

Exploring riverine zooplankton in three habitats of the Illinois River ecosystem: Where do they come from?

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Abstract

We sampled three habitats (main channel, side channels, and backwater lakes) during 2 yr along 32 km of the Illinois River to compare zooplankton distribution and dynamics, as well as evaluate the possible effects of hydrology on taxonomic abundance and distribution. Zooplankton assemblages displayed both spatial and temporal variation. Whereas the riverine zooplankton assemblage was dominated by rotifers, the backwater lake assemblage was dominated by copepods. Zooplankton densities in the main channel peaked earlier in the season in both years than the backwater lake habitats. To determine if these patterns were caused by fluvial exchanges occurring between habitats during flooding, we sampled the connections between the backwater lake and main channel habitats and found that large numbers of zooplankton entered the main channel via these connections. Further, calculations of main channel population growth, birth, and death rates showed that population growth rates most commonly exceeded birth rates during the flooding period. Seasonal inoculums from off-channel habitats could play an important role in riverine zooplankton dynamics. However, for the main channel to achieve the measured zooplankton densities, ~400,000 backwater lakes would be required and zooplankton would need to travel an unrealistic number of days and distance based on estimated growth rates. Thus, other mechanisms (hatching of resting eggs or in situ reproduction) are likely responsible for zooplankton abundances.

There is no clear understanding of how zooplankton assemblages in large rivers are structured (Davies and

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Walker 1986; Reynolds 1988) and their origin is often debated (Hynes 1970). Riverine zooplankton dynamics are thought to be controlled by factors affecting transport and growth (Hynes 1970). Main river channels produce harsh physical conditions (advection, turbulence, high turbidity) that may reduce zooplankton feeding (Hart 1988; Saiz et al. 1992), growth (McCabe and O'Brien 1983; Thorp et al. 1994), and reproduction (McCabe and O'Brien 1983; Thorp et al. 1994). Further, it is thought that these organisms are unable to swim against currents (Winner 1975). Despite harsh physical conditions, population growth does occur suggesting some taxa can successfully reproduce in the main channel of large rivers and densities often vary with shifts in the seasonal hydrologic regime. (Saunders and Lewis 1988a,b).

River-floodplain ecosystems are comprised of both lotic (the main channel) and lentic, or off-channel, habitats. Although riverine zooplankton community composition may be controlled by advection and turbulence, physical changes during flooding likely play a critical role in structuring this community. Typical floods are associated with low water temperatures, decreased residence times, increased advection and decreased transparency in main

river channels. During seasonal flood pulses, these river habitats exchange nutrients and organisms (Bayley 1995; Grosholz and Gallo 2006). In contrast, throughout the rest of the year, off-channel habitats are warmer with increased residence times and greater transparency due to decreased turbulence (Shiel et al. 1982; Rossaro 1988). These habitat-specific differences may be especially important in determining the abundance and taxonomic composition of zooplankton (Pace et al. 1992; Romare et al. 2005).

Zooplankton may be washed out of off-channel sources during flooding (Rossaro 1988; Thorp et al. 1994) providing a source of zooplankton to main river channels. Such exchanges likely enhance biological activity and increase food-web complexity in large river ecosystems (Junk et al. 1989; Brown and Coon 1994; Dewey and Jennings 1992). Increased zooplankton biomass and species diversity in main channels occurs as floodwaters recede, further suggesting washout from off-channel sources (Saunders and Lewis 1988a; Pace et al. 1992). Because hydrologic variables and habitat connectivity add complexity in these ecosystems, they are not well-understood. Previous work in large floodplain rivers has also focused on tropical ecosystems with less consideration of rivers in temperate regions.

Although off-channel habitats are recognized as being potentially important sources of riverine zooplankton (Pace et al. 1992; Casper and Thorp 2007), they are often ignored. Most studies of large river ecosystems have examined seasonal zooplankton composition and distribution in only the main river channel (Thorp et al. 1994; Basu and Pick 1995). However, seasonal connectivity of habitats and floodplain dynamics within river-floodplain ecosystems may play an important role in understanding riverine zooplankton dynamics. The objectives of this study were to (1) determine whether zooplankton assemblages differ seasonally among three river-floodplain habitats, (2) examine how flooding affects the spatial and temporal distribution of riverine zooplankton, and (3) quantify zooplankton fluxes between main and off-channel habitats.

Study sites

Data were collected from three backwater lakes, four main-channel sites, and two side-channel sites during 2 yr (1997 and 1998) along a 32-km stretch of the Alton Pool of the Illinois River (Fig. 1). Long Lake (Jersey County, Illinois), Swan Lake (Calhoun County, Illinois), and Chickahominy Lake (Calhoun County, Illinois) were each sampled at three stations. Chickahominy Lake and Long Lake were isolated from the main river channel except during the spring high water. Backwater sites had greater chlorophyll *a* concentrations ($110.9 \pm 10.6 \text{ mg L}^{-1}$ vs. $29.4 \pm 2.0 \text{ mg L}^{-1}$), lower nitrogen concentrations ($2848.6 \pm 149.6 \text{ mg L}^{-1}$ vs. $3693.3 \pm 310.4 \text{ mg L}^{-1}$) and similar phosphorous concentrations ($1092.0 \pm 98.4 \text{ mg L}^{-1}$ vs. $811.1 \pm 50.0 \text{ mg L}^{-1}$) compared to the main and side-channel sites (D. H. Wahl unpubl.). At times of inundation, three additional stations were sampled at the only point of connection (no other overland flow occurred) between the two habitats (stage height of 4.9 m for Chickahominy Lake

