

Vertical, lateral and longitudinal movement of zooplankton in a large river

JEFFREY D. JACK,* WEI FANG* AND JAMES H. THORP[†]

*Department of Biology and Center for Environmental Science, University of Louisville, Louisville, KY, U.S.A.

[†]Kansas Biological Survey and Department of Ecology and Evolutionary Biology, Higuchi Hall, University of Kansas, Lawrence, KS, U.S.A.

SUMMARY

1. The spatial distribution and movement patterns of zooplankton in large rivers are little known compared with those in lake environments. We conducted a series of studies in the Ohio River (U.S.A.) during the low flow period to assess diel vertical (DVM), longitudinal and lateral movement of crustacean zooplankton.

2. The dominant large zooplankton, the copepod *Eurytemora affinis*, showed a consistent vertical migration pattern of daytime ascent and night-time descent during all sampling periods – the reverse of the most common migratory pattern of zooplankton in lakes. The cladoceran *Bosmina* migrated in a similar way in two of the three sampling periods. Surveys taken longitudinally in the river showed similar trends for both taxa.

3. During the lateral surveys, *E. affinis* was significantly more abundant in the shallow littoral zone during the night than in the daytime. The combination of vertical and lateral movement patterns along with the diel distribution of zooplanktivorous fish suggest that these movements are a predator-avoidance mechanism.

4. Sampling programmes in large rivers should consider that larger zooplankton such as *E. affinis* may not be randomly distributed in the river channel and behaviours such as diel vertical migration may be just as evident in river habitats as in lakes.

Keywords: diel vertical migration, predation, rivers, vertical migration, zooplankton

Introduction

The phenomenon of diel vertical migration (DVM) of zooplankton has been extensively examined for over a century (Dini & Carpenter, 1992) and has been observed in both freshwater lakes and marine systems (e.g. Vuorinen *et al.*, 1999). DVM typically involves a daytime descending and night-time ascending movement, but other patterns have also been observed. Lateral migration (also called horizontal migration) and shoreline-avoidance behaviour of zooplankton has also been reported in a number of different systems (Zurek, 1989; Gliwicz & Rykowska, 1992; Wicklum, 1999; Burks *et al.*, 2002).

Many hypotheses have been proposed to explain the functional significance of DVM. Some have suggested that zooplankton that feed in warmer waters but spend a portion of their time in colder water layers would show increased metabolic efficiency (Enright & Honegger, 1977), although a recent review of the literature provided little support for this hypothesis (Hays, 2003). A better-supported hypothesis is one of predator avoidance where zooplankton undergo DVM to avoid visually orienting predators during the day (Ringelberg, 1999). This approach is supported by both observational and experimental evidence, in particular work involving the responses of zooplankton to the presence of fish or fish 'infochemicals' (Dodson, 1988; Van Gool & Ringelberg, 2002.) Recently, there have also been studies which show UV levels in some lakes may also play a role in DVM behaviours (Boeing *et al.*, 2004; Leech *et al.*, 2005).

Correspondence: Jeffrey D. Jack, Department of Biology and Center for Environmental Science, University of Louisville, Louisville, KY 40292, U.S.A. E-mail: jeff.jack@louisville.edu

However DVM behaviour has rarely been examined in river ecosystems. Zooplankton in river channels have often been regarded as organisms which have been trapped in an advective, well-mixed environment and which are being transported downstream from their sources in lakes and slackwater areas. Nevertheless, there are reasons why zooplankton in large rivers may exhibit some of the same movement behaviours seen in lake taxa. Larger and more motile zooplankton have shown negative rheotaxis and have some ability to detect, avoid, and resist moving water (Richardson, 1992). Research in large rivers such as the Ohio and the St Lawrence have revealed the presence of large zooplankters such as *Eurytemora affinis* Poppe (Thorp *et al.*, 1994; Thorp & Casper, 2002) that may be strong enough swimmers to influence their position in the river water column. Recent work in other river systems has also suggested that the zooplankton may not be as homogeneously mixed in the river water column as was once thought. Pace, Findlay & Lints (1992) described areas of the Hudson River (U.S.A.) that served as population sources and others which served as sinks, both of which resulted in changes in zooplankton abundance through their study reach. Thorp *et al.* (1994) found higher densities of zooplankton in the littoral zone of the Ohio River than in the midchannel during the low flow conditions of summer, while Shiel, Walker & Williams (1982) found the opposite trend in the River Murray in Australia. Reckendorfer *et al.* (1999) identified potential 'storage zones' in the Danube River that may affect zooplankton growth rates and thus their distributions, along a river reach. Viroux (1999) performed the first study that explicitly assessed zooplankton spatial distributions in large rivers (the Moselle and the Meuse) using cross-channel transects. He found that the larger zooplankton appeared to be patchily distributed across the channel of the Meuse and that lateral inputs of zooplankton in the Moselle led to higher abundances of zooplankton near the riverbanks.

