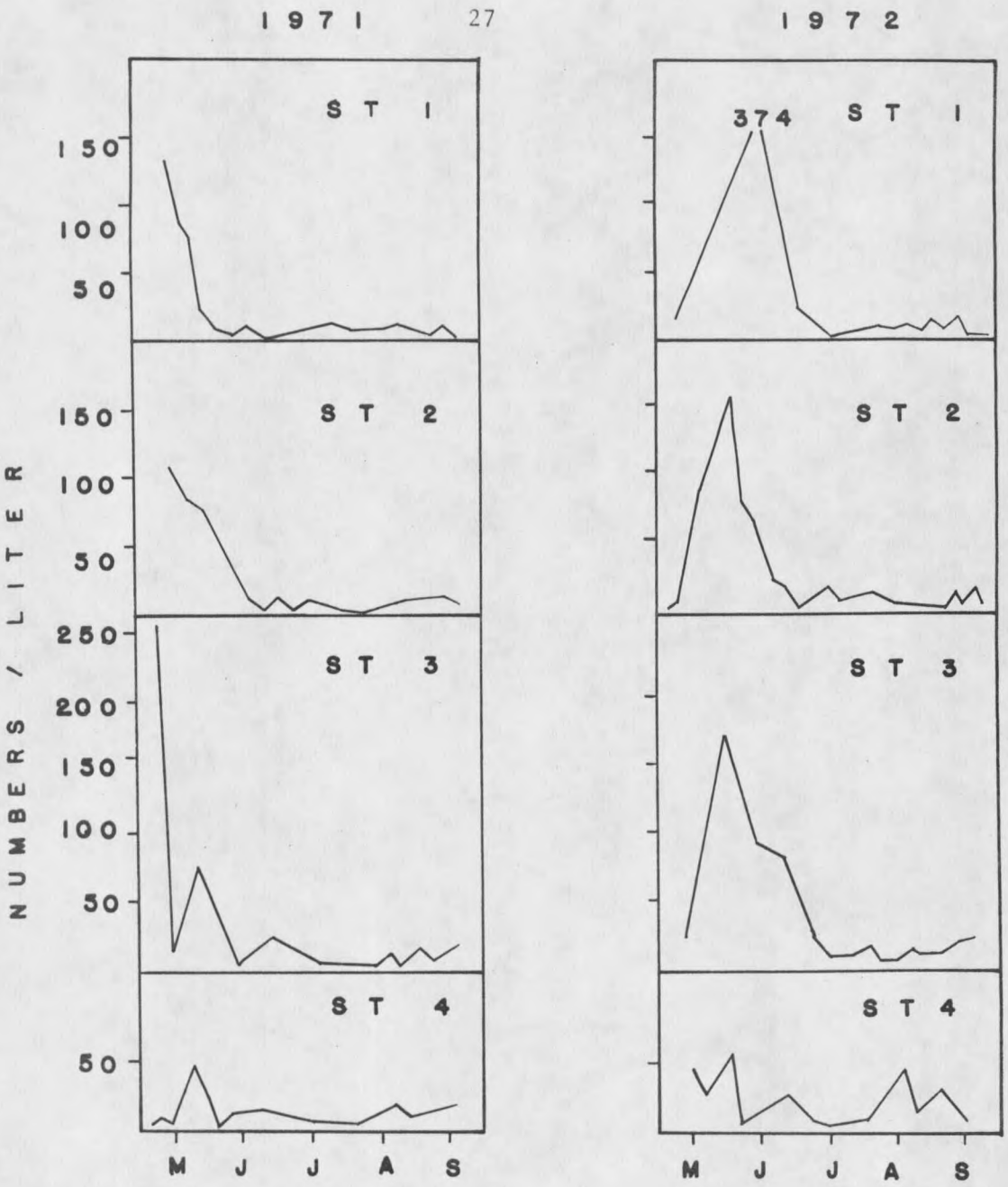

Figure 6. Concentration variations of Cyclops bicuspidatus thomasi.

Table 11. Cyclops bicuspidatus average values.