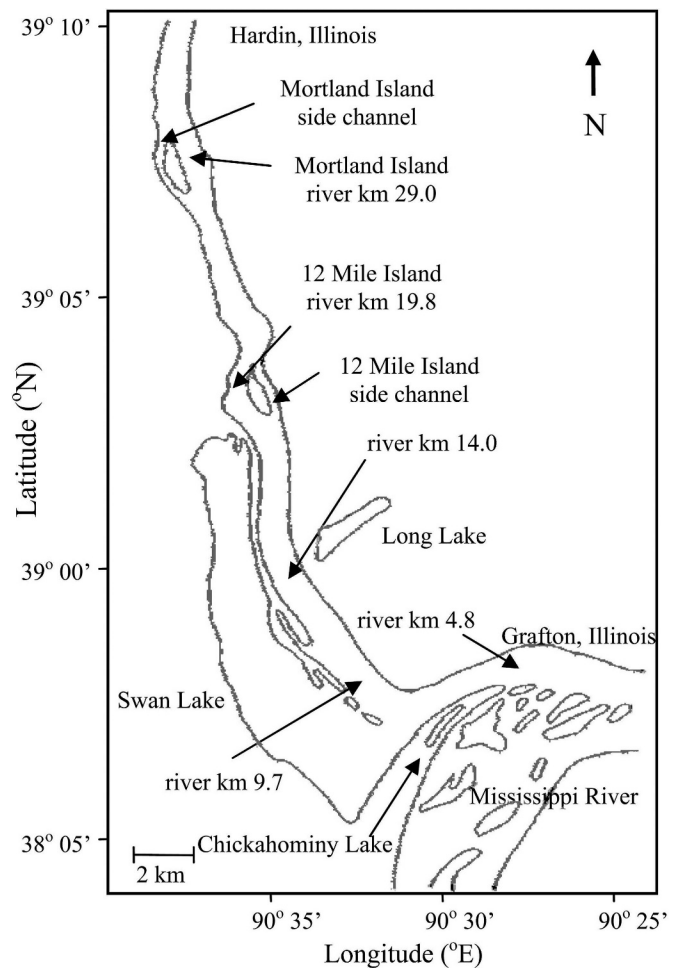


Fig. 1. Map of the three habitats sampled in the lower Illinois River from March through September in 2 yr. Two habitat comparisons were conducted using paired sites. The first comparison was between three backwater lakes (Chickahominy Lake, Swan Lake, and Long Lake) and three main-channel sites (river km 4.8, 14.0, and 19.8). The second was between two side channels (12 Mile Island and Mortland Island) and two main-channel sites (river km 19.8 and 29.0). Sampling was conducted at three stations in each of the backwater lakes and two stations in each of the side-channel and main-channel sites.

and 4.8 m for Long Lake; Fig. 2). Swan Lake was connected to the main channel throughout the year, but the three stations along the point of habitat connection were sampled only when a measurable flow was detected.

Three main-channel sites were chosen adjacent to the backwater lakes. Main-channel sites used were shifted slightly downstream in the second year (i.e., river km 19.8, 14.0, and 4.8 were used in the first year whereas river km 14.0, 9.7, and 4.8 were used in the second) since side-channel habitats were not analyzed in that year (see below). Two stations were sampled per site. Two side-channel sites were located at 12 Mile Island (river km 19.8) and Mortland Island (river km 29.0). Two stations were sampled at each site; one at the side-channel origin and a second just above the confluence with the main river channel. Main-channel sites were sampled adjacent to these

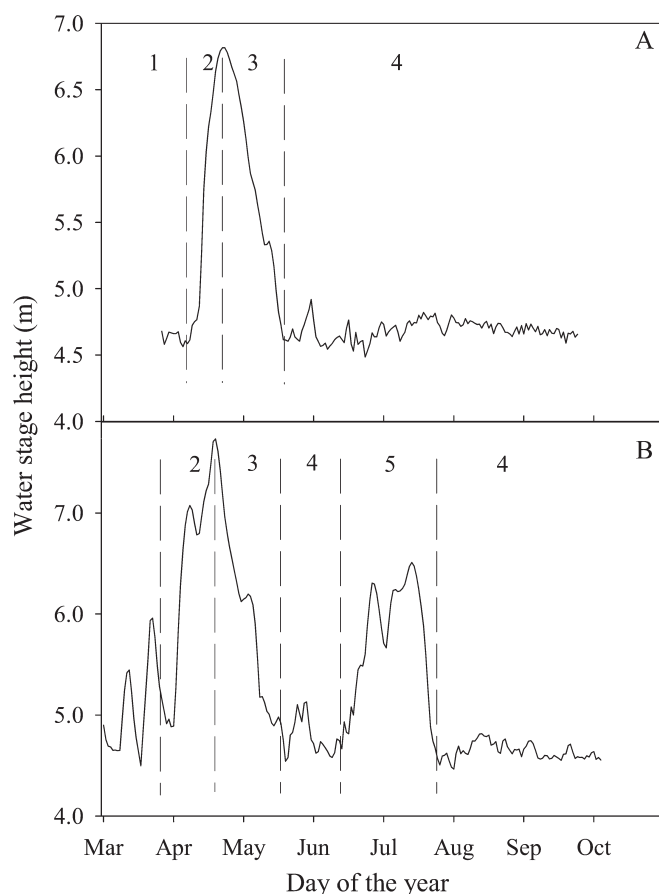


Fig. 2. Water-stage height data for the lower Illinois River from March through September (A) 1997 and (B) 1998. The seasonal flood was broken down into four stages including (1) pre-flood, (2) rising-water, (3) falling-water, and (4) post-flood periods (secondary peak (5) in 1998 was not included in the analysis). Each of the stages was divided according to hydrograph data except the falling-water phase that ended when connection between the backwater and main-channel habitats ceased.

side-channel sites. Side-channel sampling was eliminated in the second year when the data from the first year clearly showed that main-channel and side-channel habitats were similar (*see Results below*).

Methods

Zooplankton samples were collected from each site every other week from March through September in order to encompass the growing season of each year. One sample was taken at each of the stations and these samples were averaged to generate mean values for each respective site. Samples were obtained using a peristaltic pump, filtering the outflow (30 liters) through a 64- μm mesh net commonly used to sample zooplankton populations (Saunders and Lewis 1988a; Basu and Pick 1996). Though this mesh size can underestimate rotifer densities, this was a systematic bias that applies across all habitats sampled and allows comparison to previous studies. By raising and lowering the intake tube at a constant rate, vertically integrated samples were collected. Samples were immediately preserved in Lugol's solution and returned to the laboratory where the zooplankton were identified to the taxonomic level outlined in Table 1. Data from different taxa were combined for some analyses; total zooplankton included all rotifer and crustacean taxa; copepods included cyclopoids, calanoids, harpacticoids, and nauplii; and cladocerans included *Daphnia*, *Bosmina*, *Diaphanosma*, *Moina*, *Leptodora*, and *Chydorus*. Zooplankton taxa with few (<100) individuals were counted entirely. Taxa with large numbers of individuals (>100) were counted by taking 1-milliliter sub-samples until 100 individuals were counted (Thorpe et al. 1994; Basu and Pick 1996).

For selected taxa including *Bosmina*, *Daphnia*, *Daphnia lumholtzi*, *Moina*, and rotifers, egg counts were conducted. Because copepods lose eggs during sampling, accurate counts could not be obtained; instead, the number of fertile individuals was noted. Using egg and zooplankton counts

Table 1. Seasonal mean densities (No. $\text{L}^{-1} \pm \text{SE}$) of most common zooplankton taxa in the different habitats of the Illinois River during March through September in 2 yr. Total sample size is indicated in parentheses by each habitat and is comprised of a combination of each site for each sampling date.