These studies suggest that some zooplankton in large rivers may be able to influence their position in the water column to a greater degree than had once been assumed and that their vertical and horizontal distributions and interactions between temporal and spatial factors should be more thoroughly investigated. As larval and juvenile fish predation on zooplankton may have significant impacts on

zooplankton population growth rates in large rivers (Jack & Thorp, 2002), DVM behaviours may be as adaptive in the river as they have been shown to be in lakes. To assess this, we collected vertical, horizontal and lateral zooplankton samples over 24 h sampling periods during low flow in the Ohio River near Louisville, KY, U.S.A. We hypothesised that the larger copepods and cladocerans would show distributions consistent with DVM (higher densities in the upper water column at night) during these periods as a result of predation pressure from visually feeding predators such as larval fish. As macrophyte densities are low and other obvious physical cover (rootmats etc.) is limited along the sampled reach of the Ohio River, we also hypothesised that there would be little lateral movement of zooplankton in response to changing light conditions.

Methods

The Ohio River is the second largest river in the U.S.A., based on mean annual discharge ($8127 \text{ m}^3 \text{ s}^{-1}$ at its mouth) and it drains an area in excess of $1\,200\,000 \text{ km}^2$ (>7% of the continental U.S.A.; Thorp, 1992). We conducted our experiments at various locations in the McAlpine Pool section of the river (Fig. 1), where the river was at least 12 m deep in the middle channel and approximately 800 m wide; additional information about the geographical characteristics of this portion of the river is available in Thorp (1992). All experiments were conducted during the low flow period in the river (July to October).

When the spatial variations of zooplankton abundance in rivers are considered, they should be viewed longitudinally, laterally, vertically and temporally because of the four-dimensional nature of lotic systems (Ward, 1989). Vertical zooplankton movement studies were conducted near Westport, KY at Ohio River Kilometer 933 (ORK; the Ohio River is divided into 1 km reaches from the mouth to its source near Pittsburgh, PA, U.S.A.). Vertical samples were taken at 22:00 hours, 04:00 hours, 10:00 hours and 1600 hours on two sampling dates in August and October. Triplicate 30-L samples of river water were collected at 2 m intervals from 0.5 to 12.5 m using a high volume diaphragm water pump. Current was assessed at the surface using a Pygmy current meter (Gurley Meter, Troy, NY, U.S.A.). Temperatures were

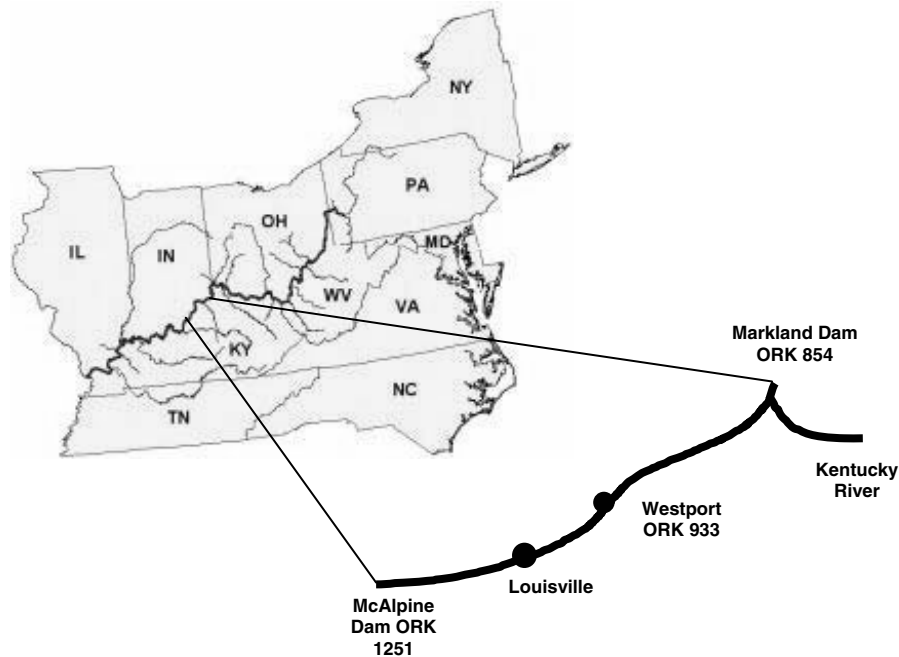


Fig. 1 Location of the Ohio River basin with inset map showing the locations of the study sites within the McAlpine Pool. Figure modified from Jack, Sellers & Bukaveckas (2002).

measured at both the surface and bottom of the river during each sampling period. Animals were filtered through a 75- μm mesh conical plankton net (Wildco, Saginaw, MI, U.S.A.), immersed in 95% ethanol to kill the animals rapidly with minimal body distortion, and were preserved in 70% ethanol.

A longitudinal study of vertical distributions was performed in July by positioning the boat in mid-channel and then allowing the boat to drift between ORK 914 to ORK 944. This procedure was followed to assess whether the downstream movement of the river water mass, which would be occurring at the same time as any vertical movement by the zooplankton, would affect the distribution patterns we observed. Samples were taken at 20:00 hours, 02:00 hours, 08:00 hours and 14:00 hours as described above with the exception that the maximum depth sampled was 10 m, not 12.5 m. No major tributary enters this portion of the river so our samples were not influenced by additional lateral inputs during the study.

For the lateral zooplankton assessment, samples were taken in July and October at the same location as the vertical samples. The boat was allowed to drift downstream with the current and zooplankton sam-

ples were collected from stations at 3, 10 and 15 m distances off-shore. Samples were taken at 20:00 hours, 05:00 hours, 10:00 hours and 15:00 hours and collected from the surface, 1 and 2 m depths (maximum depth for the 3 m inshore station). The same methods were used with the exception that a 25- μm mesh plankton net was used to filter the pumped water in the October sample. We wanted to assess whether smaller zooplankton also migrated laterally and this smaller mesh was needed to capture the rotifers and other similarly sized plankton. The samples from the different depths at each position were pooled together for analysis.

For all studies at least 100 individuals of each of the dominant taxa (comprising at least 5% of the sample's numerical abundance) were counted in subsamples (subsampling, where necessary, with a Folsom plankton splitter). Subsampling errors were assumed to be constant and negligible (Sell & Evans, 1982; Evans & Sell, 1983). All samples were counted with a stereodissecting microscope (Nikon SMZ-U, Yokohama, Japan) at 20–80 \times magnification using a plankton wheel and identified to lowest practicable taxon, usually species. Taxonomic keys used were Coste (1978), Pennak (1987) and Thorp & Covich (1991).

Hypotheses were tested by three-factor analysis of variance (ANOVA), with depth (or position in the case of the lateral migration study), time and date as the three independent variables. A significant interaction among all three factors was interpreted as a seasonal influence on DVM pattern. In such cases, data from each month were analysed individually using two-factor ANOVA with depth and time as the independent variables. Densities of each abundant species and total zooplankton density were treated as the dependent variables. Descriptive statistics were calculated with the UNIVARIATE procedure of SAS (SAS Institute Inc, 1996). Deviations from normality were judged by a combination of normal probability plots and the Shapiro-Wilk W -statistic. Data were successfully transformed using $\log_{10}(x + 1)$, when normality assumptions were not met.

Results

During each sampling period, physical conditions of the river were relatively stable. Little temperature variation was observed between surface and bottom water ($<4^{\circ}\text{C}$ for the lateral migration studies), indicating no thermocline was formed and diel changes in temperatures were minor during the study periods. Surface current velocities varied from 0.1 to 0.8 m s^{-1} during all sampling dates.

Of the 19 taxa collected in the study, only *E. affinis* Poppe and *Bosmina* were judged sufficiently abundant enough (at least 2 individuals L^{-1} at all times and locations during a sampling period) to be included in the analyses. The *Bosmina* in the river were formerly identified as *Bosmina longirostris* complex (O. F. