Hydrobiologia **525:** 101–112, 2004.

Spatial and temporal variability of zooplankton in a great plains reservoir

Randall J. Bernot[1,2,*], Walter K. Dodds[1], Michael C. Quist[1,3] & Christopher S. Guy[1,4]
[1]*Division of Biology, Kansas State University, Manhattan, KS 66506, U.S.A.*
[2]*107 Galvin Life Science Center, Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, U.S.A.*
[3]*U.S. Geological Survey – Biological Resources Division, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY 82071-3166, U.S.A.*
[4]*U.S. Geological Survey – Biological Resources Division, Montana Cooperative Fishery Research Unit, Department of Ecology, Montana State University, Bozeman, MT 59717-3460, U.S.A.*
*(*Author for correspondence: Fax: +1-574-631-7413, E-mail: bernot.1@nd.edu)*

Received 20 August 2003; in revised form 20 January 2004; accepted 26 January 2004

Key words: *Daphnia*, diel vertical migration, reservoir, Rotifera

Abstract

Seasonal and daily patterns of zooplankton populations are often predictable in natural lakes. Distinct zonation and geomorphic differences in reservoirs, however, make ecological extrapolations from lakes to reservoirs uncertain. We describe the spatial and temporal distribution of zooplankton, algae, and water clarity across reservoir zones and along a depth gradient in Glen Elder Reservoir, Kansas. *Daphnia* species were most abundant in the lacustrine zone, with *D. pulicaria* numerically dominant in early spring and *D. mendotae* dominant later in 1999 and 2000. Rotifers (*Keratella quadrata*, *Asplanchna* spp.) were dominant in the riverine zone in 1999, 2000, and 2001. Algal biomass was not significantly different between zones through most of the sampling periods, except late April in 1999 and mid-April in 2000. Chlorophyll *a* exceeded 81 μg l^{-1} in the lacustrine zone in mid- to late-April in 1999 and 2000, and exceeded 90 μg l^{-1} in the riverine zone in mid-April. Water clarity was significantly lower in the riverine zone in 1999 and 2000. Most zooplankton taxa had similar depth distributions at night and day, indicating a lack of diel vertical migration behavior on a large scale. However, in small scale (30 cm vertical enclosures) laboratory experiments, both *D. pulicaria* and *D. mendotae* occupied significantly deeper depths (>25 cm) under lighted conditions in the presence of fish chemical cues compared to shallow water (7–17 cm) under dark conditions and in the absence of fish cues. These contrasting results suggest that, as in other studies, *Daphnia* sense cues from predators and alter their depth in the water column on small scales without natural constraints on movement and choices. However, other factors in the reservoir such as wind-generated water movements and cues from other predators may prevent depth choices similar to those seen under controlled conditions. These results illustrate biotic and abiotic differences between riverine and lacustrine zones in a large reservoir, and contrast with *Daphnia* depth segregation and migration patterns in natural lakes.

Introduction

Predictable patterns of biodiversity often occur in freshwater pelagic communities over yearly cycles in temperate regions of the globe. Seasonal succession of planktonic communities is driven by the changing availability of limiting resources to phytoplankton and zooplankton populations (Sommer, 1989). In zooplankton seasonal succession, communities of a few large species give way

to communities of smaller, more diverse assemblages in late spring or early summer (Sommer, 1989; Cáceres, 1998). Most research on seasonal succession has been conducted in natural, glacially formed lakes (Marzolf, 1990). Yet the majority of lentic habitat in the United States is the result of man-made impoundments that are generally shallower, have relatively high nutrient input and productivity, and are relatively less stable than natural lakes (Thornton, 1990).

Reservoirs also often contain distinct zones (e.g., riverine and lacustrine zones) that vary widely in flow and depth, making a characterization of the reservoir more difficult than of most natural lakes (Wetzel, 2001). Depth generally increases from shallow (<2 m depth) in riverine zones to much deeper (>10 m depth) in lacustrine zones (Wetzel, 1990). Extensive erosion by water currents in riverine zones leads to high levels of suspended sediments that get deposited exponentially down reservoir (Baxter, 1977; Wetzel, 1990). High particulate turbidity often reduces light penetration and limits primary production in riverine zones (Kirk, 1985).

Decreased turbidity in lacustrine zones enhances the depth of light penetration and higher rates of phytoplankton productivity occur. Thus, reservoirs become more similar to natural lakes in the lacustrine zone. However, differences in depth, fetch, and light penetration may ultimately preclude this portion of the reservoir from assuming the physical and biotic properties of natural lakes (Baxter, 1977). Therefore, physical differences in reservoir zones may have variable effects on the interacting biota living in the riverine vs. lacustrine zones (Arruda et al., 1983; Wetzel, 1990). The biotic communities and seasonal succession patterns may differ according to these constraining physical forces, yet has received little comparative attention (Miner & Stein, 1993; Ecker & Walz, 1998).

On a smaller scale, many planktonic organisms have the ability to move among habitats (either horizontally or vertically) in search of favorable abiotic (i.e., water temperature, nutrients) and biotic (i.e., high food resources, refuge from predators) conditions (Rosenzweig, 1991; Brown, 1990; Lima, 1998). For instance, two species of competing *Daphnia* in a stratified natural lake segregate themselves along a depth gradient according to their relative susceptibility to predators (Leibold & Tessier, 1991). Similarly, *Daphnia* may move horizontally into and out of macrophyte beds to reduce their predation risk (Burks et al., 2001).

Many *Daphnia* exhibit predictable large-scale shifts in their position within the water column (i.e., diel vertical migration; DVM) that are believed to be predator-avoidance mechanisms (Lampert, 1989; Loose, 1993; DeMeester et al., 1999). While a great deal of attention has been paid to the evolutionary significance and adaptive value of these plastic behaviors in northern latitude temperate natural lakes, little empirical evidence of DVM exists in man-made reservoirs. These habitats might be less likely to have migrating zooplankton, considering constraints imposed on migration such as shallow depth and wind-generated turbulence. Shallow depths may mean that no substantial refugia are available with depth. Reservoirs tend to have elongated morphology in the direction of the river channel, leading to greater fetch, and greater potential for wind-generated vertical mixing. In relatively shallow reservoirs, wind-induced turbulence and convection cells have been theorized to constrain active zooplankton movement and influence zooplankton distribution (Stavn, 1971; Cáceres, 1998). However, the extent to which zooplankters like *Daphnia* segregate by depth or exhibit DVM in shallow reservoirs remains unclear.

Here, we describe the spatial and temporal distribution of zooplankton, algal biomass (in the form of chlorophyll *a*), and water clarity across reservoir zones and compare zooplankton densities across a depth gradient in a large Kansas reservoir. Specifically, we ask: (1) how do zooplankton densities, algal abundance, and light attenuation differ between the lacustrine and riverine portions of a reservoir, (2) if zooplankton taxa undergo DVM by exhibiting different depth distributions during day and night on a large scale, and (3) if the 2 dominant *Daphnia* species, *D. pulicaria* and *D. mendotae* undergo DVM on a small scale in a laboratory setting.

Methods

Field patterns

We studied the plankton community of Glen Elder Reservoir, a 5093 ha reservoir in Mitchell County,

Kansas USA in the spring of 1999, 2000, and 2001. Glen Elder Reservoir is relatively shallow (mean depth = 7 m, max depth = 13 m) and was not thermally stratified in 1999 or 2000 (Bernot, 2003). We monitored the zooplankton community in Glen Elder Reservoir weekly from 16 March to 8 June 1999, from 21 March to 25 May 2000, and 4 April to 24 May 2001. Zooplankton were sampled from 24 stations in 1999 (2 riverine and 22 lacustrine stations), 20 stations in 2000 (4 riverine and 16 lacustrine stations), and 4 stations (all riverine) in 2001 (Fig. 1). Riverine stations were located west of a causeway, had water depths <2 m, detectable flow (Quist et al., 2002) and were at the mouths of Granite Creek and the Solomon River. Lacustrine stations were located east of a causeway at sites with depths >2 m and no detectable flow (Quist et al., 2002). Sampling stations and frequency were designed to relate zonal differences in larval fish and zooplankton densities during the spring of 3 years and are presented elsewhere (Quist et al., 2003). Full water-column zooplankton samples were collected with a plankton net (12 cm diameter, 65 μm mesh) and immediately preserved in 70% ethanol. Organisms were identified using keys provided by Pennak (1978). Taxa were enumerated by counting all organisms in a 5 ml subsample on a counting wheel (minimum of 50 individuals per taxa). Copepod naupli were not included in analyses. To estimate algal abundance, full water column water samples were also collected with a tube sampler, filtered onto a glass fiber filter (Whatman GF/F) and immediately frozen and brought to the laboratory for chlorophyll *a* concentration analysis. To measure chlorophyll *a*, pigments were extracted for 5 min in 90% ethanol at 78 °C (Sartory & Grobbelaar, 1984). After 24 h of refrigeration, samples were centrifuged and chlorophyll *a* pigment concentration in liquid was estimated using a fluorometer set to prevent phaeophytin from causing interference with fluorescence (Welschmeyer, 1995; Greenberg et al., 1998). Light and temperature profiles were measured from the deepest part of the lacustrine zone (i.e., a dam site; 13 m max. depth) and from the riverine zone during sampling periods. Temperature was measured with a thermistor probe (Yellow Springs Instruments, Yellow Springs, Ohio). Light attenuation was calculated from measurements made with a Li-Cor (LI-1922A, Li-Cor, Lincoln, NE) photometer with a cosine-corrected sensor for photosynthetically available radiation.

Statistical differences in the density of the most common taxa (present in >80% of our samples), chlorophyll *a*, and light attenuation coefficient (LAC) among habitat zones (lacustrine vs. riverine) and dates, and zone × date interactions were assessed using repeated measures ANOVA in 1999 and 2000. Linear contrasts were performed to determine significant differences between zones on each date. Simple linear regression was used to

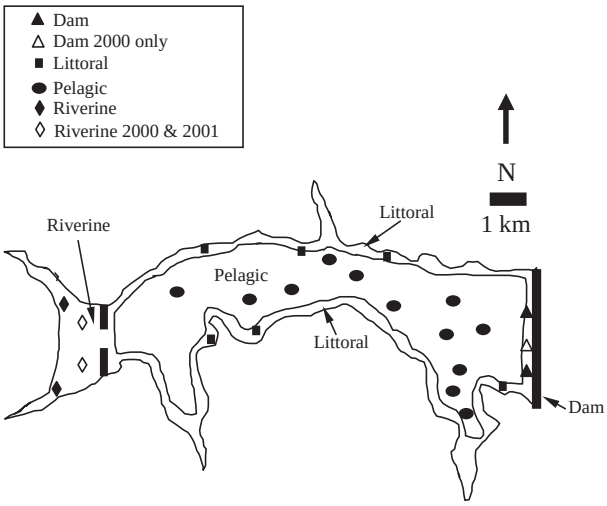

Figure 1. Locations of stations sampled on Glen Elder Reservoir, Kansas, from 1999 to 2001. Lacustrine zone stations consisted of dam, littoral, and pelagic sites.

determine if light attenuation depended on chlorophyll *a* concentration in each reservoir zone.

Zooplankton depth distribution

We assessed the depth distribution of the 6 most common (present in >80% of samples) zooplankton taxa (*Daphnia pulicaria*, *D. mendotae*, *Bosmina longirostris*, *Acanthocyclops vernalis*, *Diaptomis pallidus* and *Keratella quadrata*) in the lacustrine zone of Glen Elder reservoir weekly from 21 March to 25 May 2000. Zooplankton was sampled at 2 m depth intervals during the day (between 1000 and 1600) and at night (2300) at the deepest part of the reservoir (13 m) using a Schindler–Patalas sampler (30 l) and preserved in 70% ethanol. We also collected water samples for chlorophyll *a* analysis at 2 m depth intervals (including surface water) using a clear Van Dorn sampler. Algal biomass at each depth interval was estimated from weekly sampling periods as chlorophyll *a* concentration and determined as described above. Subsamples of all zooplankton were identified using keys provided by Pennak (1978) and counted to estimate the abundance of each taxon at each depth as described above. Differences in depth distribution between day and night samples on each sampling date for each taxon and chlorophyll *a* were assessed with two-sample Kolmogorov–Smirnov non-parametric test statistic (D) that tests the null hypothesis of equal depth distributions (Solow et al. 2000). Significance of D was determined using a randomization procedure that pooled the 2 samples into a single sample. The pooled sample was divided at random into 2 samples of which D was recalculated. This procedure was repeated 1000 times using Systat 8.0 and the significance level (p-value) was the proportion of simulated values of D that exceed the observed value (Manly, 1991; Solow et al., 2000).

Laboratory experiment

We tested if *Daphnia pulicaria* and *D. mendotae* migrated vertically on a diel cycle on a small scale using clear glass tubes (35 cm length, 5 cm diam.) in a laboratory experiment. Adult laboratory-reared clones of each species taken from culture (originally collected from Glen Elder) were used as experimental animals. Experiments were conducted in July 2000 on a laboratory bench with a light source (standard fluorescent bulb) directly above 16 glass tubes filled with aged lake water and a 12:12 light:dark cycle at 20 °C. Light was 108 μmol quanta m^{-2} s^{-1} at the surface of the water of each tube and 59 μmol quanta m^{-2} s^{-1} at the bottom of each tube. Thus, we created a gradient of light within each tube, but did not provide a completely dark refuge for *Daphnia*. The temperature of each tube was 21 ± 0.45 °C (mean ± SE, $n = 16$) at the surface and 21 ± 0.87 °C at the bottom at the conclusion of each experiment, so there was no temperature gradient experienced by *Daphnia*. We used chemical cues generated by zooplanktivorous fish to simulate a perceived predation risk on individual *Daphnia* without the direct effects of predation (Tollrian & Dodson, 1999; Brönmark & Hansson, 2000; Turner et al., 2000). We conducted two experimental trials (one per species) in which we measured the depth of individual *Daphnia* in lighted and dark conditions, both in the presence and the absence of chemical cues from separately housed bluegill sunfish (*Lepomis macrochirus*). One litre of water was taken from eight separately housed juvenile *L. macrochirus* that were fed *Daphnia* daily and thus contained chemical cues. Chemical cue water was stirred for 2 min and 10 ml was pipetted into each glass tube designated as a fish cue treatment. Filtered and aged (>48 h) lake water (10 ml) was added to each of the glass tubes designated as no-fish cue controls. One individual *Daphnia* was carefully pipetted into each glass tube. We recorded the depth of each animal 4 h after stocking into tubes (light) and then again 6 h later (dark; 10 h after stocking). Observations in the dark were aided by the use of a flashlight with a red filter to minimize disturbing the *Daphnia*. Thus, for each species we analyzed the effects of time (light vs. dark) and predation risk (fish cues vs. no fish cues) with a repeated measures ANOVA ($n = 8$ per treatment combination).