Taxa	Mean density (No. L^{-1})				
	1997		Side channel (n=24)	1998	
	Backwater lake (n=34)	Main channel (n=39)		Backwater lake (n=30)	Main channel (n=30)
<i>Bosmina</i>	4.12(± 1.71)	6.44(± 1.90)	6.92(± 2.35)	3.87(± 2.51)	2.83(± 0.96)
<i>Chydorus</i>	0.12(± 0.05)	0.10(± 0.02)	0.12(± 0.04)	0.07(± 0.02)	0.14(± 0.06)
<i>Daphnia</i>	3.82(± 0.85)	3.28(± 0.76)	2.73(± 1.11)	0.35(± 0.15)	0.46(± 0.11)
<i>Daphnia lumholtzi</i>	0.98(± 0.61)	0.19(± 0.04)	0.31(± 0.15)	0.85(± 0.50)	0.04(± 0.02)
<i>Diaphanosoma</i>	0.07(± 0.05)	0.04(± 0.02)	0.07(± 0.02)	0.03(± 0.02)	0.01(± 0.01)
<i>Leptodora</i>	0.01(± 0.00)	0.00(± 0.00)	0.01(± 0.00)	0.00(± 0.00)	0.00(± 0.00)
<i>Moina</i> spp.	13.32(± 3.41)	13.11(± 3.44)	16.00(± 5.70)	0.04(± 0.02)	0.00(± 0.00)
Calanoids	3.59(± 1.22)	0.74(± 0.13)	0.47(± 0.07)	0.34(± 0.21)	0.20(± 0.06)
Cyclopoids	98.92(± 17.16)	34.04(± 3.42)	37.74(± 5.77)	24.94(± 5.92)	12.65(± 1.93)
Harpacticoids	0.46(± 0.11)	0.26(± 0.07)	0.69(± 0.68)	0.04(± 0.03)	0.03(± 0.02)
Nauplii	96.59(± 15.34)	30.80(± 2.84)	28.83(± 3.49)	34.92(± 14.42)	22.13(± 4.29)
Rotifers	83.21(± 20.90)	122.92(± 32.85)	112.63(± 39.82)	18.95(± 8.75)	19.58(± 7.00)
Ostracods	0.07(± 0.03)	0.06(± 0.02)	0.07(± 0.06)	0.02(± 0.01)	0.00(± 0.00)

with temperature data, calculations were made to determine intrinsic growth (r), birth (b), and death (d) rates for both the main-channel and backwater lake habitats. Intrinsic growth rates were calculated using the equation

$$r = (\ln N_{t_0} - \ln N_{t_1}) (t_0 - t_1)^{-1} \quad (1)$$

where $t_0 - t_1$ represents the number of days between two sampling dates and N_{t_0} and N_{t_1} represent the number of organisms captured on the respective sampling dates under the assumptions of the exponential growth equation (Paloheimo 1974). Birth rates were calculated using the equation

$$b = \ln(1 + E) D^{-1} \quad (\text{Edmondson 1968}) \quad (2)$$

where E = the number of eggs per animal and D = egg development time and is calculated using the equation

$$\ln D = \ln a + b \ln T + c(\ln T)^2 \quad (3)$$

where a , b , and c are taxon-specific constants and T represents temperature (Bottrell et al. 1976). Death rates were calculated as the difference between the birth rate and intrinsic growth rate.

Concurrent with zooplankton collections, various chemical (surface-water samples were collected for total phosphorus, total nitrogen, and chlorophyll a [Chl a]) and physical measurements (secchi depth, temperature, current velocity, depth, and water-stage height) were taken to characterize the habitats. Velocity was measured at 0.5 m below the surface using a Flo-Mate 2000 portable flowmeter (Marsh McBirney). Water stage and discharge data were obtained from the United States Army Corps of Engineers, St. Louis office.

During periods of measurable flow, connection period (duration of connection), water-depth transects, and velocity measurements were taken at each connection site weekly. These data were used to determine discharge rates, as well as flux rates (calculated as zooplankton density at the connection per volume of water moving through the connection as a function of time) of zooplankton between habitats. The number of organisms entering the main channel per second was determined for each site by date and averaged over connection period to calculate the number of organisms passing into the main channel from each backwater lake. The number of organisms passing per second for each main-channel site was also determined for each date and averaged during the time of connection. The connection input and main-channel zooplankton data were used to estimate the total number of backwater lakes having similar zooplankton discharge that would be needed to account for observed densities in the main channel. The calculated intrinsic growth rate data was used to determine how far a population of zooplankton would have to travel to reach the densities observed in the main channel through population growth alone. To represent an instantaneous measure of the number of organisms (N) in a unit area, the time factor (seconds) was dropped from previous calculations. Assuming that the riverine zooplankton assemblage was determined solely by inputs from off-channel sources

and no death, the number of days (D) required to achieve N was calculated by dividing N by the population growth rate (r). Velocity data collected from each main-channel location was then converted to meters day⁻¹ and multiplied by D to calculate the distance zooplankton would have traveled to reach a sample location.

Because sample sites were not chosen randomly and were sampled through time, split-plot repeated-measures analysis of variance (RM ANOVA) was used to characterize physical differences and to compare zooplankton distribution among habitats through time (Maceina et al. 1994). The main plot variable was habitat type (main channel, side channel, or backwater) with site (Swan, Long, Chickahominy, Three Mile, or Mortland) being the replicate and date being the subplot. The habitat \times site interaction was set as the error term for all split-plot analyses that evaluated differences across habitats. Analyses that evaluated date or habitat \times date interactions employed the full model error term. To conform to assumptions of normality, density data were log-transformed. To further assess the effects of flood events, data were divided into four groups: pre-flood (sample dates prior to initial water-level increase), rising water (increasing water levels), falling water (decreasing water levels), and post-flood (sample dates occurring after water levels reached pre-flood conditions). Each time period was determined from hydrograph readings (Fig. 2). Samples taken on dates during a second peak occurring in the second year were not used in the flood-stage analysis. One-way ANOVAs were used to compare among these flood stages. All analyses were conducted using general linear model procedures (SAS Institute 1991).

Results

Current velocity in the main channel ranged from 0.15 m s⁻¹ to 1.11 m s⁻¹ in the first year and from 0.15 m s⁻¹ to 1.20 m s⁻¹ in the second year. Current velocity was highest in early spring then declined in both years (Fig. 3) and did not differ between main and side-channel habitats (split-plot RM ANOVA, $F_{1,3} = 27.38$, $p = 0.12$). Water temperatures in both years showed a similar pattern being coolest early in the year and peaking in June (first year) or July (second year). Temperatures were warmer in the backwater lakes than in the main channel (Fig. 3; split-plot RM ANOVA, $F_{1,2} = 44.45$, $p = 0.02$). However, temperature did not differ among sites within the main-channel, side-channel, or backwater habitats ($p > 0.20$). Secchi depths varied greatly across years and season (Fig. 3) showing a significant three-way interaction among year, season, and habitat (split-plot RM ANOVA, $F_{6,66} = 2.09$, $p = 0.06$). Within the backwater lakes, secchi depth was higher in Long Lake than in Swan Lake ($F_{2,27} = 4.31$, $p = 0.024$; Tukey's honestly significantly difference [HSD] $p < 0.05$). Chickahominy Lake was intermediate and did not differ from either of the other two.

