Zooplankton Assemblages in the Ohio River: Seasonal, Tributary, and Navigation Dam Effects

James H. Thorp, A. Ross Black, and Kim H. Haag

Large River Program, Biology Department, University of Louisville, Louisville, KY 40292, USA

and John D. Wehr

Louis Calder Center of Fordham University, P.O. Drawer K, Armonk, NY 10504, USA


Ohio River zooplankton were collected monthly or quarterly for 1 yr from littoral and pelagic (main channel) areas in three navigation pools (constricted and floodplain) with four intrapool locations (lower pool and above, below, and within major tributaries). Total densities were minimal (1.64/L) when discharge and turbidities peaked (December–April) but were relatively high otherwise (21.63/L). Seasonal rises in rotifer density preceded increases in cladocerans and copepods; rotifers were nearly twice as abundant as cladocerans and copepods. Diversity (species richness) was not correlated with temperature, velocity, or turbidity. Density was positively linked with temperature and negatively correlated with river velocity and turbidity. Diversities in littoral and pelagic areas were not different, but densities were higher nearshore (mostly copepods and cladocerans); rotifers were usually more common in the main channel. Neither proximity to low-head navigation dams nor channel morphology had detectable effects on zooplankton. Although total diversity and density were similar in tributaries and the main channel, rotifers were more abundant in tributaries, and the Ohio contained more cladocerans and copepods. Densities in the Ohio were greater below than above tributaries for rotifers and cladocerans but lower for copepods, primarily because of nauplii.

Le zooplancton de la rivière Ohio a fait l’objet de prélèvements mensuels ou trimestriels pendant 1 an dans des régions littorales et pélagiques (chanel principal) dans trois bassins de navigation (étanglement et plaines inondables) avec quatre emplacements à l’intérieur du bassin (bassin inférieur et au-dessus, en dessous et à l’intérieur des principaux tributaires). Les densités totales sont minimales (1,64/L) lorsque le débit et la turbidité sont au maximum (décembre à avril), mais relativement élevées dans les autres cas (21,63/L). Les augmentations saisonnières de la densité des rotifères précèdent les augmentations de la densité des cladocères et des copépodes. L’abondance des rotifères est près de deux fois plus élevée que celle des cladocères et des copépodes. Aucune corrélation n’a été observée entre la diversité (richesse des espèces) et la température, la vitesse ou la turbidité. On a observé une corrélation positive entre la densité et la température et une corrélation négative entre la densité et la vitesse du cours d’eau et sa turbidité. Aucune différence n’a été observée sur le plan de la diversité entre les régions littorales et pélagiques; cependant, les densités sont plus élevées près du rivage (pour l’essentiel, copépodes et cladocères). Les rotifères sont en général plus répandus dans le chenal principal. Ni la proximité des barrages de canalisation à faible hauteur de charge, ni la morphologie du chenal ne semblent avoir d’effet détectable sur le zooplancton. Si l’on a observé des valeurs similaires pour la densité et la diversité totale dans les tributaires et dans le chenal principal, les rotifères sont cependant plus abondants dans les tributaires, tandis que l’on retrouve davantage de cladocères et de copépodes dans la rivière Ohio. Les densités observées dans la rivière Ohio sont plus élevées en aval qu’en amont des tributaires pour les rotifères et les cladocères, mais plus faibles pour les copépodes, principalement à cause des larves de nauplii.

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Large rivers have not been examined in an ecosystem context nearly as often as lakes or headwater streams; consequently, they represent ecological “black boxes” from a functional perspective (Thorp 1992a). Indeed, only about 4% of all studies conducted on flowing waters have dealt with large (greater than sixth order) rivers (Hynes 1989), and much of this research has concerned the distribution and relative abundance of fish and unionid mussels. Scientific studies of riverine plankton, or "otamoplankton," at organismal, population, and community levels are particularly rare. Of the relatively few papers published on riverine zooplankton, most report spatial and temporal community patterns in relation to hydrodynamics (e.g., Rossaro 1988; Saunders and Lewis 1988a, 1988b; Ferrari et al. 1989; Pace et al. 1992), hydrographic gradients (e.g., De Ruyter van Steveninck et al. 1990), suspended inorganic sediment and organic matter concentrations (e.g., Moghraby 1977; Shiel 1979), seasonal water temperatures (e.g., Neitzel et al. 1982; Rossaro 1988), and/or phytoplankton abundances (e.g., Shiel 1985).
One focal area of process-oriented research in large tropical and temperate rivers has been an analysis of sources and fates of energy and nutrients. An early comprehensive view of energy flow was embodied in the river continuum concept (RCC) (Vannote et al. 1980; Minshall et al. 1983, 1985). The RCC stated that streams should be viewed as longitudinally interlocked systems in which ecosystem dynamics of downstream reaches are linked with processes occurring upstream. Biotic assemblages, such as the potamoplankton and riverine benthos, were thought to follow an orderly longitudinal shift in community composition primarily in response to upstream processes and changing stream morphology. Recent studies have concluded, however, that allochthonous organic matter derived from sources other than upstream processes (Junk et al. 1989) as well as autochthonous primary production and direct riparian inputs (Thorp and Delong 1994) are of crucial importance to large river food webs. In systems where extensive river–floodplain interactions occur, productivity of riparian vegetation and organic processing within floodplains may greatly modify longitudinal patterns of ecosystem processes predicted by the RCC (Junk et al. 1989). While it is increasingly recognized that large floodplain rivers do not conform to predictions of the RCC (Sedell et al. 1989), the applicability of this pivotal theory to large rivers with constricted channels is still debatable (Thorp and Delong 1994).