Results

Field patterns

Densities of zooplankton taxa varied within and among each sampling year (Figs 2 and 3). In

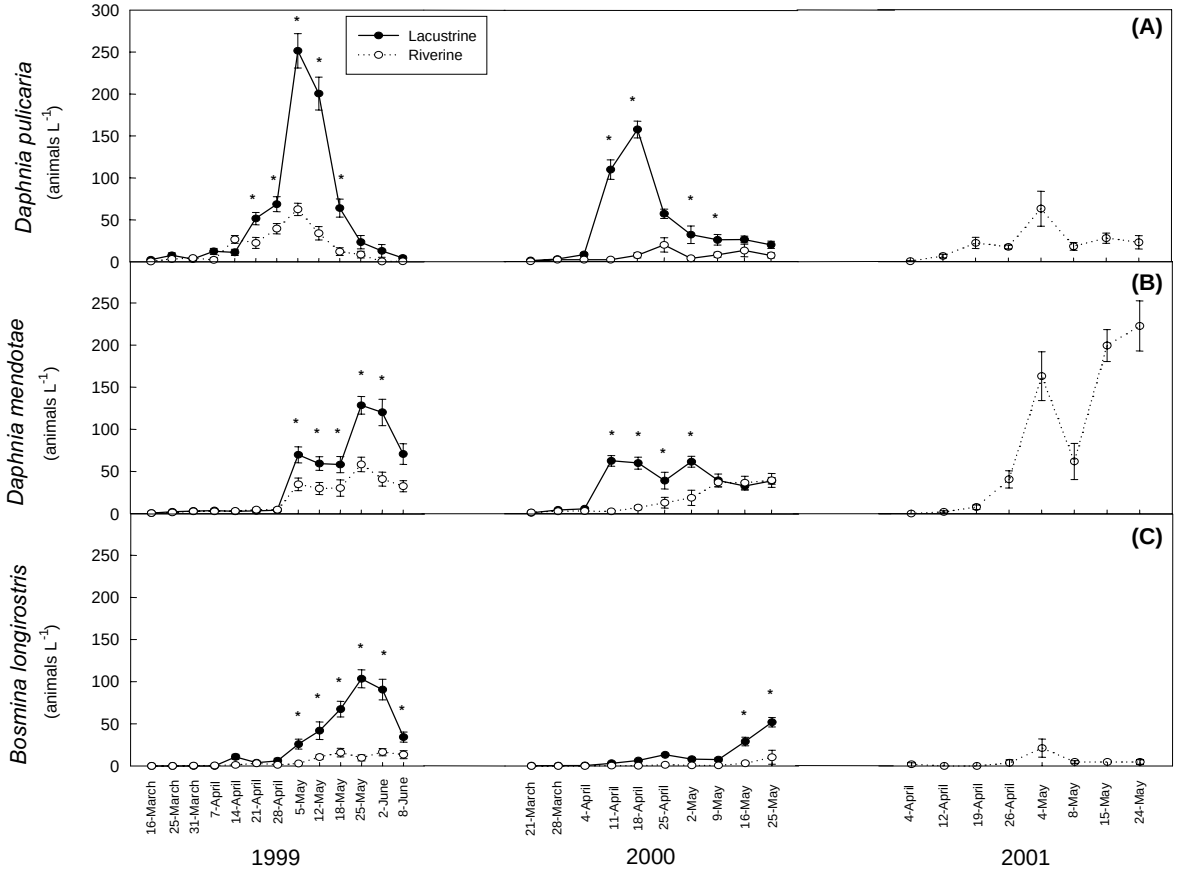

Figure 2. Density of (A) *Daphnia pulicaria*, (B) *D. mendotae*, and (C) *Bosmina longirostris* in lacustrine and riverine zones in Glen Elder Reservoir, Kansas in 1999, 2000, and 2001. Asterisks represent significant differences between reservoir zones within sampling dates.

general, cladocera (*Daphnia pulicaria*, *D. mendotae*, and *B. longirostris*) were significantly more abundant in the lacustrine zone than the riverine zone in 1999 and 2000 across most sampling periods (linear contrasts: p-values range from <0.01 to 0.18, Fig. 2). *Daphnia pulicaria* density exceeded 250 animals l^{-1} in May 1999 and 150 animals l^{-1} in April 2000 (Fig. 2A), but only reached 60 animals l^{-1} in the riverine zone in 2001. *Daphnia mendotae* density peaked at 145 animals l^{-1} in 1999 and 70 animals l^{-1} in 2000. This peak occurred later than the *D. pulicaria* density peaks in both years, and *D. mendotae* became very abundant in the riverine zone in late May 2001 (>200 animals l^{-1}; Fig. 2B). *Bosmina longirostris* exceed 100 animals l^{-1} in May 1999 lacustrine samples, but only reached 60 and 20 animals l^{-1} in 2000 and 2001 respectively (Fig. 2C). Densities of cladocerans differed significantly over the course of each season depending on the habitat zone (zone × date: 1999, $F_{12,252}$ ranged from 33.58 to 51.52, $p < 0.01$; 2000, $F_{9,153}$ ranged from 17.76 to 41.90, $p < 0.01$).

Adult copepod densities varied over the course of all sampling periods (Fig. 3). In general, the calanoid copepod, *Diaptomis pallidus*, and the cyclopoid copepod, *Acanthocyclops vernalis*, were significantly more abundant in the lacustrine zone than the riverine zone early in the spring, but became more abundant in the riverine zone later in the spring (Fig. 3). Densities of copepods differed significantly over the course of each season depending on the habitat zone (zone × date: 1999, $F_{12,252} > 4.50$, $p < 0.01$; 2000, $F_{9,153} > 11.98$, $p < 0.01$).

Rotifer (*Keratella quadrata*, *Asplanchna* spp.) densities varied over the course of all sampling periods (Fig. 4). Rotifer densities differed

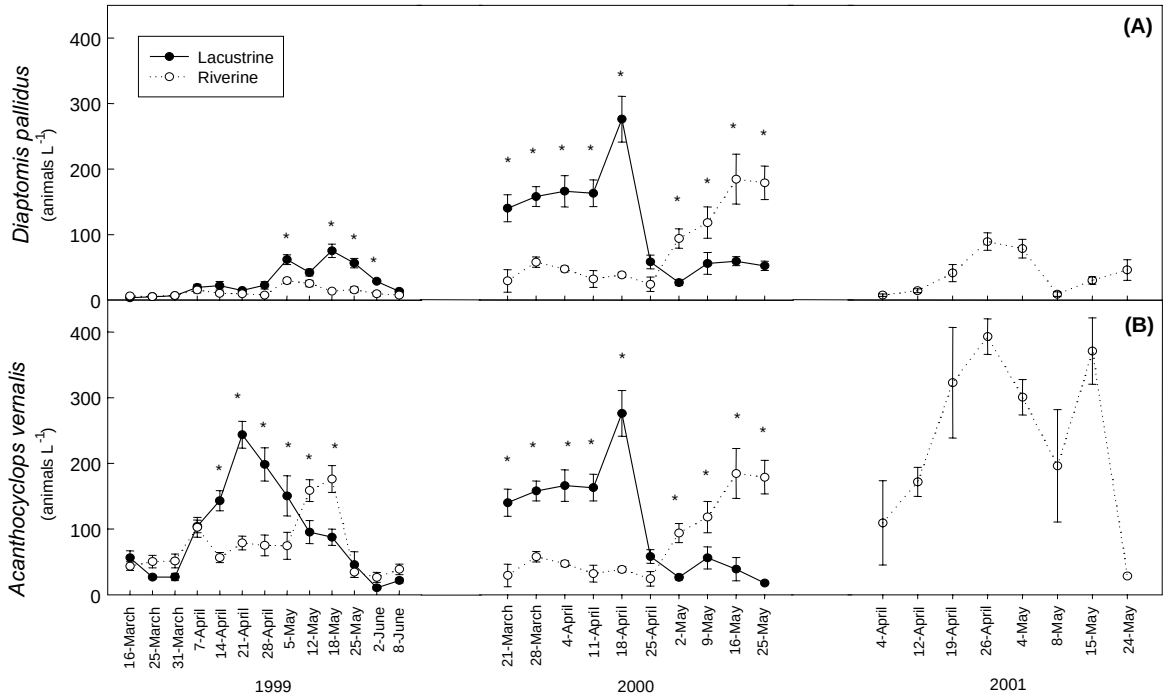

Figure 3. Density of (A) adult *Diaptomis pallidus*, and (B) adult *Acanthocyclops vernalis* in lacustrine and riverine zones in Glen Elder Reservoir, Kansas in 1999, 2000, and 2001. Asterisks represent significant differences between reservoir zones within sampling dates.

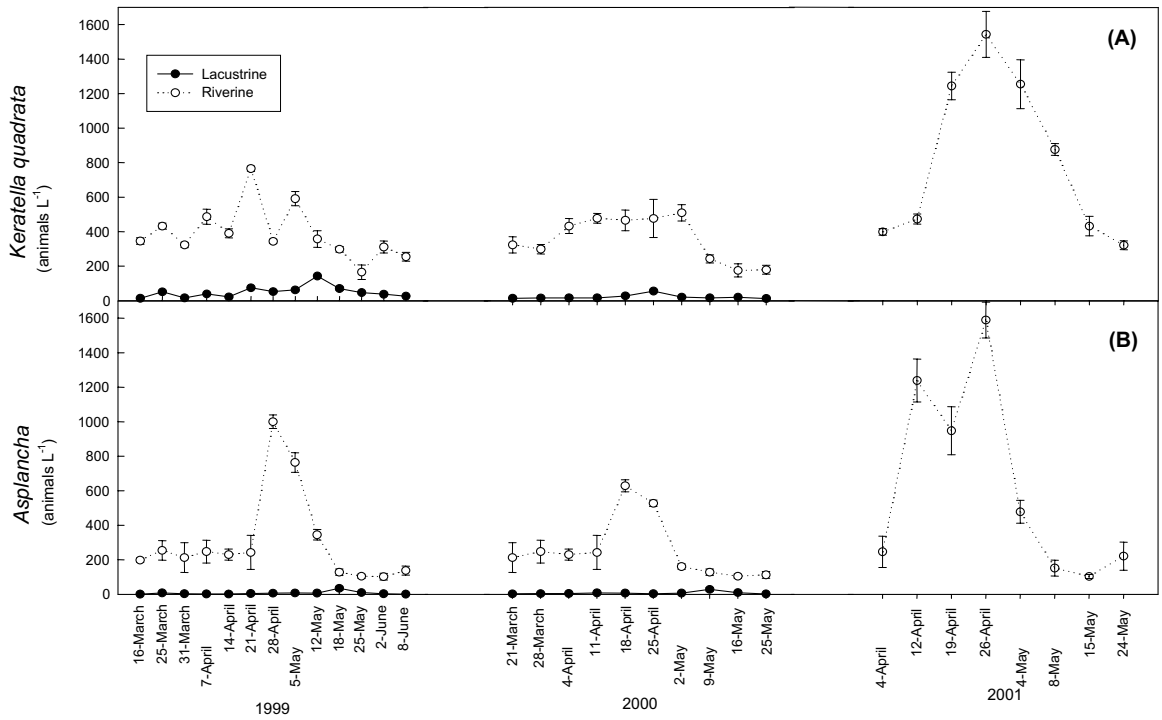

Figure 4. Density of (A) *Keratella quadrata*, and (B) *Asplanchna* spp. in lacustrine and riverine zones in Glen Elder Reservoir, Kansas in 1999, 2000, and 2001. Reservoir zones differed significantly in rotifer densities on all sampling dates.

significantly over the course of each season depending on the habitat zone (zone × date: 1999, $F_{12,252} > 10.21$, $p < 0.01$; 2000, $F_{9,153}$ ranged from 17.76 to 41.90, $p < 0.01$), but were generally higher in the riverine zone.

Algal biomass differed significantly over the course of each season depending on the habitat zone (zone × date: 1999, $F_{12,252} > 11.50$, $p < 0.01$; 2000, $F_{9,153} > 20.41$, $p < 0.01$) and was generally greater in the lacustrine zone (Fig. 5C). Algal biomass peaked in mid-April in 1999 and 2000 reaching 90 μg l^{-1} chlorophyll *a* in the lacustrine zone. Chlorophyll *a* concentrations only reached 41 μg l^{-1} in 1999 and 70 μg l^{-1} in 2000 in the riverine zone (Fig. 5C). LAC was positively dependent on chlorophyll *a* concentration in the lacustrine zone ($R^2 = 0.59$, $p < 0.01$; Fig. 6) but not the riverine zone ($R^2 = 0.06$, $p = 0.19$).