Habitat comparisons—Total zooplankton densities in the backwater lakes and main-channel habitats appeared similar throughout much of the year (Fig. 4). In fact, total zooplankton densities did not differ between the backwater

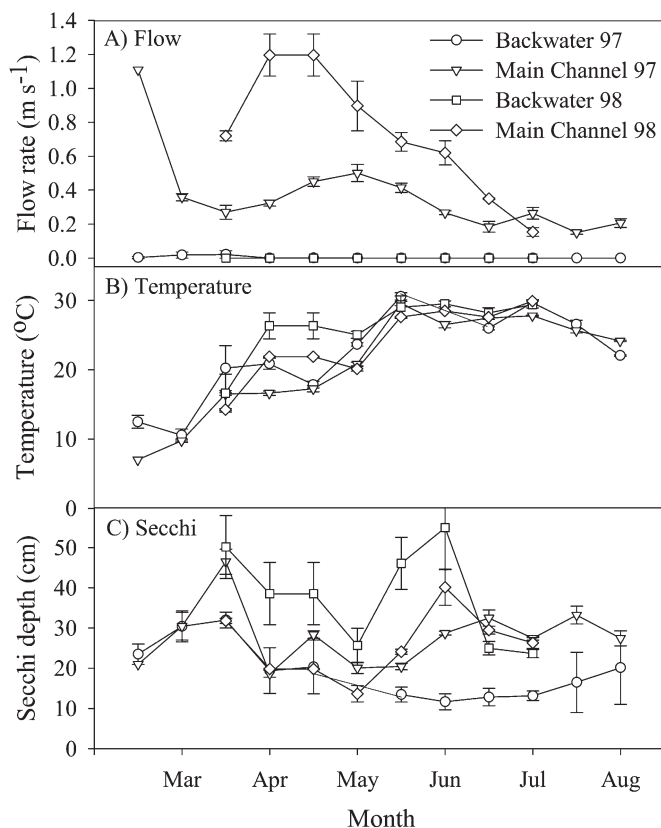


Fig. 3. (A) Mean (\pm SE) velocity (m s^{-1}), (B) temperature ($^{\circ}\text{C}$), and (C) secchi depth (cm) measured in backwater, main-channel, and side-channel habitats on the lower Illinois River from March through September in 2 yr.

lake and main-channel habitats (split-plot RM ANOVA, $F_{1,2} = 0.50$, $p = 0.55$) nor was there a significant interaction between date and habitat (split-plot RM ANOVA, $F_{11,67} = 1.22$, $p = 0.29$). Zooplankton densities were lower in the second year than in the first year (split-plot RM ANOVA, $F_{1,67} = 154.48$, $p < 0.0001$). In addition, the pattern of abundance in both habitats varied between years with a secondary peak in early June of the first year (Fig. 4) causing a significant interaction among year, date, and habitat (split-plot RM ANOVA, $F_{8,67} = 3.76$, $p = 0.0011$).

In contrast, the pattern of abundance for individual taxa differed between habitats (Fig. 4), and was consistent between years (Fig. 4). Whereas peak zooplankton densities were primarily due to rotifers in the riverine habitats, crustaceans were numerically most important in the backwater lake habitat (Table 1). The crustacean zooplankton assemblage in both habitats was dominated by copepods, primarily cyclopoids and nauplii (Fig. 4). Cyclopoids in backwaters reached peak densities during May through July in the first year, unlike riverine cyclopoids, that remained at relatively low levels throughout the year. In the second year, backwater cyclopoids peaked briefly, in May (Fig. 4), with a smaller peak in the main channel in late June and early July. Differences between years and habitats resulted in a significant interaction among year, date, and habitat (split-plot RM

ANOVA, $F_{10,79} = 3.53$, $p = 0.0007$). Densities of nauplii were greater in backwater lakes than riverine habitats in the first year. Nauplii peaked twice, once in May and again in July in backwaters, whereas no peak was observed in the main channel in the first year (Fig. 4). In the second year, densities peaked early in the season and then declined to low levels (Fig. 4). This pattern produced a significant interaction among year, date, and habitat (split-plot RM ANOVA, $F_{10,79} = 2.55$, $p = 0.01$). Densities of other copepods, including calanoids and harpacticoids, were very low and did not differ between habitats ($p > 0.09$).

For rotifers, a significant interaction between habitat and date occurred (split-plot RM ANOVA, $F_{13,79} = 2.63$, $p = 0.004$). Main-channel rotifer densities were much greater during the month of May in both years (Fig. 4). Rotifer densities were also higher in the first year than in the second year (split-plot RM ANOVA, $F_{1,79} = 123.46$, $p < 0.0001$).

Cladocerans in backwater lakes were observed slightly prior to riverine cladocerans (Fig. 4). Peak densities occurred earlier in the main channel and peaked at higher levels than in backwater lakes in the first year. In the second year, the rise in cladocerans in backwater lakes and main channels occurred simultaneously, although peak densities occurred earlier in backwater lakes than in the main channel (Fig. 4). This pattern produced a significant interaction between date, habitat, and year (split-plot RM ANOVA, $F_{10,79} = 2.08$, $p = 0.04$).

In contrast to differences observed between backwater lakes and main-channel habitats, total zooplankton densities did not differ between the two riverine habitats (split-plot RM ANOVA, $F_{1,1} = 0.99$, $p = 0.50$). In fact, there were no differences between the main and side-channel habitats in any of the major taxonomic groups examined (all $p > 0.05$).

Flood stage and zooplankton composition—Total zooplankton densities in the main channel were significantly greater during the post-flood than during the pre-flood and rising-water stages, but were not higher than during the falling-water stage (one-way ANOVA, $F_{3,10} = 26.89$, $p < 0.0001$; Tukey's HSD $p < 0.05$). While rotifers contributed strongly to the zooplankton assemblage in the main channel until the post-flood stage, they reached maximum density in the falling-water phase ($F_{3,10} = 41.55$, $p < 0.0001$; Tukey's HSD $p < 0.05$). In contrast, cladoceran densities increased until peaking in the post-flood stage ($F_{3,10} = 190.14$, $p < 0.0001$; Tukey's HSD $p < 0.05$). *Bosmina* ($F_{3,10} = 175.13$, $p < 0.0001$) and *Daphnia* ($F_{3,10} = 69.18$, $p < 0.0001$) followed this same pattern (Tukey's HSD $p < 0.05$). Copepod densities increased until the peak flooding period and then declined ($F_{4,9} = 15.02$, $p = 0.0005$; Tukey's HSD $p < 0.05$). Nauplii ($F_{3,10} = 33.53$, $p < 0.0001$) peaked in both the post-flood stage and the rising-water stage, whereas cyclopoids ($F_{3,10} = 29.95$, $p < 0.0001$) peaked during the post-flood stage (Tukey's HSD $p < 0.05$).