A major impediment to studying large rivers is that long, relatively pristine, and unregulated reaches of very large rivers have nearly vanished from developed nations and are rapidly disappearing from less-developed countries as a result of impoundment, channelization, and other regulatory processes undertaken for flood control, electrical power generation, water storage, navigation, and recreation (Benke 1990; Thorp 1992a). Effects of high-head dams on lotic ecosystems are relatively well known because of extensive research on reservoirs and the rivers flowing from them. Their influences depend partially on the dam's location along the river continuum and on factors such as the dam's height and water-release pattern (see discussion of serial discontinuity concept in Ward and Stanford 1983). In contrast, ecological effects of low-head navigation locks and dams, such as those on the Ohio and upper Mississippi rivers, are poorly known.

Some regulated rivers such as the Ohio are subdivided by lowhead dams into “pools.” Despite their name, pools bear little resemblance to lakes, have seasonally high current velocities, and are not equivalent to the pool–riffle sequence of shallow streams (for a comparative review of lake and river attributes, see Ryder and Pesendorfer 1989). Current velocities, depth, suspended sediment concentration, and substrates vary from upper to lower portions of pools (Thorp 1992a), with likely effects on zooplankton residing in channel and nearshore areas. Many pools within the Ohio receive potentially important organic and inorganic contributions from tributaries. The structure and function of potamoplankton communities within these pools are presumably modified to some degree by inputs of drifting animals and phytoplankton, particulate organic matter (POM) and dissolved organic matter (DOM), inorganic sediment, and local differences in water quality. The impacts of these factors probably vary seasonally and may be influenced by the relationship between the wetted channel and its catchment (e.g., whether the pool resides within a constricted or floodplain region).

As part of a broader study of the Ohio River ecosystem, we investigated seasonal dynamics of potamoplankton in three pools of the Ohio River: two entirely within a constricted reach and one mostly confined to a floodplain segment. Our principal objectives were to determine seasonally (a) whether potamoplankton assemblages in the deepwater channel are significantly different from those near the banks, (b) effects of dams (partially by identifying community patterns along a gradient from the upstream to the downstream dam), (c) influences of major tributaries on potamoplankton, and (d) whether plankton assemblages differ in constricted-channel and floodplain regions of the river.

Methods

Study Sites

Based on mean annual discharge, the Ohio River is the second largest river in the United States, surpassed only by the lower Mississippi (below its confluence with the Ohio at Cairo, Ill.). The average annual discharge of the Ohio at Louisville (which is 604 km from the river's mouth) is 3273 m³/s (115 500 ft³/s), with a historical (63 yr of data) daily range of 59–31 432 m³/s (McClain et al. 1993). It is divisible into (1) a region of constricted channel and relatively narrow floodplains (constricted by former glacial activity) which characterize approximately two thirds of the river (from Pittsburgh, Pa., to just below Louisville, Ky.) and (2) a floodplain region from just below Louisville to the confluence of the Ohio River and the smaller, middle Mississippi River (Ray 1974).

Data were collected from three pools along a 361-km stretch of the Ohio (Fig. 1): the 155-km-long Markland Pool (most upstream reach), the 119-km McAlpine Pool, and the 185-km Cannelton Pool (most downstream reach). The Markland and McAlpine pools have relatively constricted channels with narrow floodplains generally alternating between right and left banks. The upper portion of the Cannelton Pool (near Louisville) is also constricted, but the pool gradually becomes a floodplain river below its confluence with the Salt River and has wide floodplains near the Cannelton dam.