Term*	Station	$\bar{X}$ Total of Summers		$\bar{X}$ First Half of Summers		$\bar{X}$ Second Half of Summers		Maximum of Summers	
		1971	1972	1971	1972	1971	1972	1971	1972
Co	1	20.62	33.56	41.83	66.89	3.65	3.57	127.0	344.6
	2	22.86	21.59	42.33	39.91	3.40	5.10	105.2	129.0
	3	24.49	33.29	42.49	56.36	4.23	7.34	222.7	166.5
	4	10.40	14.26	14.52	19.80	5.69	7.93	45.3	47.2
A	1	2.05	4.92	2.29	8.03	1.86	2.12	3.8	29.2
	2	1.79	5.46	1.88	8.90	1.70	2.36	4.6	23.9
	3	4.69	7.04	7.04	10.53	2.04	3.12	34.4	28.4
	4	2.89	5.70	2.24	4.12	3.54	7.06	7.4	19.4
Co	1	22.67	38.48	44.12	74.92	5.10	5.69	134.4	373.8
+	2	24.65	27.04	44.20	48.80	5.43	7.46	108.0	152.9
A	3	29.17	40.33	49.53	66.89	6.27	10.45	257.1	192.3
	4	13.29	19.96	16.76	23.92	9.24	14.99	48.1	53.1
Na	1	46.19	30.12	88.81	52.85	12.09	9.66	295.7	205.4
	2	38.78	24.59	69.94	40.57	7.61	10.21	215.0	105.8
	3	18.60	23.76	29.85	36.98	7.35	8.89	69.9	101.7
	4	11.31	12.15	13.90	18.33	8.35	3.90	55.8	63.6
ES/L	1	.445	.583	.337	.884	.517	.312	1.09	2.30
	2	.579	.832	.411	1.195	.705	.577	2.64	3.20
	3	.951	.848	.882	.848	1.003	.849	2.26	2.35
	4	1.376	1.491	.843	.916	1.833	2.064	3.48	3.33
E/L	1	6.62	10.88	6.78	17.69	6.51	4.75	21.98	39.07
	2	11.95	14.11	8.24	18.41	14.73	11.10	52.82	37.59
	3	15.18	13.35	15.76	15.50	14.74	10.93	37.49	36.75
	4	25.52	26.55	16.90	17.33	32.92	35.76	44.77	165.12

* Symbols: Co = number of copepodids per liter, A = number of adults per liter, ES/L = number of egg sacks per liter, E/L = number of eggs per liter, Na = number of nauplii per liter.

Table 12. Cyclops bicuspidatus statistical analysis of station and summer patterns. *

		Nonparametric Analysis (number of Exceptions)				Analysis of Variance Probability Values		
Term	Trend	$\bar{X}$ for Total of Summer	$\bar{X}$ for First Half of Summer	$\bar{X}$ for Second Half of Summer	Maximum of Summer	$\bar{X}$ for Total of Summer	$\bar{X}$ for First Half of Summer	$\bar{X}$ for Second Half of Summer
Co**	1971	3	3	3	3			
Ad	More	4	4	4	3			
Co+Ad	Than	4	4	4	3	.0511	.0854	.0696
Na	1972	2	2	2	2			
ES/L		3	3	1	3			
E/L		3	3	1	2	.3500	.1203	.3815
Co	Values	8	8	1	10			
Ad	Increase	3	6	1	6			
Co+Ad	From	7	8	0	9	.069	.050	.077
Na	Station	12	12	10	12			
ES/L	One	0	4	0	2			
E/L	Through Four	1	4	1	6	.008	.692	.003

Table 13. Cyclops bicuspidatus statistical comparison of the first half to the second half of the summer.

Trend	First half less than second half of the summer.					
Term	Co	Ad	Co+Ad	Na	ES/L	E/L
Nonparametric	8	6	8	8	2	5

* Nonparametric probability values for number of exceptions on p 12.

** Symbols: Co = number of copepodids, Ad = number of adults, Na = number of nauplii, ES = number of egg sacks, E = number of eggs, L = liter.

station one through four during the second half of the summers. Production may have decreased during the first half of the summers and not varied appreciably among the stations for the total summers.

ANØV p-values may be too low for copepodid + adult for total summers due to one or more relatively extreme values. Copepodids, adults, and nauplii generally had higher concentrations the first half of the summers than the second half. Egg concentrations were similar between the summer halves, thus, productivity was probably higher the first half than the second half of the summers (Table 13).

DIAPTOMUS LEPTOPUS

Diaptomus leptopus concentration variations were different than concentration varieites of Daphnia schodleri and Cyclops bicuspidatus (Fig. 7). Total and second half of the summer concentrations of adult and copepodid Diaptomus leoptopus were similar in 1971 and 1972 (Tables 14 and 15). Copepodid and adult concentrations for the first half of the summer were greater in 1971 than 1972.

All 1971 nauplii concentrations were similar to 1972 concentrations. All 1971 egg sac concentrations and egg concentrations for the second half of the summer were similar to 1972 concentrations. Egg concentrations for the second half of the summer were greater during 1971 than 1972.

Total and first half of the summer production in 1971 was similar to 1972 production. The ANØV p-value for the egg concentration probably was too high.