Light attenuation coefficients were significantly greater in the riverine than the lacustrine zone on all dates except the first sampling dates of each year (16 March 1999 and 21 March 2000; Fig. 5A), suggesting greater turbidity in the riverine zone. LAC also differed significantly over the course of each season depending on the habitat zone (zone × date: 1999, $F_{12,252} > 15.32$, $p < 0.01$; 2000, $F_{9,153} > 19.98$, $p < 0.01$). Water temperature rose steadily in 2000 and 2001, but varied more in 1999 due to a late May cool period (Fig. 5B).

Zooplankton depth distribution

The depth distribution of *D. pulicaria* did not significantly differ between day and night ($p > 0.10$) except on 5 April 2000 when an even distribution during the day was significantly different than a bottom-skewed distribution at night ($p = 0.04$, Fig. 7). No consistent skew in the depth distribution of *D. pulicaria* was observed, though a shallow-water skew appeared on 23 May 2000. The depth distribution of *D. mendotae* had a marginally significant bottom skewed night distribution on 5 April 2000 ($p = 0.07$), but did not differ on other dates ($p > 0.10$, Fig. 7). *Daphnia mendotae* distributions also had a shallow-water

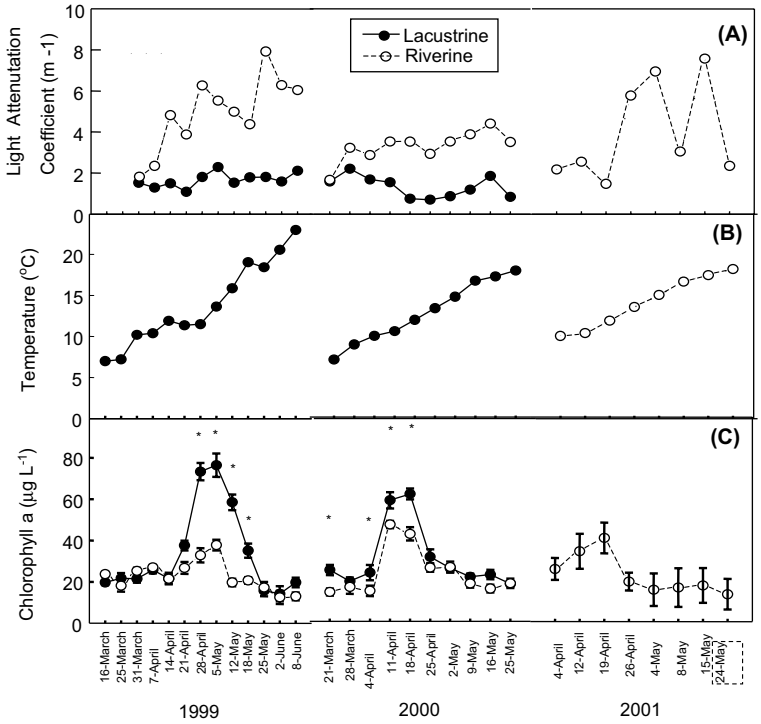

Figure 5. (A) Light attenuation coefficient, (B) water temperature, and (C) algal biomass (chlorophyll *a*) in lacustrine and riverine zones sampled in springtime weekly samples from Glen Elder Reservoir in 1999, 2000, and 2001. Asterisks represent significant differences between zones within sampling dates. Note that because water temperature differed little between zones, lines overlap.

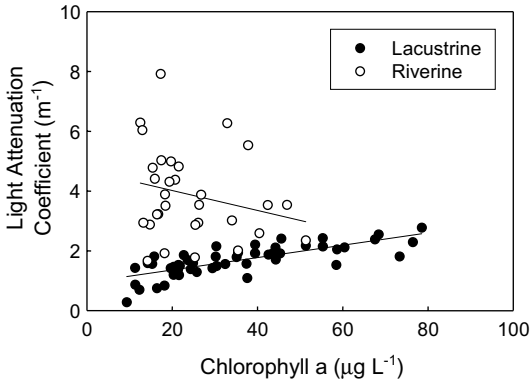

Figure 6. Relationship between chlorophyll *a* concentration and light attenuation coefficient (LAC) in the lacustrine (closed circles) and riverine (open circles) zones of Glen Elder Reservoir. The lines represent simple linear regression equations for the lacustrine ($R^2 = 0.59$, LAC = 0.021(chlorophyll *a*) + 0.948) and riverine ($R^2 = 0.06$, LAC = −0.033 (chlorophyll *a*) + 4.685) zones.

skew on 23 May 2000, but not on other dates. *Acanthocyclops vernalis* depth distribution was surface-skewed during the day but bottom-skewed at night on 5 April 2000 ($p = 0.03$, Fig. 8), but did not differ on any other date ($p > 0.10$). No general depth skew was observed for *A. vernalis*. *Bosmina longirostris*, *Diaptomis pallidus*, and *Keratella quadrata* depth distributions did not differ between day and night on any date ($p > 0.10$, Figs 7 and 8). *Bosmina longirostris* did exhibit a shallow-water skew across day and night samples, however (Fig. 7). The depth distribution of chlorophyll *a* was skewed toward the surface and did not differ diurnally on any sampling date ($p = 0.41$).

Laboratory experiment

Both *D. pulicaria* and *D. mendotae* used deeper water (>25 cm depth) in the day in the presence of fish chemical cues compared to shallow water (7–17 cm depth) at night and in the absence of fish chemical cues (Fig. 9). Both species had significant time by fish chemical cue effects (*D. pulicaria*: $F_{1,13} = 12.12$, $p < 0.01$, *D. mendotae*: $F_{1,13} = 13.60$, $p < 0.01$) indicating the potential for predator-induced vertical movement in the water column *in situ*.

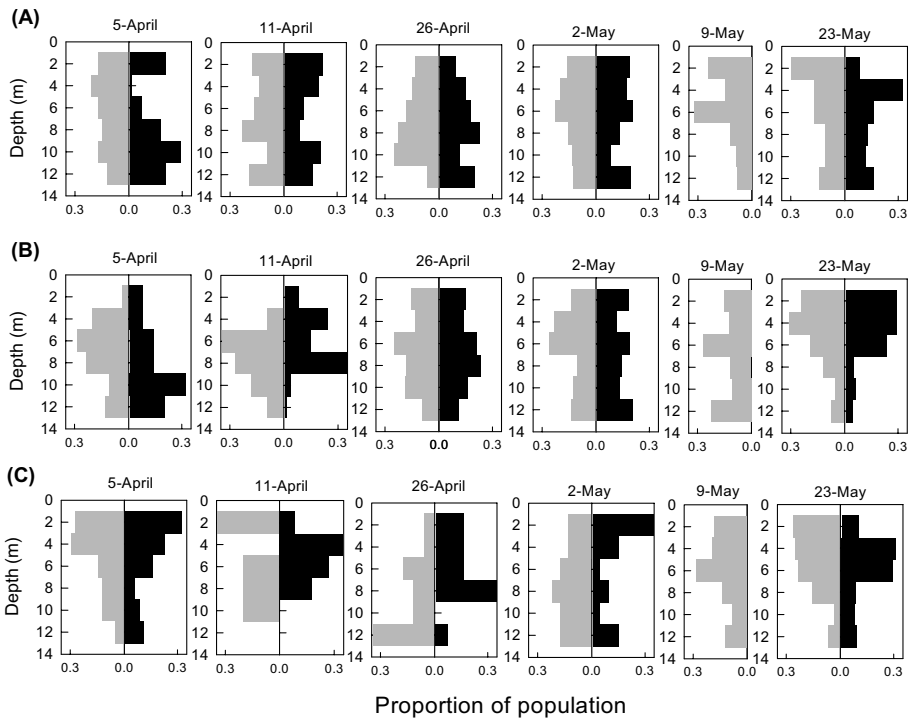

Figure 7. Depth distributions of *Daphnia pulicaria* (A), *Daphnia mendotae* (B), and *Bosmina longirostris* occupying depths ranging from 2 to 12 m in Glen Elder Reservoir in day (shaded) and night (filled) samples in the spring of 2000.

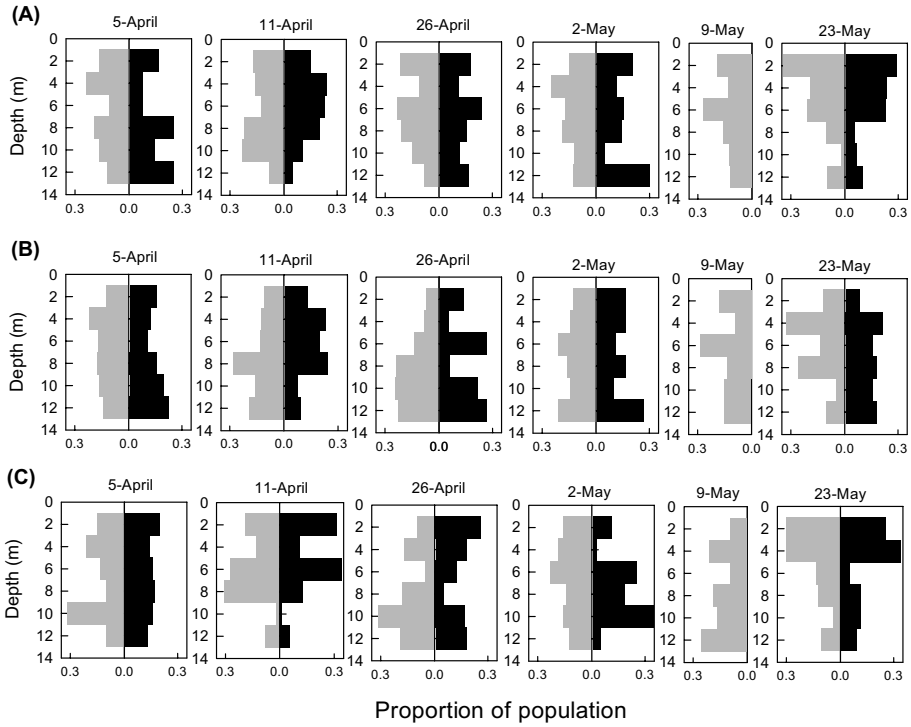

Figure 8. Depth distributions of adult *Diaptomis pallidus*, adult *Acanthocyclops vernalis*, and *Keratella quadrata* occupying depths ranging from 2 to 12 m in Glen Elder Reservoir in day (shaded) and night (filled) samples in the spring of 2000.

Discussion

Zooplankton densities, algal abundance, and water clarity differed between the riverine and lacustrine portions of Glen Elder Reservoir. The lacustrine zone resembled the *Daphnia*-dominated communities of natural lakes (Mills & Forney, 1987), but the riverine zone differed significantly in biotic and abiotic parameters. While much limnological research has focused on natural lake ecosystems and extended to reservoirs, differences in geomorphology and hydrology could lead to biotic differences as well (Thornton, 1990).

Daphnia densities were greater in the lacustrine zone than the riverine zone, while rotifer densities were much greater in the riverine zone. Competitive interactions between these groups of algal grazers depend on suspended solid content in the water column as well as the size and quality of algae (Kirk & Gilbert, 1990; Abrahams & Kattenfeld, 1997; Pollard et al., 1998). Flow and greater suspended solids often favor rotifers over crustaceans in riverine conditions because of short rotifer development time (Ecker & Walz, 1998) and the ability of rotifers to selectively feed (Kirk & Gilbert, 1990). Suspended solids negatively affect *Daphnia* populations by interfering with feeding (Kirk, 1992). Although we did not measure turbidity directly, the lack of a relationship between algal biomass and LAC in the riverine zone suggest that some other factor such as suspended solids reduced water clarity and affected *Daphnia*. In environments without suspended sediments, cladocerans tend to suppress rotifers through exploitation competition for the same algal resources (Gilbert, 1988) and mechanical interference (Gilbert & Stemberger, 1985). The positive relationship between algal biomass and LAC in the lacustrine zone of Glen Elder reservoir suggest that algal biomass controlled light attenuation when concentrations of suspended solids were low (Davies-Colley & Smith, 2001).

Algal abundance was greater in the lacustrine zone in April, then declined throughout May in all 3 years, and did not differ between zones. As water temperatures rose, algal production presumably

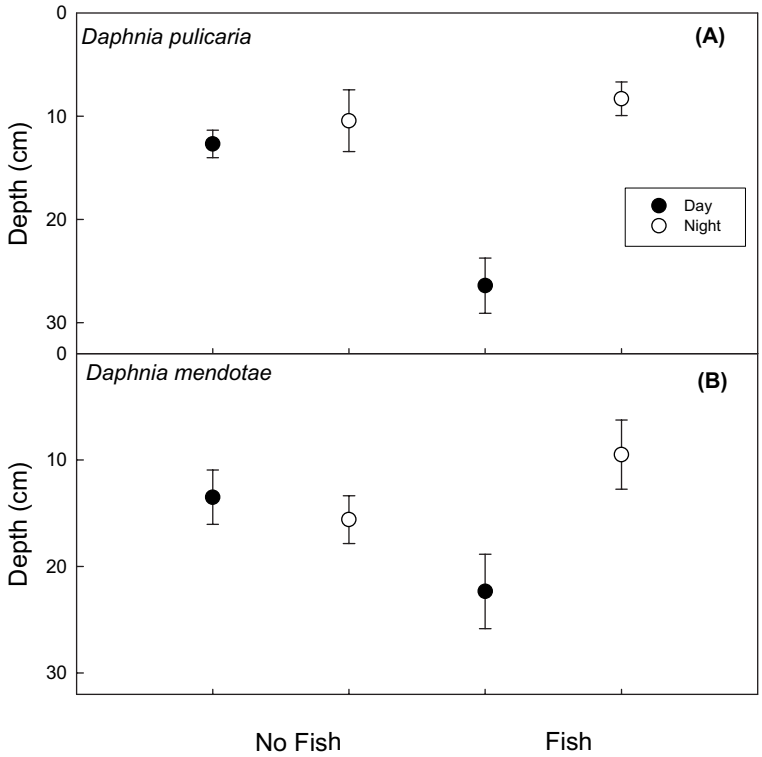

Figure 9. Mean depth of (A) *Daphnia pulicaria*, and (B) *Daphnia mendotae* in glass tubes during the day and at night in the absence and presence of bluegill sunfish (*Lepomis macrochirus*) kairomones. Symbols represent mean depth ±1 standard error.

increased, algal abundance increased until zooplankton densities and grazing pressure (primarily *Daphnia* in the lacustrine zone and rotifers in the riverine zone) peaked, resulting in lower algal standing crop later in the spring (May–June). Taken together, these data indicate patterns of lacustrine plankton succession similar to that of natural lakes (Sommer, 1989) and patterns of riverine succession similar to that of rivers (Basu & Pick, 1996; Baranyi et al., 2002).

In Glen Elder, distributions of zooplankton taxa generally did not exhibit diurnal changes in depth distributions. This contrasts with a large number of studies showing diel vertical migration in cladoceran species (Lass & Spaak, 2003). Moreover, as predation risk increases from early spring to summer due to higher fish activity and density, it has been hypothesized that the extent of DVM should increase (Post et al., 1992; Mehner, 2000). We did not find this to be the case as no consistent pattern of depth distribution occurred, even though larval fish density increased from March through June of each year (Bernot, 2003). On a smaller scale in the laboratory, though, both *D. pulicaria* and *D. mendotae* occupied deeper water during the day than at night when exposed to fish chemicals. The discrepancy may be attributed to differences in scale, such that *Daphnia* did migrate in Glen Elder, but not more than a few centimeters, making DVM undetectable with our methods. It may also be due to physical differences between the two venues: Glen Elder was mixing due to wind-driven turbulence (wind speeds often exceeded 15 m s^{-1} (National Weather Service, U.S. National Oceanic and Atmospheric Association), maximum fetch = 7 km), but glass tubes experienced little mixing except perhaps slight convective mixing from water heating. Thus, water motions may have constrained *Daphnia* movement upward at night or downward during the day (Anthony & Downing, 2003). Finally, clonal differences in *Daphnia* DVM behavior may occur in natural systems (Lass & Spaak, 2003). We used only one clone of each species in our laboratory

experiment that may not represent the full range of clones in the reservoir.

In nature, *Daphnia* experience predation risks from a number of predators, including the invertebrate predator *Chaoborus*, that can obscure single predator effects on large-scale migration patterns (Sih et al., 1998, Burks et al. 2001). For example, Gonzalez and Tessier (1997) found *Daphnia* to move up in the water column during day, and down at night due to *Chaoborus* predation. This is the opposite of the migration pattern found in most other DVM studies of *Daphnia* movement due to fish predation risk (Tollrian & Harvell, 1999). Thus, the combination of cues may have resulted in little or no *Daphnia* movement, or movement of some individuals up at night simultaneous to other individuals down at night, resulting in no net observed change in population depth distribution. *Chaoborus* were collected from Glen Elder in at least one sample per sampling date using both Schindler–Patalas traps and full water-column plankton tows, but in low densities ($<0.03\ l^{-1}$) relative to other studies (Gonzalez & Tessier, 1997).

In conclusion, the riverine and lacustrine zones of Glen Elder Reservoir differed in zooplankton population characteristics as well as water clarity. Relatively low water clarity and high densities of rotifers characterized the riverine zone. Relatively higher water clarity, low densities of rotifer, and high densities of *D. pulicaria* early in the spring, and then high densities of *D. mendotae* characterized the lacustrine zone later in the spring. None of the most common zooplankton taxa exhibited diel vertical migration on the scale of 2 m intervals in the reservoir. However, on a small scale in the laboratory, both *D. pulicaria* and *D. mendotae* occupied deeper depths during the day in the presence of fish chemical cues, suggesting that these species have the ability for DVM but may not swim upwards or downwards due to physical constraints or the influence of multiple predators.

Acknowledgements

We thank M. Bernot, C. Oppert, S. Butler, J. Delp, J. Hart for their assistance in the field and laboratory. D. Gudder, C. Smith, J. Nechols, K. Kemp, S. Dodson, and anonymous reviewers commented on previous versions of the manuscript. We also thank K. Austin and the staff at Glen Elder State Park for their assistance with this and other research on Glen Elder Reservoir. Funding was provided by the Kansas Department of Wildlife of Parks through Federal Aid in Sport Fish Restoration, Project F-45-R2 and Kansas State University.

References

Abrahams, M. & M. Kattenfeld, 1997. The role of turbidity as a constraint on predator–prey interactions in aquatic environments. Behavioral Ecology and Sociobiology 40: 169–174.

Anthony, J. L. & J. A. Downing, 2003. Physical impacts of wind and boat traffic on Clear Lake, Iowa, USA. Lake and Reservoir Management 19: 1–14.

Arruda, J. A., G. R. Marzolf & R. T. Faulk, 1983. The role of suspended sediments in the nutrition of zooplankton in turbid reservoirs. Ecology 64: 1225–1235.

Baranyi, C., T. Hein, C. Holarek, S. Keckeis & F. Schiemer, 2002. Zooplankton biomass and community structure in a Danube River floodplain system: effects of hydrology. Freshwater Biology 47: 473–482.

Basu, B. K. & F. R. Pick, 1996. Factors regulating phytoplankton and zooplankton biomass in temperate rivers. Limnology and Oceanography 41: 1572–1577.

Baxter, R. M., 1977. Environmental effects of dams and impoundments. Annual Review of Ecology and Systematics 8: 255–283.

Bernot, R. J., 2003. Consequences of *Daphnia* phenotypic plasticity in a Great Plains reservoir. PhD Dissertation, Kansas State University, Manhattan, Kansas USA, 127pp.

Brönmark, C. & L. A. Hansson, 2000. Chemical communication in aquatic systems: an introduction. Oikos 88: 103–110.

Brown, J. S., 1990. Habitat selection as an evolutionary game. Evolution 44: 732–746.

Burks, R. L., E. Jeppesen, & D. M. Lodge, 2001. Littoral zone structures as *Daphnia* refugia against fish predators. Limnology and Oceanography 46: 230–237.

Cáceres, C. E., 1998. Seasonal dynamics and interspecific competition in Oneida Lake *Daphnia*. Oecologia 115: 233–244.

Davies-Colley, R. J. & D. G. Smith, 2001. Turbidity, suspended sediment, and water clarity: a review. Journal of the American Water Resources Association 37: 1085–1101.

DeMeester, L., P. Dawidowicz, E. Van Gool & C. J. Loose, 1999. Ecology and evolution of predator-induced behavior of zooplankton: depth selection behavior and diel vertical migration. In Tollrian, R. & C. D. Harvell (eds), *The Ecology and Evolution of Inducible Defenses*. Princeton University Press, Princeton, New Jersey: 160–176.

Ecker, B. & N. Walz, 1998. Zooplankton succession and thermal stratification in the polymictic shallow Müggelsee (Berlin, Germany): a case for the intermediate disturbance hypothesis? Hydrobiologia 337/338: 199–206.

Gilbert, J. J., 1988. Suppression of rotifer populations by *Daphnia*: a review of the evidence, the mechanisms and the effects on zooplankton community structure. Limnology and Oceanography 33: 1286–1303.

Gilbert, J. J. & R. S. Stemberger, 1985. Control of *Keratella* populations by interference competition by *Daphnia*. Limnology and Oceanography 30: 180–188.

Gonzalez, M. J., & A. J. Tessier, 1997. Habitat segregation and interactive effects of multiple predators on a prey assemblage. Freshwater Biology 38: 179–191.

Greenberg, A. E., L. S. Clesceri & A. D. Eaton, 1998. Standard Methods for the Examination of Water and Wastewater, 20th edn. American Public Health Association joint publication with American Water Works Association and Water Environment Federation.

Hansson, L. A., 1995. Diurnal recruitment patterns in algae: effects of light cycles and stratified conditions. Journal of Phycology 31: 540–546.

Kirk, J. T. O., 1985. Effects of suspensoids (turbidity) on penetration of solar radiation in aquatic ecosystems. Hydrobiologia 125: 195–208.

Kirk, K. L., 1992. Effects of suspended clay on Daphnia body growth and fitness. Freshwater Biology 28: 103–109.

Kirk, K. L. & J. J. Gilbert, 1990. Suspended clay and the population dynamics of planktonic rotifers and cladocerans. Ecology 71: 1741–1755.

Lampert, W., 1989. The adaptive significance of diel vertical migration of zooplankton. Functional Ecology 3: 21–27.

Lass, S. & P. Spaak, 2003. Chemically induced anti-predator defences in plankton: a review. Hydrobiologia 491: 221–239.

Leibold, M. A. & A. J. Tessier, 1991. Contrasting patterns of body size for coexisting *Daphnia* species that segregate by habitat. Oecologia 86: 342–348.

Leibold, M. A., J. M. Chase, J. B. Shurin & A. Downing, 1997. Species turnover and the regulation of trophic structure. Annual Review of Ecology and Systematics 28: 467–494.

Lima, S. L., 1998. Nonlethal effects in the ecology of predator-prey interactions. Bioscience 48: 25–34.

Loose, C. J., 1993. *Daphnia* diel vertical migration behavior: response to vertebrate predator abundance. Archiv fur Hydrobiologie 39: 29–36.

Manly, B. F., 1991. Randomization and Monte Carlo Tests In Biology. Chapman and Hall.

Marzolf, G. R., 1990. Reservoirs as environments for zooplankton. In Thornton, K. W, B. L. Kimmel & F. E. Payne (eds), Reservoir Limnology: Ecological Perspectives. Wiley-*Interscience*, New York: 195–208.

Mehner, T., 2000. Influences of spring warming on the predation rate of underyearling fish on *Daphnia* – a deterministic simulation approach. Freshwater Biology 45: 253–263.

Mills, E. L. & J. L. Forney, 1987. Trophic dynamics and development of freshwater pelagic food webs. In Carpenter, S.R. (ed.), Complex Interactions in Lake Communities. Springer, New York: 11–30.

Miner, J. G. & R. A. Stein, 1993. Interactive influence of turbidty and light on larval bluegill (*Lepomis macrochirus*) foraging. Canadian Journal of Fisheries and Aquatic Science 50: 781–788.

Pennak, R. W., 1978. Fresh-Water Invertebrates of the United States, 2nd edn. Wiley, New York.

Persson, L., 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. Oikos 85: 385–397.

Polis, G. A., A. L. W. Sears, G. R. Huxel, D. R. Strong & J. Maron, 2000. When is a trophic cascade a trophic cascade? Trends in Ecology and Evolution 15: 473–475.

Pollard, A. I., M. J. Gonzalez, M. J. Vanni & J. L. Headworth, 1998. Effects of turbidity and biotic factors on the rotifer community in an Ohio reservoir. Hydrobiologia 387–388: 215–223.

Post, J. R., L. G. Rudstram, D. M. Scahael & C. Luecke, 1992. Pelagic planktivory by larval fishes in Lake Mendota. In Kitchell, J. (ed.), Food Web Management: A Case Study of Lake Mendota. Springer-Verlag, New York, pp. 303–318.

Quist, M. C., C. S. Guy, & R. J. Bernot, 2002. Ecology of larval white bass in a large Kansas reservoir. North American Journal of Fisheries Management 22: 637–642.

Quist, M. C., C. S. Guy, & J. L. Stephen, 2003. Recruitment dynamics of walleyes (Stizostedion vitreum) in Kansas reservoirs: generalities with natural systems and effects of a centrarchid predator. Canadian Journal of Fisheries and Aquatic Science 60: 830–839.

Rosenzweig, M. L., 1991. Habitat selection and population interactions: the search for mechanism. American Naturalist 137: 385–387.

Sartory, D. P. & J. E. Grobbelaar, 1984. Extraction of chlorophyll a from freshwater phytoplankton for spectrophotometric analysis. Hydrobiologia 114: 177–187.

Sih, A., G. Englund, & D. Wooster, 1998. Emergent impacts of multiple predator species on prey. Trends in Ecology and Evolution 13: 350–355.

Solow, A. R., S. M. Bollens & A. Beet, 2000. Comparing two vertical plankton distribution. Limnology and Oceanography 45: 506–509.

Sommer, U., 1989. Plankton Ecology: Succession in Plankton Communities. Springer-Verlag, New York.

Stavn, R. H., 1971. The horizontal-vertical distribution hypothesis: Langmuir circulations and *Daphnia* distributions. Limnology and Oceanography 16: 453–466.

Thornton, K. W., 1990. Perspectives on reservoir limnology. In Thornton, K. W., B. L. Kimmel & F. E. Payne (eds), Reservoir Limnology: Ecological Perspectives. John Wiley and Sons, Inc., New York: 1–13.

Tollrian, R. & S. I. Dodson, 1999. Inducible defenses in Cladocera: constraints, costs, and multipredator environments. In Tollrian, R. & C. D. Harvell (eds), Ecology and Evolution of Inducible Defenses. Princeton University Press, Princeton, USA.

Turner, A. M., R. J. Bernot & C. M. Boes, 2000. Chemical cues modify species interactions: the ecological consequences of predator avoidance by freshwater snails. Oikos 88: 148–158.

Welschmeyer, N. A., 1995. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. Limnology and Oceanography 39: 1985–1992.

Wetzel, R. G., 1990. Reservoir ecosystems: conclusions and speculations. In Thornton, K. W., B. L. Kimmel & F. E. Payne (eds), Reservoir Limnology: Ecological Perspectives. Wiley-Interscience, New York: 227–238.

Wetzel, R. G., 2001. Limnology: Lake and River Ecosystems, 3rd edn. Academic Press, New York.