In addition to studying the Ohio River mainstem, we took samples from the largest tributary entering each pool: the greater Miami River in the Markland Pool, the Kentucky River in the McAlpine Pool, and the Salt River in the Cannelton Pool (Fig. 1). The Miami River flows generally south and historically has a mean annual discharge near its mouth of 93 m³/s. Both the Kentucky and Salt rivers flow northwest and have average annual discharges of 239 m³/s (31 yr) and 51 m³/s (6 yr), respectively.

Data on the species composition, diversity (species richness), and density of potamoplankton were collected monthly (McAlpine Pool) or quarterly (Cannelton and Markland pools) for 1 yr beginning in February 1991 from 24 sites (Fig. 1). Samples were taken from littoral (nearshore) and main channel (pelagic) areas in three navigation pools (constricted and floodplain) with four intrapool locations (lower pool and above, below, and within three major tributaries). The lower portion of each pool was sampled 8–16 km above the dam; samples in the upper portion of each pool were taken approximately 3 km above and below the Ohio's confluence with a major tributary. Zooplankton were also collected within the tributary itself at a distance of about 3 km
upstream from its mouth. This provided information on the influence of both dams and tributaries on Ohio River potamoplankton. Samples of potamoplankton, along with physical data, were collected in a midchannel area and near the bank (1 ± 0.5 m in depth) at all sample sites. This afforded information on potentially distinct populations of littoral and pelagic potamoplankton.

Sample Methods

On each sample date, five zooplankton samples were collected from each of eight sites/pool, producing a total of 800 zooplankton samples. We obtained quantitative samples from a depth of 0.25 m with multiple dips of a 5-L bucket; sample volume (10–20 L) was varied monthly depending on zooplankton relative abundance. After pouring the water sample through a 63-μm net, the trapped zooplankton were transferred to 60-mL bottles, killed using hot water, and preserved with a modified Lugol’s solution. Depending on the absolute abundance of zooplankton (especially nauplii), samples were either entirely identified or, more commonly, subsampled with a plankton splitter. A stereomicroscope and inverted compound microscope were used for sorting and identification.

Various physical and chemical measurements were taken at 0.5–1 m depth to characterize sample sites during each collection period. Current velocities in the channel and nearshore areas were measured with a Marsh McBirney velocity meter (model 201-D), and water temperatures were recorded with a YSI temperature probe. Water samples were retrieved for turbidity analysis from the 12 midchannel sites and measured in NTU units with a Hach turbidimeter (=nephelometer) standardized with known samples. Water samples for chemical analysis were filtered in line (Whatman GF/F) and frozen (−15°C) for later processing. Samples were analyzed for concentrations of soluble-reactive phosphorus (SRP) using the antimony–ascorbate–molybdate method (APHA 1985; Bran+Luebbe Analyzing Technologies 1986a). NH$_4^+$-N concentrations were measured using phenol–hypochlorite, and NO$_3^−$ concentrations were quantified (after reduction to NO$_2^−$ in a Cd–Cu column) via reaction with sulfanilamide–NED (APHA 1985; Bran+Luebbe Analyzing Technologies 1986b, 1987a). Soluble reactive Si (as SiO$_2$) was measured via the molybdosilicate method (APHA 1985; Bran+Luebbe Analyzing Technologies 1987b), and SO$_4^{2−}$ was analyzed using the BaCl$_2$ method (APHA 1985; Bran+Luebbe Analyzing Technologies 1989). Methods were modified for automated analysis and run on a Traacs 800 automated analyzer (Bran+Luebbe Inc.). Na was measured using flame atomic absorption spectrophotometry (Perkin-Elmer model 1100B).

Statistical Analyses

Most data analyses employed nonparametric statistical procedures because normality tests in the SAS program

Fig. 1. Schematic drawing of the study area in the Ohio River showing the position of the three dams, pools, and tributaries and the collection sites within each pool. The Ohio changes from a constricted-channel river to a floodplain river just downstream of the Salt River.
Results

Site Characteristics

Current velocities during the year-long study were greatest in the late winter and early spring and lowest in late summer. The maximum velocity we measured at 1 m depth in the

Ohio River was 1.7 m/s in midchannel. Velocities in the channel were always greater than those nearshore, which averaged <0.10 m/s but peaked at 0.55 m/s. Average monthly discharge patterns at the McAlpine dam for the period of our study and for the period of record (1928–92) are similar (Fig. 2), with high discharge in winter and early to midspring followed by a precipitous drop in late spring through mid-autumn. This two-phase pattern of discharge is reflected in the monthly patterns of suspended sediment concentration and water temperature (Fig. 3). Nearly all the winter–spring turbidity maximum is associated with resuspended sediments and is relatively uninfluenced by phytoplankton abundance (J.D. Wehr et al., unpublished data). River water chemistry also changed considerably during the year (Fig. 4). Most key variables varied inversely with discharge, especially SRP, NO₃, and SO₄. Maximum levels of these nutrients were observed during late summer and early autumn and declined in December (first substantial rise in discharge); however, SiO₂ concentrations decreased during summer low-flow periods and were greatest during the winter.

Seasonal Dynamics of Potamoplankton

Species richness, total zooplankton density, and densities of rotifers, cladocerans, adult copepods, and nauplii varied among months ($P < 0.01$ in all groups). Although species richness differed among months, consistent seasonal patterns were not evident. In contrast, patterns of zooplankton density corresponded well with the two-phase model of discharge...
TABLE 1. Densities (no./L) of the most common zooplankton from the McAlpine Pool of the Ohio River. Data were compiled from three main channel sites sampled monthly during 1991–92. \( n = 190 \) in Phase I and 277 in Phase II.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Phase I (Dec.–Apr.)</th>
<th>Phase II (May–Nov.)</th>
<th>Annual</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>Max.</td>
</tr>
<tr>
<td>Cladocerans</td>
<td>0.136</td>
<td>0.048</td>
<td>9.00</td>
</tr>
<tr>
<td>Bosmina</td>
<td>0.077</td>
<td>0.009</td>
<td>1.10</td>
</tr>
<tr>
<td>Ceriodaphnia</td>
<td>0.001</td>
<td>0.001</td>
<td>0.10</td>
</tr>
<tr>
<td>Daphnia</td>
<td>0.005</td>
<td>0.001</td>
<td>0.10</td>
</tr>
<tr>
<td>Rotifers</td>
<td>0.390</td>
<td>0.031</td>
<td>2.10</td>
</tr>
<tr>
<td>Ascomorpha</td>
<td>0.018</td>
<td>0.003</td>
<td>0.20</td>
</tr>
<tr>
<td>Brachionus</td>
<td>0.076</td>
<td>0.014</td>
<td>1.20</td>
</tr>
<tr>
<td>B. calyciflorus</td>
<td>0.011</td>
<td>0.003</td>
<td>0.25</td>
</tr>
<tr>
<td>B. rubens</td>
<td>0.009</td>
<td>0.003</td>
<td>0.25</td>
</tr>
<tr>
<td>Euchlanis</td>
<td>0.050</td>
<td>0.011</td>
<td>1.15</td>
</tr>
<tr>
<td>Keratella</td>
<td>0.058</td>
<td>0.008</td>
<td>0.95</td>
</tr>
<tr>
<td>K. quadrata</td>
<td>0.002</td>
<td>0.001</td>
<td>0.15</td>
</tr>
<tr>
<td>Polyarthra</td>
<td>0.039</td>
<td>0.005</td>
<td>0.40</td>
</tr>
<tr>
<td>Calanoida</td>
<td>0.038</td>
<td>0.008</td>
<td>0.80</td>
</tr>
<tr>
<td>Cyclopoida</td>
<td>0.187</td>
<td>0.015</td>
<td>1.15</td>
</tr>
<tr>
<td>Nauplii</td>
<td>0.712</td>
<td>0.046</td>
<td>3.10</td>
</tr>
</tbody>
</table>

* Phase I consisted of data from February, March, April, and December of 1991 and January and February of 1992; Phase II was May–November of 1991.
* Other cladocerans collected: *Diaphanosoma, Eubosmina, Moina, Simocephalus*. In the summer of 1992, large populations of the exotic species *Daphnia lumholtzi* were collected.
* Copepods described primarily of *Eurytemora* (Calanoida) and *Diacyclops* (Cyclopoida).

FIG. 5. Mean number of rotifers, cladocerans, and copepods during the study period. Solid circles and dashed line = rotifers; open circles and solid line = cladocerans; solid triangles and dotted line = copepods.

...described above (Fig. 5). During the period when discharge and suspended sediment concentration are high and temperatures are low (Phase I: December–April in our sample year), average zooplankton densities were low (1.6/L). In contrast, during Phase II (May–November in our sample year), densities were relatively high (21.6/L, with a maximum monthly density of 34.6/L). Although a portion of this effect may have been due to dilution (mean monthly discharge was roughly six times greater in Phase I than in Phase II), a considerable portion of the disparity in densities between Phases I and II was due to differences in absolute population size. The seasonal patterns of abundance for major groups were similar to total density and to each other; however, a seasonal rise in density was first observed for rotifers, then for cladocerans, and lastly for copepods (Fig. 5). Of the 14 most abundant taxa, 13 were highly variable over time (\( P < 0.0001 \)) and the fourteenth was almost significant (\( P = 0.07 \)). All 14 taxa were most abundant during Phase II (Table 1).