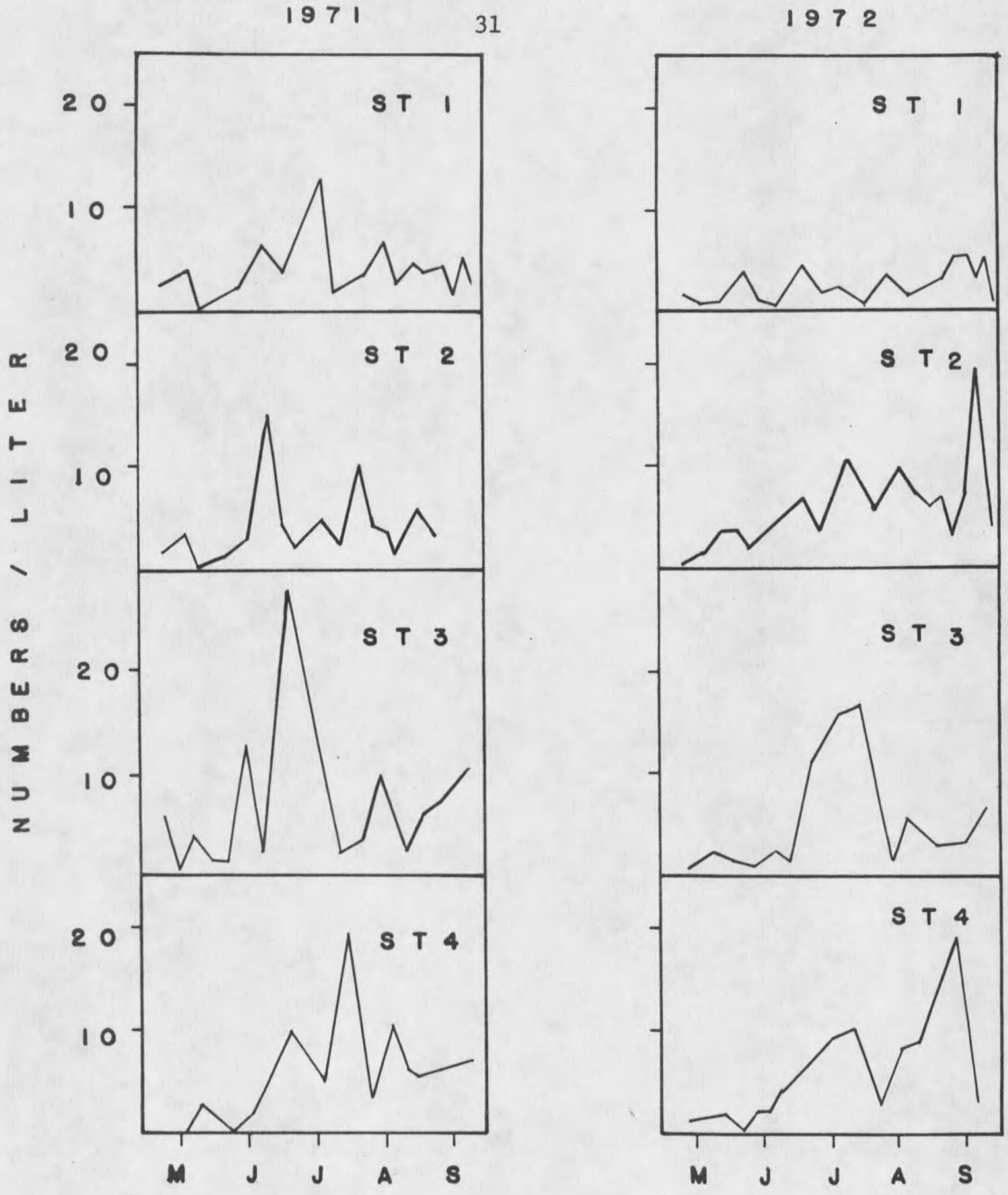

Figure 7. Concentration variations of Diaptomas leptopus.

Table 14. Diaptomus leptopus average values.

Term*	Station	$\bar{X}$ Total of Summers 1971	$\bar{X}$ Total of Summers 1972	$\bar{X}$ First Half of Summers 1971	$\bar{X}$ First Half of Summers 1972	$\bar{X}$ Second Half of Summers 1971	$\bar{X}$ Second Half of Summers 1972	Maximum of Summers 1971	Maximum of Summers 1972
Co	1	2.89	1.32	3.86	1.16	2.22	1.46	11.81	3.71
	2	3.34	3.89	3.46	3.01	3.23	4.68	11.81	16.16
	3	3.72	4 23	3.24	5.06	4.20	3.29	12.75	14.05
	4	3.56	2.88	2.45	1.37	4.50	4.60	11.75	13.17
A	1	.95	.94	.90	.68	.99	1.09	2.70	2.64
	2	1.17	1.65	1.21	1.14	1.15	2.00	3.25	3.19
	3	2.82	1.30	3.75	1.00	1.90	1.64	20.97	2.83
	4	2.44	2.41	1.33	.75	3.23	3.60	4.35	5.37
Co	1	3.85	2.26	4.75	1.84	3.21	2.56	13.6	4.83
+	2	4.51	5.53	4.64	4.15	4.38	6.68	15.06	18.67
A	3	6.54	5.53	6.99	6.07	6.10	4.93	27.10	15.31
	4	5.99	5.29	3.78	2.12	7.73	8.19	18.10	18.50
Na	1	6.46	3.40	9.42	2.88	4.38	3.87	20.53	18.60
	2	5.61	7.99	5.79	8.13	5.46	7.86	15.97	25.21
	3	4.63	9.31	2.97	5.63	6.29	13.44	13.33	72.11
	4	3.67	3.53	1.92	1.42	5.42	6.92	10.71	21.95
ES/L	1	.221	.205	.440	.066	.166	.316	.805	.820
	2	.387	.343	.298	.310	.417	.363	.987	.134
	3	.484	.260	.327	.290	.543	.240	1.070	.500
	4	.756	.790	.375	.585	.864	.872	1.790	1.460
E/L	1	3.357	1.849	6.610	1.965	2.544	1.756	5.46	4.05
	2	4.260	5.449	3.555	7.364	4.495	4.253	9.87	14.25
	3	6.285	5.065	3.937	6.958	7.165	2.643	15.71	14.67
	4	10.148	11.340	4.500	13.085	11.762	10.642	23.25	19.51

* Symbols: Co = number of copepodids per liter, A = number of adults per liter, ES/L = number of egg sacks per liter, E/L = number of eggs per liter, Na = number of nauplii per liter.

Table 15. Diaptomus leptopus statistical analysis of station and summer patterns. *

Term	Trend	Nonparametric Analysis (Number of Exceptions) $\bar{X}$ for Total of Summer	$\bar{X}$ for First Half of Summer	$\bar{X}$ for Second Half of Summer	Maximum of Summer	Analysis of Variance Probability Values $\bar{X}$ for Total of Summer	$\bar{X}$ for First Half of Summer	$\bar{X}$ for Second Half of Summer
Co**	1971	2	1	2	3			
Ad	More	1	0	3	1			
Co+Ad	Than	1	0	2	2	.3863	.0668	.7753
Na	1972	2	2	3	3			
ES/L		1	2	2	2			
E/L		2	3	0	1	.9211	.3999	.1832
Co	Values	3	8	3	6			
Ad	Increase	2	4	1	2			
Co+Ad	From	4	4	1	4	.097	.049	.069
Na	Station	8	10	4	8			
ES/L	One	1	4	2	2			
E/L	Through Four	1	4	1	0	.015	.707	.023

Table 16. Diaptomus leptopus statistical comparison of the first half to the second half of the summer.

Trend	First half less than second half of the summer.					
Term	Co	Ad	Co+Ad	Na	ES/L	E/L
Nonparametric	3	2	4	3	1	5

* Nonparametric probability values for number of exceptions on page 12.

** Symbol definitions on page 29.

Copepodid and adult concentrations indicated no difference among the stations for maxima, total, and first half of the summer populations. They increased from station one through four during the second half of the summers. No difference in nauplii numbers was evident among the stations.

Egg and egg sac concentrations for the total, second half, and maxima of the summers increased from stations one through four. No pattern among the stations was evident for egg and egg sac concentrations the first half of the summers. Since number Cop. A per liter, and number eggs per liter, increased, total and second half of the summer production increased from station one through four. Production the first half of the summer appeared similar among the stations.

ANØV p-values for total and first half of the summer copepodid and adult concentrations were probably too low due to one or more relatively large values. They are not indicative of a pattern among the stations. All D. leptopus groups indicate little difference between the first and second half of the summers (Table 16).

LEPTODORA KINDTII

Leptodora kindtii populations usually appeared bimodal with peaks earliest and most extensive at stations three and four (Fig. 8). L. kindtii concentrations were greater in 1971 than 1972 (Tables 17 and 18). Although concentrations varied considerably during the first half of the summers, 1971 concentrations probably were greater than 1972 concentrations.

Total and second half of the summers L. kindtii concentrations definitely increased from station one through four. Although concentrations during the first half of the summer varied greatly, concentrations apparently increased from station one through four. L. kindtii concentrations were generally less the first half of the summer than the second half (Table 19).

L. kindtii predation affected Daphnia schodleri populations. L. kindtii concentrations paralleled Daphnia schodleri death rates (Fig. 8). Wright (1965) also found this. Only at station four were D. galeata death rates suggestive of strong L. kindtii predation. At this station the death rate of D. schodleri plus the death rate of D. galeata was a better approximation of L. kindtii predation. At this station death rate for D. schodleri plus the death rate for D. galeata was a better approximation of L. kindtii concentrations than either Daphnia species alone.

Cummins et al. (1969) said, "The results indicate that the predator - prey relationships are quite complex, with the Leptodora population depending on at least two prey species at any given time." Although L. kindtii depended on a wide variety of prey species throughout the summer, Cummins et al. found that Daphnia and Cyclops were the predominant food source. Cummins said, "Smaller animals (2-5 mm) probably depend on bacteria, algae, and detrital particles. Therefore, only one percent of the population in the 6-12 mm size classes should be considered predaceous on any given sample date."

Table 17. Leptodora kindtii average values.

Term* Station		$\bar{X}$ Total of Summers 1971	$\bar{X}$ Total of Summers 1972	$\bar{X}$ First Half of Summers 1971	$\bar{X}$ First Half of Summers 1972	$\bar{X}$ Second Half of Summers 1971	$\bar{X}$ Second Half of Summers 1972	Maximum of Summers 1971	Maximum of Summers 1972
N	1	.0358	.0349	.0222	.0300	.0373	.0373	.0792	.0600
	2	.0715	.0397	.0645	.0288	.0824	.0505	.1481	.1281
	3	.1200	.0686	.0905	.0830	.1453	.0586	.2792	.2379
	4	.2142	.1517	.2062	.1660	.2188	.1346	.5616	.4275

* Symbol: N = number or organisms per liter.

Table 18. *Leptodora kindtii* statistical analysis of station and summer patterns. *

Term	Trend	Nonparametric Analysis (Number of Exceptions) $\bar{X}$ for Total of Summer	$\bar{X}$ for First Half of Summer	$\bar{X}$ for Second Half of Summer	Maximum of Summer	Analysis of Variance Probability Values $\bar{X}$ for Total of Summer	$\bar{X}$ for First Half of Summer	$\bar{X}$ for Second Half of Summer
LC**	1971 More Than 1972	0	1	0	0	.0641	.1979	.0948
LC	Values Increase From Station One Through Four	0	1	0	0	.014	.007	.060

Table 19. *Leptodora kindtii* statistical comparison of the first half to the second half of the summer.

Trend	First half less than second half of the summer.
Term	LC
Nonparametric	2
ANØV	.3706

* Nonparametric probability values for number of exceptions on page 12.

** Symbols: LC = *L. kindtii* number per liter, ANØV = analysis of variance.

Overall, L. kindtii predation may not have affected total zooplankton production. Hall, Cooper, and Warner (1970) said, "Nutrients generally increased production of zooplankton but had little effect on community composition. Fish predation had profound effects on the diversity and size distribution of the zooplankton but only affected production at low nutrient levels."

L. kindtii concentrations approximated Daphnia spp. instantaneous death rates more closely during 1972 as there was comparatively low Daphnia spp. production (Fig. 8).

ADDED NUTRIENT EFFECT

The effect on zooplankton production of the 1971 drawdown increased from station one through three. Zooplankton production at station four was less affected than at station three, though usually more than at station two. Table 20 gives parameter differences between 1971 and 1972 (1971 minus 1972) for the first half of the summers and second half of the summers.

No consistant pattern was evident for the first half of the summer 1971 minus 1972 differences.

The second half of the summer differences for birth rates, death rates, egg concentrations, and L. kindtii concentrations increased from station one through three with four less than three.

One explanation for the station three - four difference is that station three had a higher percentage of diatoms and a lower percentage

---- Daphnia schodleri instantaneous birth rate.
____ Leptodera kindtii concentrations.

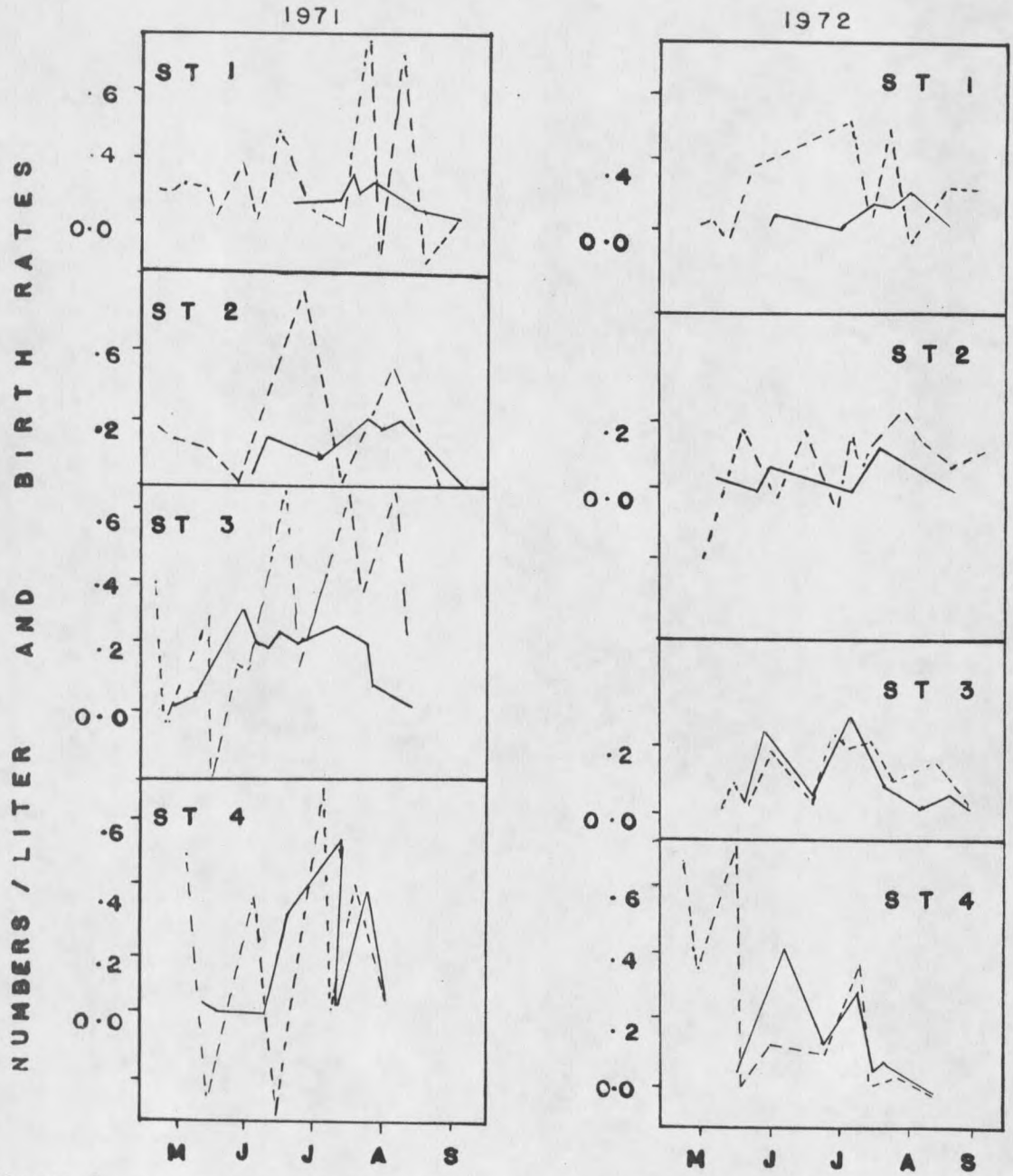

Figure 8. Comparison of Daphnia schodleri instantaneous birth rates of Leptodora kindtii concentrations.

of blue-green algae in 1971 than in 1972, thus algae at station three may have been more edible in 1971 than 1972 (Fig. 9, Rada, 1974). Another explanation for the difference is that blue-green algae concentrations at station four were high enough during both summers to possibly inhibit zooplankton production by either indigestibility or toxicity. The author believes that both factors influenced the station three-four differences.

Second half of the summer differences in species concentrations for D. schodleri and C. bicuspidatus increased from station one through four. D. galeata and D. leptopus differences yielded no substantial pattern among the stations (Table 16).

Second half of the summer D. schodleri and C. bicuspidatus concentration differences did not indicate this trend. Selective L. kindtii predation on D. schodleri and C. bicuspidatus could explain these data.

Second half of the summer 1971 - 1972 differences for station four compared to station three were less for L. kindtii and more for C. bicuspidatus and D. schodleri concentrations. Relatively high concentrations of another predator such as Cyprinus carpio (carp) could explain this discrepancy.

MINOR SPECIES

Alona sp. was most abundant during the second part of the summer at station one.

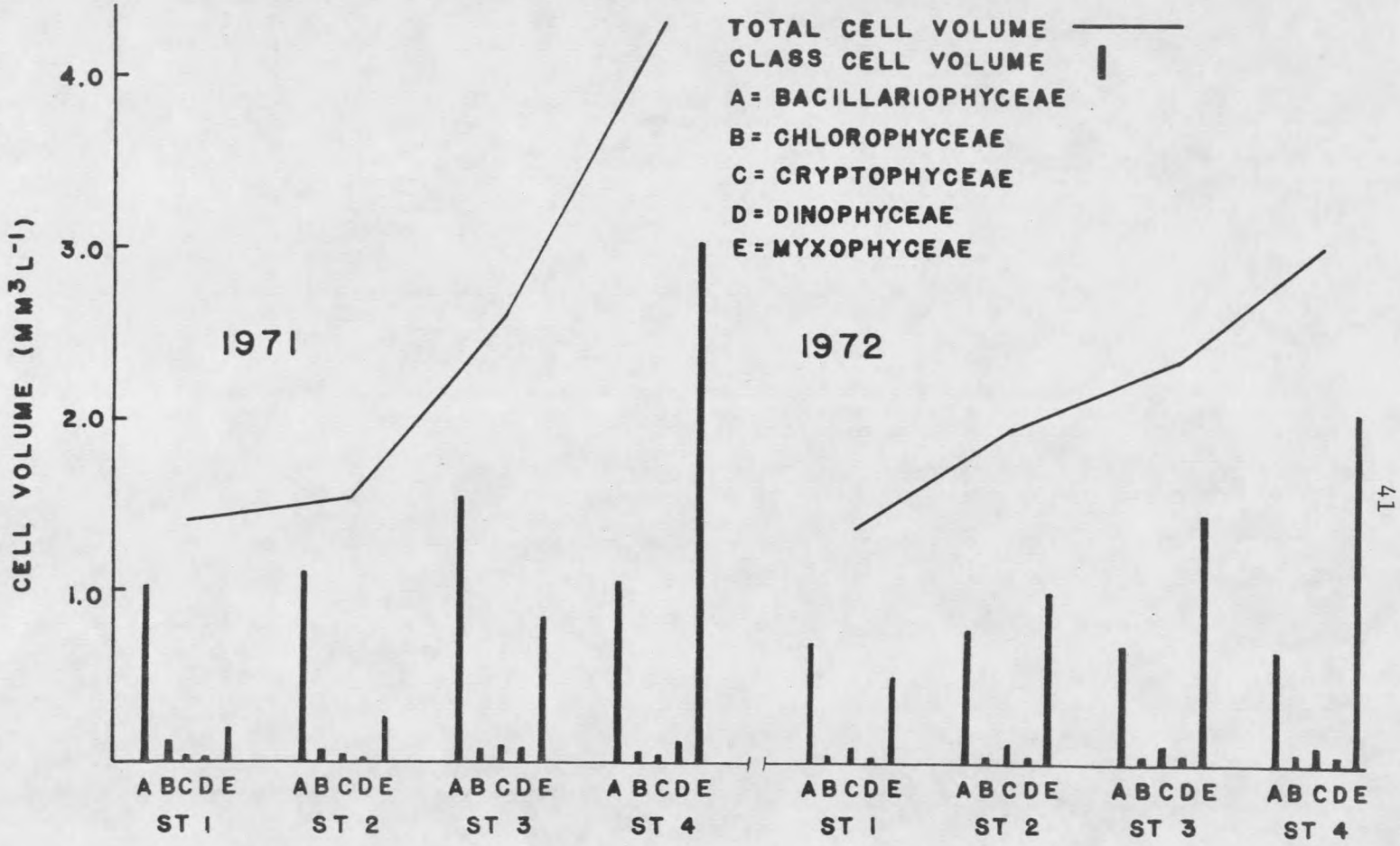

Figure 9. Yearly mean cell volumes of phytoplankton at each station for the periods: May 15, 1971 - September 18, 1971 and May 13, 1972 - September 18, 1972 (Rada, 1974).

Table 20. Average values for the first half of the 1971 sampling period minus the average values of the first half of the 1972 sampling period and the average values for the second half of the 1971 sampling period minus the average values for the second half of the 1972 sampling period.

Species	T*	S	First Half 71-72	Second Half 71-72	Species	T	S	First Half 71-72	Second Half 71-72
Daphnia schodleri	b	1	-.087	.046	Daphnia galeata	b	1	-.039	.093
		2	.059	.242			2	.004	.283
		3	-.004	.644			3	.058	.536
		4	-.209	.478			4	.104	.433
Daphnia schodleri	d	1	-.095	.062	Daphnia galeata	d	1	-.149	.182
		2	.134	.247			2	-.030	.316
		3	.053	.734			3	.132	.566
		4	-.249	.506			4	.260	.296
Cyclops bicuspidatus	E/L	1	-10.91	1.76	Diaptomus leptopus	E/L	1	4.65	.79
		2	-10.17	3.64			2	-3.81	.24
		3	.26	3.81			3	-3.02	4.52
		4	-.43	2.84			4	-8.59	1.12
Daphnia schodleri	N*	1	9.91	-1.70	Daphnia galeata	N	1	.42	-.40
		2	5.67	-2.80			2	.63	-1.04
		3	-4.23	-7.61			3	.60	-.08
		4	-2.34	-19.88			4	-5.17	2.09

Table 20. (Continued)

Species	T*	S	First Half 71-72	Second Half 71-72	Species	T	S	First Half 71-72	Second Half 71-72
Cyclops bicuspidatus	Co + Ad/L	1	-30.80	-.59	*Diaptomus leptopus*	Co + Ad/L	1	2.19	.657
		2	-4.60	-2.03			2	.489	-2.30
		3	-17.36	-4.18			3	.925	1.17
		4	-7.16	-5.75			4	1.66	-.46
Leptodora kindtii	LC	1	-.0078	.00001					
		2	.0357	.0319					
		3	.0075	.0867					
		4	.0402	.0842					

* Symbols: T = term, S = station, N = adults + juvenile number per liter, Co + Ad = copepodid + adult number per liter, LC = L. *kindtii* number per liter.

Bosmina sp. peaked during the first part of the summer of 1971 at all stations. Peaks occurred on June 5, June 21, June 28, and July 6 at stations one, two, three, and four, respectively.

No significant Bosmina sp. peaks occurred during 1972 except on July 5 at station one.

1957 - 1958 vs. 1971 - 1972 COMPARISONS

Comparison of zooplankton in Canyon Ferry during 1957-1958 with 1971-1972 shows little difference in concentrations (Table 21).

Number per liter of adult + copepodid C. bicuspidatus, adult + copepodid D. leptopus, and adult + juvenile D. galeata + D. schodleri had similar maxima and averages. Low 1957 and 1958 nauplii counts may have been due to losses through the number of 10 net that was used.

Daphnia spp. b and d, and C. bicuspidatus number of eggs per liter were higher in 1957 and 1958 than 1971 and 1972. Thus, Canyon Ferry may have been more productive during 1957 and 1958 than 1971 and 1972.

1957 and 1958 D. galeata concentrations were much higher than 1971 and 1972 D. galeata concentrations. This may mean that the conditions have changed so as to favor D. schodleri over D. galeata. Since the 1957 and 1958 study was done at only station one, a statement about the change in species concentrations for the whole reservoir would be tenuous.

Table 21. Comparison of 1957 and 1958 values to 1971 and 1972 values.

Species	Term	Maxima				Average			
		1957	1958	1971	1972	1957	1958	1971	1972
Daphnia Schodleri	N *		22.10	79.91	90.82		8.31	16.71	13.83
	E/L		11.26	73.03	44.68		.17	7.80	6.75
	b		.59	.20	.36		.15	.09	.11
	r		.21	.24	.31		.01	-.03	-.01
	d		.08	.22	.06		-.14	-.12	-.10
Daphnia galeata	N		24.75	1.19	2.52		6.20	.71	.79
	E/C		10.67	5.50	2.00		4.23	2.49	1.23
D. schodleri + D. galeata	N	61.62	43.28	79.91	93.04	14.5	14.5	17.4	14.6
Cyclops bicuspidatus	Ad		9.29	3.81	29.23		2.47	2.05	4.92
	Co		265.5	127.0	344.6		41.2	20.6	33.6
	Na	36.4	31.2	295.7	205.4	10.1	13.3	46.2	30.1
	E/L		146.0	22.0	39.1		31.64	6.6	10.8
	Ad + Co/L	466.4	260.8	134.4	373.8	40.3	43.6	22.7	38.5
Diaptomus leptopus	Ad + Co/L	7.8		13.6	4.8	3.32		3.85	2.26

* Symbols: Ad = number of adults, b = instantaneous birth rate, C = clutch, Co = number of copepodids, d = instantaneous death rate, E = number of eggs, N = number of juveniles + adults, Na = number of nauplii, L = liter.

SUMMARY

Canyon Ferry Reservoir was formed by the closure of Canyon Ferry Dam in 1953. Limnological investigations were conducted by Dr. J. C. Wright from the fall of 1956 to the spring of 1959. A follow-up study was conducted during the summers of 1971 and 1972. The objectives of the follow-up study were to determine whether or not Canyon Ferry had become more eutrophic since 1959 and to analyze general limnological paramaters.

This thesis dealt with zooplankton populations. The species analyzed were Daphnia schodleri Sar, Daphnia galeata mendotae, Cyclops bicuspidatus thomasi S. A. Forbes, and Leptodora kindtii Focke.

Production in 1971 and 1972 was less than or equal to 1957 and 1958 production. Apparently, 1971 production was greater than 1972 production due to an early summer drawdown and reflooding in 1971 and subsequent increased nutrient release and increase in phytoplankton production. The effects of this drawdown on productivity were most evident during the second half of the summer and at stations three and four, which were closest to the nutrient release source. Station differences in zooplankton parameters may have been influenced by phytoplankton, turbidity, and Leptodora kindtii predation and flushing rate. Zooplankton differences between the first and second halves of the summers may have been influenced by temperature, food availability, Myxophycean toxins, and L. kindtii predation and flushing rate. Zooplankton production increased from the dam toward the inlet (the

nutrient release source).

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