Total zooplankton densities in backwater lakes after flooding were significantly higher than densities were before flooding ($F_{3,11} = 8.17$, $p = 0.004$). Cladoceran densities were low before flooding, increasing and peaking

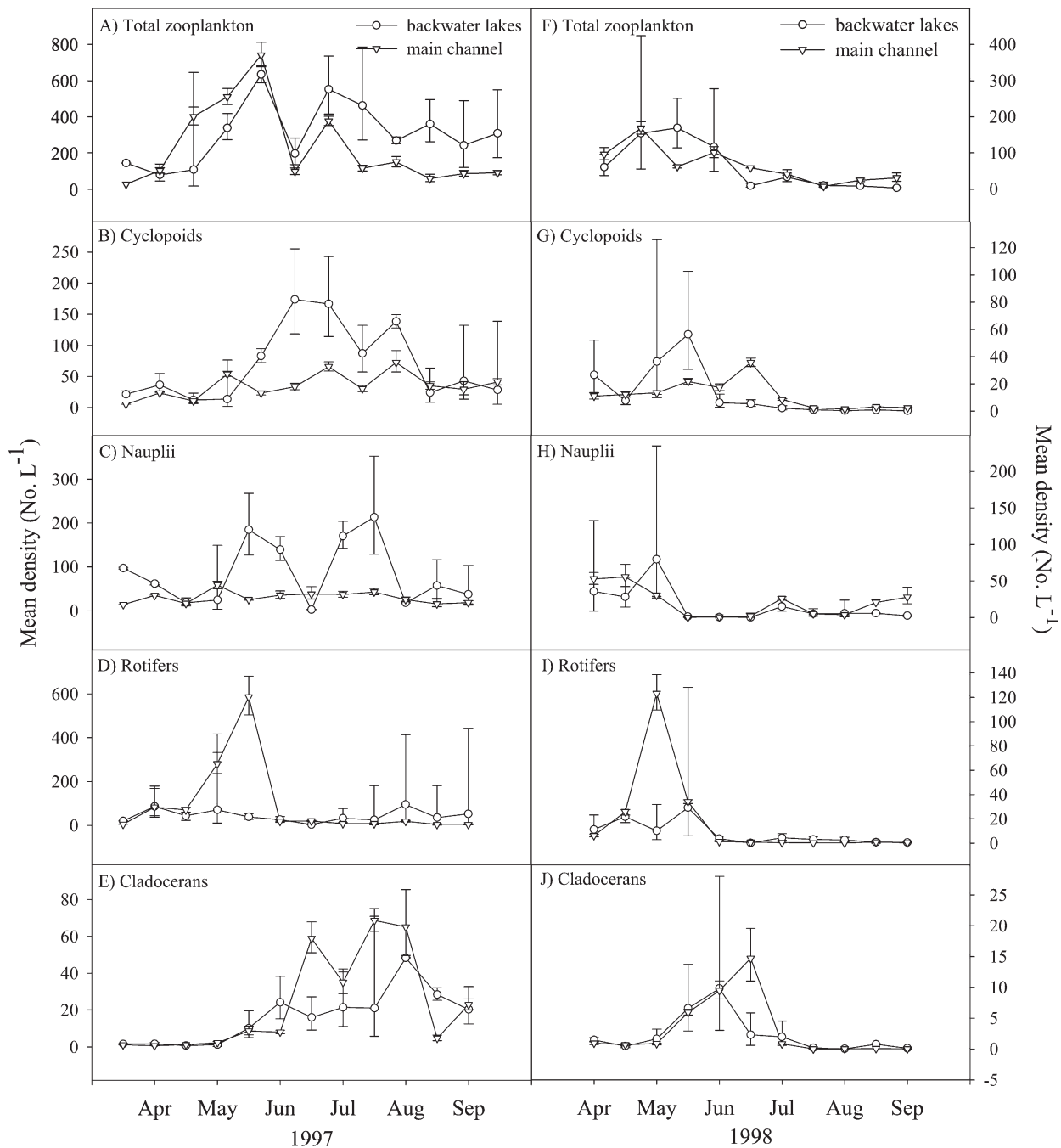


Fig. 4. (A, F) Mean (\pm SE) total zooplankton, (B, G) cyclopoid, (C, H) nauplii, (D, I) rotifer, and (E, J) cladoceran densities (No. L⁻¹) collected in backwater and main-channel sites in the lower Illinois River from March through September 1997 (panels A–E) and 1998 (panels F–J).

during the falling-water and post-flood stages ($F_{3,11} = 12.75$, $p = 0.0007$; Tukey's HSD $p < 0.05$). Differences in cladoceran taxa between stages were primarily due to *Bosmina* ($F_{3,11} = 8.45$, $p = 0.0034$) and *Daphnia* ($F_{3,11} = 16.14$, $p = 0.0002$) both of which peaked during the falling-water and post-flood stages (Tukey's HSD $p < 0.05$). The only copepod taxon showing differences between flood stages was cyclopoids, which were highest during the falling-water and post-flooding stages ($F_{3,11} = 7.76$, $p = 0.0046$; Tukey's HSD $p < 0.05$).

Reproduction, birth, and death rates—All zooplankton taxa examined carried eggs in all habitats, but the proportion of individuals was generally low and did not differ among habitats (Table 2; ANOVA, $p > 0.05$). Although riverine zooplankton appeared to carry fewer eggs per individual than zooplankton from the other two habitats (Table 2), a significant difference occurred only for *Bosmina*, which carried more eggs in the connections than in either the riverine or backwater lake habitats (split-plot RM ANOVA, $F_{3,5} = 47.01$, $p = 0.0004$; Tukey's HSD $p < 0.05$).

Table 2. Percentage (\pm SE) of zooplankton taxa which carried eggs and the mean number of eggs (\pm SE) carried per individual in each of the habitat types sampled in the Illinois River during March through September.

Taxa	Backwater lakes		Main channel		Side channels		Connections	
	Carrying eggs (%)	Mean No. eggs (ind. ⁻¹)	Carrying eggs (%)	Mean No. eggs (ind. ⁻¹)	Carrying eggs (%)	Mean No. eggs (ind. ⁻¹)	Carrying eggs (%)	Mean No. eggs (ind. ⁻¹)
Cladocera	5.8(\pm 1.1)	4.1(\pm 0.8)	8.2(\pm 0.8)	3.8(\pm 0.5)	4.6(\pm 0.3)	10.0(\pm 0.3)	7.1(\pm 1.5)	5.2(\pm 0.7)
<i>Bosmina</i>	13.5(\pm 3.3)	3.2(\pm 0.2)	17.6(\pm 1.5)	3.0(\pm 0.1)	18.7(\pm 2.4)	3.5(\pm 0.2)	13.3(\pm 2.6)	5.9(\pm 1.0)
<i>Daphnia</i>	2.7(\pm 0.6)	6.2(\pm 0.7)	4.5(\pm 0.7)	4.7(\pm 0.4)	8.4(\pm 1.2)	5.2(\pm 0.4)	2.8(\pm 1.0)	6.3(\pm 1.2)
<i>Daphnia lumholtzi</i>	5.2(\pm 2.8)	7.8(\pm 1.1)	6.8(\pm 2.1)	6.4(\pm 1.0)	8.0(\pm 2.7)	4.4(\pm 0.6)	0.0(\pm 0.0)	0.0(\pm 0.0)
<i>Moina</i>	1.6(\pm 0.5)	4.1(\pm 0.4)	2.6(\pm 0.5)	3.7(\pm 0.2)	3.8(\pm 1.7)	4.5(\pm 0.3)	0.0(\pm 0.0)	0.0(\pm 0.0)
Rotifers	2.9(\pm 0.6)	1.6(\pm 0.1)	4.1(\pm 1.1)	1.3(\pm 0.1)	1.5(\pm 0.5)	1.1(\pm 0.0)	0.3(\pm 0.2)	2.5(\pm 0.7)

For selected taxa, population growth, birth, and death rates were compared between the backwater lakes and main-channel sites (Fig. 5). Because patterns among main-channel sites were very similar, these data were pooled. Population growth patterns varied significantly for all taxa both within backwater lakes and between these backwater lakes and the main-channel sites. *Bosmina* birth rates in the main channel and Swan Lake dramatically increased in June. Birth and population growth rates of *Daphnia* in the main channel remained low until early July, when birth rates increased. *Daphnia* population growth rates in backwater lakes exceeded birth rates twice (one mid-season

and one late in the season). Excluding Chickahominy Lake, *Moina* did not appear until late in the season and their population growth rates exceeded birth rates only in late June. Rotifer population growth rates in the backwater lake habitat remained near zero with a small positive increase observed around June. A similar pattern was seen in the main channel with the only positive growth rate occurring at the beginning of August.

Habitat connections—Total zooplankton densities flowing from the connection points were similar to those in the main channel and backwater lakes (Table 3; split-plot RM

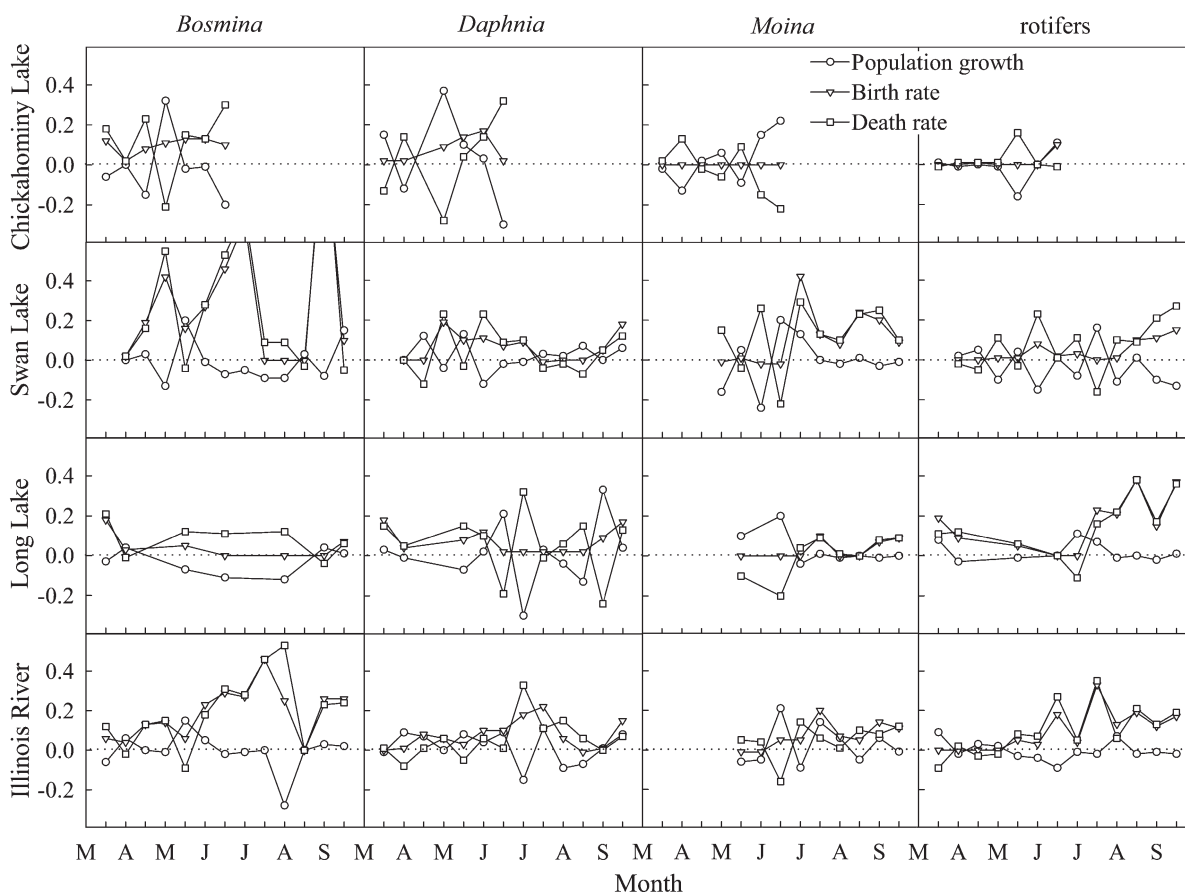


Fig. 5. Population growth, birth, and death rates for *Bosmina*, *Daphnia*, *Moina*, and rotifers in three backwater lakes and the main channel of the lower Illinois River in March through September.

Table 3. Mean (\pm SE) zooplankton density (No. L⁻¹) during March through May when a measurable flow existed between the backwater lakes and main channel of the Illinois River. Habitats were compared using a split-plot RM ANOVA and Tukey's HSD. Within a row, values with the same letter are not significantly different. Taxa in boldface show a statistically discernible difference across habitat types.

	Zooplankton density (No. L ⁻¹)		
	Connections (n=10)	Backwater lakes (n=16)	Main channel (n=15)
Total zooplankton	192.51(\pm 57.10) ^a	263.71(\pm 43.55) ^a	356.52(\pm 65.33) ^a
Cladocerans	4.34(\pm 1.51) ^a	9.25(\pm 3.90) ^a	2.81(\pm 0.82) ^a
<i>Bosmina</i> spp.	1.71(\pm 0.65) ^a	5.71(\pm 3.11) ^a	1.53(\pm 0.66) ^a
<i>Chydorus</i> spp.	0.62(\pm 0.26) ^a	0.24(\pm 0.09) ^a	0.18(\pm 0.03) ^a
<i>Daphnia</i> spp.	1.99(\pm 0.68) ^a	2.75(\pm 0.98) ^a	0.91(\pm 0.23) ^a
<i>Diaphanosoma</i> spp.	0.01(\pm 0.01) ^a	0.00(\pm 0.00) ^a	0.01(\pm 0.01) ^a
<i>Moina</i> spp.	0.01(\pm 0.01) ^a	0.54(\pm 0.33) ^a	0.19(\pm 0.07) ^a
Copepods	135.14(\pm40.83)^a	177.04(\pm33.94)^a	55.43(\pm9.88)^b
calanoids	1.70(\pm1.06)^a	0.95(\pm0.23)^{ab}	0.19(\pm0.04)^b
cyclopoids	58.67(\pm 19.91) ^a	71.67(\pm 19.65) ^a	23.02(\pm 4.83) ^a
harpacticoids	0.07(\pm 0.04) ^a	0.58(\pm 0.19) ^a	0.38(\pm 0.12) ^a
nauplii	74.69(\pm23.96)^a	103.80(\pm21.09)^a	31.59(\pm5.19)^b
Ostracods	0.92(\pm 0.45) ^a	0.13(\pm 0.07) ^a	0.02(\pm 0.01) ^a
Rotifers	52.11(\pm25.94)^b	77.29(\pm26.29)^{ab}	298.25(\pm63.54)^a

ANOVA, $F_{2,4} = 0.61$, $p = 0.59$). Both copepod ($F_{2,4} = 41.49$, $p = 0.002$) and copepod nauplii ($F_{2,4} = 18.82$, $p = 0.01$) densities in the connection points and backwater lakes were greater than in the main channel (Tukey's HSD $p < 0.05$). Calanoid densities in the connection points were greater than in the main channel ($F_{2,4} = 24.89$, $p = 0.006$; Tukey's HSD $p < 0.05$), backwater lake densities were intermediate, but not different from the main-channel sites.

Long Lake was connected to the main channel five of the six dates sampled and contributed the largest number of organisms ($\sim 850,000$ s⁻¹) to the main channel. Chickahominy Lake was connected during four sampling dates and also made a very large contribution ($\sim 286,000$ zooplankton s⁻¹). A measurable flow between Swan Lake and the main channel existed on only one date and made the smallest contribution ($\sim 55,000$ zooplankton s⁻¹). Although the number of organisms flowing out of the backwaters into the main channel was high, the estimated number of organisms in the main channel flowing past each of the backwaters was much higher ($>10^6$). Using the mean number of organisms added into the main channel from Chickahominy and Long lakes, we estimated that 369,780 backwater lakes were needed to achieve zooplankton numbers found in the main channel. In addition, we estimated the distance and number of days zooplankton input by the backwater lakes would need to travel to reach their observed densities using the previously estimated population growth rates. Population growth rates of *Bosmina* spp. were most commonly negative so that both distance and number of days traveled estimates were either near zero or negative. In contrast, when either *Daphnia* or rotifer population growth rates were positive, both the distance ($>10^{10}$ km) and number of days ($>10^9$) traveled were extremely high. These results clearly indicated that an unattainable number of backwater lakes were needed to explain the zooplankton density observed and that main-channel densities are the result of processes unrelated to transport from backwater lakes. As a result, we did not

estimate intrinsic growth rates or zooplankton transfer between the backwater lakes and the main channel in the second year of the study.

Discussion

Although advection and decreased residence times found within main river channels create a harsh environment apparently unfavorable to the survival of most zooplankton taxa (Rzoska 1978; Thorp et al. 1994), zooplankton are often abundant (van Dijk and van Zanten 1995; Bass et al. 1997; our study). Total zooplankton abundance in the Illinois River was temporally variable, but the system is highly eutrophic and peak zooplankton densities (~ 700 L⁻¹ in 1997, ~ 200 L⁻¹ in 1998) exceeded those found in other tropical and temperate rivers (<200 L⁻¹; Hoxmeier and DeVries 1997; Casper and Thorp 2007). In the first year, but not in the second, total zooplankton abundance in Illinois River backwater lakes also exceeded zooplankton densities found in most other riverine off-channel habitats (>200 L⁻¹; Bass et al. 1997; Hoxmeier and DeVries 1997). High zooplankton abundance in the Illinois River could be the result of several environmental factors, but is likely due to the relatively high primary productivity.

The temporal distribution of zooplankton taxa differed between main and off-channel habitats and this pattern differed between years. Zooplankton densities within the main channel in the first year exceeded densities in the backwater lakes until flood waters receded and flow rates decreased. However, in the second year the pattern of abundance through the season for total zooplankton was much more similar between habitat types. The composition of zooplankton taxa was similar between years. Riverine zooplankton assemblages are typically dominated numerically by rotifers and the backwater assemblage dominated by cyclopoids and nauplii (Ferrari et al. 1989; van Dijk and van Zanten 1995; Dettmers et al. 2001). Main-channel

zooplankton densities peaked in the late spring, with rotifers comprising almost this entire peak. Unlike the riverine habitats, no definitive peak in rotifer densities occurred in the backwater lake habitat and densities remained low throughout the season.

In contrast to rotifers, the pattern of abundance of copepods (primarily nauplii and cyclopoids) varied considerably between years, being highly variable over the season in the first year with no single peak being evident. In the second year, copepod abundance showed a single peak in late May and early June, followed by a decrease in abundance for the remainder of the season. Copepods in the backwater lakes achieved very high densities compared to the main channel for much of the season. The observed seasonal pattern was consistent with river (Saunders and Lewis 1988a,b; Pace et al. 1992) and reservoir (Dettmers and Stein 1992; Welker et al. 1994) studies. Copepod densities in the backwater lakes were much higher than in these previous studies, whereas main-channel densities tended to be greater than (Saunders and Lewis 1988a,b) or similar to other riverine systems (Popp et al. 1996; Moore and Cotner 1998).

Differences in zooplankton composition between the backwater lake and riverine habitats may be the result of variations in feeding or reproductive strategies. In contrast to lakes, riverine zooplankton assemblage structure seems to be dominated by rotifers (Shiel et al. 1982; Burger et al. 2002). Short generation times of small species may reduce effects caused by advective losses. Further, advection and high flow rates create turbid environments, which often contain high concentrations of filamentous and/or toxic algae (Pace et al. 1992), and small zooplankton species may feed more successfully in such environments (Gilbert 1990; Kirk and Gilbert 1990).

Comparable to other studies conducted in large river ecosystems (Nietzel et al. 1982; Saunders and Lewis 1988a), *Moina* and *Bosmina* were the most abundant whereas *Daphnia* were the least abundant cladoceran taxa. Cladocerans began to appear following the decline of rotifers. *Daphnia* and *Bosmina* were the first to increase, but *Moina* increased as these taxa declined and quickly became the dominant cladoceran taxon. Although they achieved similar densities between habitats, cladocerans in the main channel peaked later than those in the backwater lakes. Cladoceran densities did not begin to increase until after floodwaters receded and main-channel flow rates decreased, suggesting discharge regulates their seasonal dynamics. The Illinois River is an extremely turbid, low-gradient, highly eutrophic river. In contrast to the peak flow rates in the Ohio (1.70 m s^{-1} ; Thorp et al. 1994) and Mississippi (1.80 m s^{-1}) rivers, maximum flow rates of the Illinois River reached only 1.28 m s^{-1} . Whereas high residence times and temperatures throughout the summer may have permitted the accumulation of *Bosmina* and *Moina*, the turbid environment may also have reduced predation pressure by altering the feeding efficiency of fish (Zaret 1979). Unlike other cladocerans (i.e., *Daphnia*), *Moina* have high turbidity tolerance and feeding rate is not suppressed by suspended sediments (Hart 1988). In the Illinois River, a combination of high water-residence times, feeding efficien-

cy, and low predation risk likely play an important role in structuring the riverine cladoceran assemblage.

Although it is clear that zooplankton can withstand the harsh physical conditions within riverine ecosystems, reproduction within these environments has not been previously well-described. The origin of riverine zooplankton is among the major debates in large river ecology (Hynes 1970; Saunders and Lewis 1988a; Thorp et al. 1994). Many believe zooplankton can reproduce in riverine areas during periods of low-flow conditions (Talling and Rzoska 1967; Pace et al. 1992), and may rarely reproduce at velocities $>0.4 \text{ m s}^{-1}$ (Rzoska 1978). Others contend that seasonal flooding flushes zooplankton out of off-channel habitats, which provide high residence times allowing for increased growth and reproduction, and import them into the main channel (Thorp et al. 1994). Although it has been suggested that rising water levels flush zooplankton out of off-channel habitats into the main channel, possible dilution effects have also been proposed (Saunders and Lewis 1988a,b; Thorp et al. 1994). Others believe that riverine zooplankton assemblages are the result of resting eggs released from river-bottom sediments during flood events and hatch as conditions become favorable (Moghraby 1977).

We found the timing of peak zooplankton densities were related to the seasonal flood-pulse (Saunders and Lewis 1988a; Pace et al. 1992). Densities for many taxa were highest just after the peak flooding period, providing evidence for a flushing effect. Further, if dilution effects were a factor in main-channel density increases, then densities should be lowest during rising water and highest in the post-flood period. Instead, main-channel rotifers achieved their maximum densities at the rising and falling-water phases, suggesting possible washout from the backwater lake habitats (Ferrari et al. 1989; Thorp et al. 1994). Evidence of a flushing effect also occurred with cyclopoids and cladocerans with densities at their highest during the falling-water and post-flood events for both groups. Peaks of taxa after flooding could be due to a concentrating effect caused by receding water levels.

Strong evidence of flushing from the backwater lake habitat was observed when examining connections between the riverine and backwater habitats. We found that up to 10^6 zooplankton s^{-1} were exported into the main channel from one lake alone. Copepods, nauplii, and rotifers were exported at the highest numbers from each of the three lakes. However, riverine cladoceran densities peaked several months after habitat connections between the main channel and side channels, suggesting that these were not the direct result of exchanges between the two habitats. In comparison to the total volume of the river, only small volumes of water and numbers of zooplankton flowed out of the backwaters into the main channel. Like many large rivers, the Illinois River has a tremendous number of adjacent backwater and oxbow lakes (~ 200) that collectively could contribute to the zooplankton assemblage. However, our estimates suggest that these inputs alone are not sufficient to support the large number of zooplankton found within the Illinois River. Further, the distance and time the zooplankton assemblage must travel to attain such high numbers is unrealistic.

In addition to backwater lakes, side channels with high residence times may permit zooplankton population growth and provide the main channel with continuous inoculums of animals (Saunders and Lewis 1988b; Thorp et al. 1994). If this were true, then either the density of zooplankton in side channels should be greater than in main channel or zooplankton density should increase between the side-channel origin and its confluence with the main channel. We found no difference in zooplankton densities either between the side and main-channel habitats or within the side channels. However, side channels in this study were short (~1 km), meandered very little, and were similar to the main channel with respect to flow rate. Such attributes likely prevented large changes from occurring in the zooplankton assemblage.

We found evidence of in situ reproduction of riverine zooplankton assemblages. The proportions of zooplankton carrying eggs in this study were consistent with those reported elsewhere (Saunders and Lewis 1988a,b). Of the taxa examined, *Bosmina* were found carrying eggs most often (~15%, average of 3 eggs individual⁻¹), suggesting that this taxon can reproduce in large rivers. Other taxa (*Daphnia*, *Daphnia lumholtzi*, *Moina*, and rotifers) also carried eggs in all three habitats. Both calanoid and cyclopoid copepods from the riverine habitats were occasionally found carrying egg sacs. Ephippia and resting eggs were found in some samples in contrast to other riverine studies where none were observed (Saunders and Lewis 1988a,b). To some extent, it appears that all of the taxa commonly found in the Illinois River can reproduce within the main-channel habitat.

Population growth and birth-rate data provide additional evidence of in situ reproduction and importation. Growth rates of main-channel populations were generally lower than birth rates throughout the season. The exception was often in late May, indicating zooplankton were hatching from resting eggs or being imported from off-channel habitats into the main channel as flood waters receded. This suggests that flooding may have cued a reproductive event. Flooding stirs sediments along the river channel and adjacent floodplain, releasing nutrients and possibly buried resting eggs. Although birth rates increased, population growth rates decreased by early June and remained near zero. This pattern was likely due to high predation rates by larval fish, which peaked during this time period (M. A. Nannini unpubl.). Thus, it appears that flooding causes importation from off-channel habitats and may cue a reproductive event within the main-channel habitat. Further, the main-channel assemblage can maintain itself through in situ reproduction. However a combination of physiologic death, river loss, and predation likely prevent population growth.

There has been no general consensus as to which factors most strongly regulate zooplankton assemblages in large river ecosystems. Although zooplankton may lack the ability to swim against currents (Rzoska 1978), they are abundant in the Illinois River and other large rivers throughout the world (Bass et al. 1997; Pace et al. 1992). Many researchers suggest that these organisms are imported from low-flow areas within the main-channel or off-

channel habitats (Shiel et al. 1982; Pace et al. 1992). We found that zooplankton densities increased after the inundation of backwater lakes and other off-channel habitats, suggesting that zooplankton are washed out of these areas and into the main channel (Rossaro 1988; Saunders and Lewis 1988b). Further, we demonstrated that flooding causes a substantial number of zooplankton to be exported from backwater lake habitats into the main channel. However, these inputs are not adequate to support the number of zooplankton found within the river.

Advection (Pace et al. 1991), turbidity (Threlkeld 1986; Hart 1987), and poor-quality food (Arruda et al. 1983; Pace 1984) may have negative effects on growth and reproduction of riverine zooplankton. Although off-channel habitats such as side channels and backwaters may provide a more favorable environment for zooplankton growth and reproduction (Saunders and Lewis 1988a,b; Pace et al. 1992), no previous studies examined the spatial and temporal distribution of riverine zooplankton across multiple habitats. By examining three habitats within the Illinois River ecosystem, our study shows that off-channel habitats provide the channel with an inoculum of zooplankton. However, other mechanisms (egg release, or in situ reproduction) are responsible for zooplankton abundances found throughout the year.

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