As a group, rotifers were nearly twice as abundant as either cladocerans or copepods (exclusive of nauplii) and typically represented more than 50% of the individuals in the community (Table 1). The rotifer genus *Polyarthra* (principally *P. vulgaris* and *P. dolichoptera*) was the most abundant taxon on an annual basis; however, the next three numerically dominant taxa were the cladoceran *Bosmina longirostris*, calanoid copepods (mostly *Eurytemora affinis*), and cyclopoid copepods (primarily *Diacyclops thomasi*). All other numerically dominant zooplankton (defined here as present at \( > 0.1/L \)) were rotifers: *Brachionus calyciflorus* and *Keratella* spp. (*K. quadrata* and several other species). *Polyarthra* spp. and *Brachionus* spp. were more abundant early in Phase II whereas *Keratella* spp. were more plentiful.
in the autumn (i.e., late Phase II). Data on density patterns for the most common of 23 species of rotifers, seven species of cladocerans, and various copepods encountered in our riverine samples are given in Table 1.

Although our study was not designed to establish causal relationships between densities of various taxa and abiotic and biotic variables, some possible relationships are suggested by correlation statistics. Species richness of zooplankton was not significantly correlated with water temperature, velocity, or turbidity. In contrast, of the 18 taxonomic density variables examined, 12 were positively correlated with water temperature \( P < 0.01 \). Density was correlated with water velocity in 13 cases \( P < 0.05 \), all of which were negative except for Brachionus rubens \( P < 0.001 \) which reached its greatest densities in early Phase II (May) when water velocities were still moderately high. Sixteen density variables were negatively correlated with turbidity \( P < 0.05 \).

Our data are generally not useful for suggesting biological interactions among species because all significant comparisons were positive. This probably resulted because maximum densities for all species clustered in Phase II. Nonetheless, it is noteworthy that densities of rotifer species, in contrast with those of cladocerans and copepods, were rarely significantly correlated with other taxa (rotifers with copepods: 21%; with cladocera: 4%; and with other rotifers: 4%).

Influence of Low-head Dams

One means of analyzing effects of dams on zooplankton is to compare assemblages in the lower and upper portions of a pool (in this case, above the confluence with a major tributary; see Fig. 7). Plankton assemblages could be different because in comparison with the lower-pool habitat, the upper

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**Fig. 6.** Mean number of species (SPP) and individuals (±1 SE) in shallow nearshore areas (depth = 1 ± 0.5 m) (hatched bars) and in deeper midchannel areas (solid bars) of the Ohio River. In this and subsequent graphs, DEN = total zooplankton density (including copepod nauplii) and ROT, CLA, COP, and NAU = densities of rotifers, cladocerans, copepods (excluding nauplii), and nauplii, respectively. Data drawn from the Ohio River only.

**Fig. 7.** Mean number of species and individuals (±1 SE) in the lower (hatched bars) and upper regions (solid bars) of a pool.

Density variables examined: total zooplankton, rotifers, cladocerans, copepods (without nauplii), and nauplii and densities of *B. longirostris*, *Ceriodaphnia reticulata*, *Daphnia* spp., *Ascomorpha* sp., total *Brachionus*, *B. caeciflorus*, *B. rubens*, *Euchlanis* (probably *E. dilatata*), total *Keratella*, *K. quadra*, *Polyarthra* spp., *Calanoida* (mostly *Eurytemora affinis*), and Copepoda (mostly *D. thomasi*).
pool has higher current velocity, more variable depth, and greater suspended sediment concentration. (J.H. Thorp, personal observation). When data from all three pools were combined, species richness was similar in upper and lower portions of the pools ($F = 0.487, P = 0.4857$), but total zooplankton densities were much higher in the upper segment ($F = 8.070, P < 0.01$). Differences in total zooplankton density were almost exclusively attributable to nauplii, which were vastly more abundant ($F = 9.168, P < 0.01$) in upstream areas of two of the three pools. Juvenile and adult copepods and both rotifers and cladocerans evinced no such pattern as groups. Other than copepod nauplii, only the densities of the rotifers *B. rubens* and *Ascomorpha* sp. were significantly different between upstream and downstream areas of pools; the former was significantly more dense upstream (mean = 0.01/L versus 0.002/L) whereas the latter showed the opposite pattern (0.01 and 0.36/L, respectively).

Therefore, the presence of navigation dams had no detectable effect on either zooplankton species diversity or densities of almost all taxonomic groups. Moreover, significant values which were present were neither consistent among taxonomic groups on a yearly basis nor constant within groups among sample months.

Contrasts with, and Contributions from, Tributaries

Two principal questions were posed in relation to tributaries. First, “Are zooplankton assemblages within tributaries significantly different from those in the Ohio River?” This was examined by comparing zooplankton immediately above a tributary with potamoplankton within a tributary. Second, “Are the diversity and density of the Ohio River zooplankton assemblage significantly influenced by inputs from tributaries?” This was addressed by comparing potamoplankton above and below the tributaries.

Although species richness and total zooplankton density did not differ significantly between tributaries and the main channel of the Ohio River, rotifers were more abundant in tributaries ($F = 8.403, P < 0.01$), and the Ohio contained more cladocerans ($F = 4.374, P < 0.05$), copepods ($F = 10.947, P < 0.001$), and crustacean nauplii ($F = 13.773, P < 0.001$) (Fig. 8). The rotifer genera *Keratella* and *Polyarthra* were both more abundant in tributaries ($F = 5.209$ and $5.589$, respectively, $P < 0.05$), and *Ascomorpha* sp. was almost significantly different ($F = 3.649, P = 0.0568$).

The input of tributaries enhanced diversity ($F = 11.677, P < 0.001$) and total density ($F = 7.167, P < 0.01$) of potamoplankton in the Ohio River (Fig. 8). Densities in the main channel of the Ohio were greater below than above tributaries for rotifers ($F = 4.152, P < 0.05$) and cladocerans ($F = 3.793, P < 0.05$) but were lower for copepods ($F = 4.883, P < 0.05$), primarily because of decreased densities of nauplii. Numbers of the rotifers *Brachionus* spp. and *Polyarthra* spp. were especially affected. These community shifts occurred without significant changes in physical and chemical conditions downstream of each of the three tributaries. These community patterns were consistent in all tributaries for species richness and densities of rotifers and copepods; but sites above the confluence of the Kentucky River contained greater numbers of total zooplankton, and areas above the mouth of the Miami River had higher densities of cladocerans. In the McAlpine Pool, where all 12 monthly samples were analyzed, diversity and densities tended to be higher below the mouth of the northwest-flowing Kentucky River from July through December but were lower from January through April and mixed in May through June.

Interpool Comparisons

To determine effects of channel/floodplain morphology, we compared average densities and diversities of zooplankton in the lower portion of each pool during the four months.
when samples from all pools were analyzed. Total species density was related to pool type ($F = 4.315, P < 0.05$), as were densities of adult and juvenile copepods, nauplii, and four species of rotifers; species richness was not significantly influenced by pool type. Although total zooplankton densities were highest in the constricted Markland Pool, this was entirely due to nauplii, which were more than seven times as abundant there than in the other two pools. When these larval copepods were excluded from the analysis, however, the highest densities occurred in the floodplain portion of the Cannelton Pool. Rank order of pools (i.e., 1–3, with 1 = highest density) for densities varied substantially among taxa. Indeed, average ranks among pools were Cannelton (mean = 1.89), McAlpine (1.89) and Markland (2.22) for all significant comparisons, or McAlpine (1.89), Cannelton (2.00), and Markland (2.11) when nauplii were removed. Therefore, clear distinctions among pools were not evident according to channel morphology and floodplain width.

When all sample sites were included in the analysis (rather than just the lower pool), species richness ($F = 9.229, P < 0.0001$), total zooplankton density ($F = 9.629, P < 0.0001$), and most other taxonomic comparisons were significantly related to pool type (Fig. 9). The average rank orders were 1.50, 2.00, and 2.50 for McAlpine, Markland, and Cannelton pools, respectively.

**Discussion**

Knowledge of lotic plankton communities is extremely limited in comparison with data available for either lotic benthos or lentic plankton. A contributing factor is the lack of consensus on the nature of potamoplankton assemblages. Do they constitute independent, reproducing communities, or are they merely assortments of transient organisms whose densities are maintained only by constant immigration from backwaters and tributaries? Although production rates have not yet been identified, it is clear from frequent observations of ovigerous individuals that Ohio River zooplankton are a reproducing community (A.R. Black and J.H. Thorp, unpublished data). The lack of consensus on potamoplankton is exacerbated by a common misconception that conclusions drawn from lentic studies can be easily applied to large rivers, negating the need to conduct “superfluous” riverine studies. The spurious nature of this comparison has been admirably demonstrated by Ryder and Pesendorfer (1989). Planktonic communities in navigable rivers probably differ more from lake assemblages than do the more frequently studied reservoir communities because the physical parameters of larger navigable rivers are relatively more disparate. In comparison with lakes and reservoirs, for example, main channels in rivers are well mixed vertically and, therefore, rarely show thermal or chemical stratification. Concentrations of key nutrients (especially N and P) are high in the Ohio River, compared with many lentic systems; more importantly, their seasonal dynamics are apparently regulated by variations in river discharge (i.e., physical processes), rather than by aquatic biota. Advective transport and suspended sediment concentration also have substantial effects on diversity and net secondary production of riverine zooplankton (e.g., Saunders and Lewis 1988b: Pace et al. 1992). Neither factor is consequential in lakes, and except for highly turbid impoundments, both parameters are less significant in reservoirs.

Despite the paucity of studies, several conclusions can be drawn from past research on riverine zooplankton. Density tends to peak in late spring through midsummer (e.g., Neitzel et al. 1982), often with different density modes for rotifers and microcrustaceans. We found similar results for potamoplankton in the Ohio during the period of our study, although peak densities occurred in mid- to late summer. The seasonal timing of the initial rise in densities varied among major taxa, but peak numbers overlapped within a month in the Ohio. Although rotifers are often the numerically dominant group in large rivers, followed in relative importance by copepods and cladocerans (e.g., Shiell 1985; Saunders and Lewis 1988a; Ferrari et al. 1989), this can vary among rivers and seasons (De Ruyter van Steveninck et al. 1990; Pace et al. 1992). During 1991–92 in the Ohio River, the order of numerical abundance averaged over the year (ignoring nauplii) was rotifers (especially Polyarthra), cladocerans (predominately Bosmina), and copepods (mostly Eurytemora and Diacyclops); rotifers were nearly twice as abundant as other taxa. Bosmina and rotifers are also important in the Hudson River, which like the Ohio is dominated by small zooplankton (Pace et al. 1992). Pace et al. (1992) hypothesized that this size phenomenon could arise because small species should be favored in advective systems, especially turbid rivers with higher concentrations of filamentous and/or toxic algae. The average density of the total zooplankton community was lower in the Ohio than in the tidally influenced Hudson, which fits with the prediction of Pace et al. (1992) that densities should be highest in lakes followed by tidal and then nontidal rivers.

The consensus of opinion dating at least as far back as Hynes (1970) seems to be that plankton assemblages in rivers are physically controlled; while our present data are not at odds with this conclusion, it is noteworthy that biological control mechanisms remain essentially unexplored. Our data for Ohio River zooplankton show a distinct two-phase pattern of species abundance. Phase I (December–April in our sample year) was characterized by high discharge and suspended sediment concentrations, cooler temperatures, mostly diminished nutrient levels, and low zooplankton densities (1.6/L). Phase II (May–November) was characterized by the opposite physical/chemical patterns and relatively high densities (21.6/L; maximum monthly density = 34.6/L). The causal factor or factors for low densities in Phase I are not entirely evident. Densities and reproductive rates of zooplankton in rivers (exclusive of riverine reservoirs) are often not significantly correlated with phytoplankton abundance (Pace et al. 1992) but are closely tied to current velocities and suspended sediment concentrations (e.g., Saunders and Lewis 1988b). While it is true that the low suspended sediment concentrations associated with the slow currents in Phase II should have a positive influence on the ingestion of food particles and body growth of zooplankton (c.f. Kirk and Gilbert 1990), the higher phytoplankton densities and warmer temperatures might make an equal or greater contribution to population size of potamoplankton.

**Littoral versus Pelagic Potamoplankton**

Habitat characteristics of lakes and rivers (including those with navigation dams) possess significant similarities and differences. Like the littoral zone of lakes, nearshore areas in the Ohio River feature snags (woody debris), vascular macrophytes, and benthic algae which rarely occur in the pelagic zone; they are also more turbulent because of wave
action. Unlike lentic habitats, however, distinctive horizontal or vertical thermal zones are lacking through most or all of the year. Consequently, the littoral zone of a lake typically has a different mixture of species from that present in its pelagic zone. Is the same contrast present between the littoral and pelagic zones of well-mixed rivers?

Our results may suggest that littoral and pelagic areas of rivers differ to a certain degree. Although species richness was similar in shallow (nearshore) and deepwater (midchannel) areas, average annual densities of total zooplankton were significantly higher nearshore (principally in summer). On an annual basis, copepods and cladocerans tended to be more abundant in the littoral zone whereas nonattached rotifers were usually more dense in deeper and faster main channel waters. These trends may not reflect distinctive niches for zooplankton, however, because the greater density in shoreline areas may be a simple result of lower velocities which tend to retain species and magnify densities. Our sampling methods were not designed to collect benthic cladocerans (e.g., chydorids), copepods, and attached rotifers, and presumably they are much more abundant in the littoral zone. The ecology of benthic rotifers and microcrustaceans in lotic systems is a fertile area for future research.

Influence of Low-head Dams and Tributaries

Ecological perspectives on the effects of dams on lotic ecosystems are based almost entirely on studies of high dams. By integrating the effects of high dams and tributaries on the RCC, Ward and Stanford (1983) developed the serial discontinuity concept. This theory indicates that high dams and large tributaries will cause the downstream biotic community to be "reset" toward an ecosystem state more representative of lower order streams. If the serial discontinuity concept is applicable to rivers with low-head dams, one would expect substantial differences in density, diversity, and/or species composition of potamoplankton in waters above and below a dam or major tributary. Our data suggest, however, that this theory cannot easily be applied to the Ohio River because we found no significant effects of the low-head navigation dams on species diversity or density of zooplankton (with the exception of copepod nauplii).

The influence of tributaries on Ohio River zooplankton appears more substantial and complex than the effect of navigation dams on this community. In their model of the Hudson River zooplankton community, Pace et al. (1992) assumed that tributaries were not a source of the cladoceran B. longirostris (the dominant zooplankter in their study) because those streams "...are small, have high current velocities, and are unlikely to support populations of zooplankton" (p. 1065). Our data indicate that a similar assumption would clearly be inappropriate for a model of the Ohio River and its larger tributaries because the Miami, Kentucky, and Salt rivers contribute substantial numbers of zooplankton to the Ohio. Although species richness and total zooplankton density did not differ significantly between tributaries and the main channel of the Ohio River during our study, rotifers were significantly more abundant in tributaries, and the Ohio contained significantly more cladocerans and copepods. The input of major tributaries significantly enhanced diversity and total density of potamoplankton in the Ohio River. Densities in the main channel of the Ohio were greater below than above tributaries for rotifers and cladocerans but were lower for copepods, primarily because of decreased densities of nauplii. Even though tributaries significantly influenced zooplankton assemblages in the Ohio River, evidence of a tributary-induced reset phenomenon is lacking over the 361-km stretch of the river studied here. While this may reflect unique characteristics of this very large river, we suspect that a primary reason for nonconformance with this theory is that the serial discontinuity concept was based principally on the behavior of benthic insects, whose food resources change dramatically along the river continuum.

Interpool Comparisons

Recent studies of large river ecosystems (Junk et al. 1989; Sedell et al. 1989) predict that rivers with constricted channels should more nearly conform to the RCC (Vannote et al. 1980) than lotic systems with wide floodplains. A comparison of zooplankton assemblages in the lower portions of two constricted-channel pools and one floodplain pool of the Ohio River produced no evidence supporting this important theory. In contrast, when all samples within a pool were averaged (i.e., both upper and lower reaches), differences among floodplain and constricted-channel pools were highly significant. These dramatic contrasts in results suggest that assemblages in the upper portion of the pools are being affected by different environmental variables than those in lower areas of the three pools. A factor likely to be highly influential is the upstream proximity of large urban areas with point-source and non-point-source inputs of pollutants. Specifically, the upper portion of the more floodplain Cannelton Pool is immediately below Louisville, and the upper reach of the Markland Pool is downstream from Cincinnati. In contrast, the upper McAlpine Pool is in a more rural area.

In North America, freshwater zooplankton biologists work almost exclusively in lentic habitats, while stream zoologists rarely study large rivers or species other than vertebrates or benthic invertebrates (e.g., insects, snails, and crayfish). Consequently, the fundamental biological knowledge of large rivers in general and potamoplankton in particular is abysmal, making it especially difficult now to tackle ecological questions as complex as those addressed in other habitats or with other species. It is evident from our Ohio River study, however, that physical factors (current velocity, turbidity, and temperature) strongly influence potamoplankton. In this navigable river with low-head dams, zooplankton assemblages appear to vary between some habitats (littoral versus pelagic) but not others (upper versus lower pool and floodplain versus constricted-channel pools). Zooplankton clearly reproduce within the Ohio, but immigrants from tributaries also may contribute significantly to the community of the main channel. Future studies are needed to determine whether internal production alone can sustain potamoplankton and whether biological interactions are important in regulating these species. Use of novel experimental techniques, such as drifting, Nitex mesh pelagic enclosures, or "potamocorals" (Thorpe 1992b; J.H. Thorp et al., unpublished data), may be necessary to understand more fully the ecology of potamoplankton in large rivers.

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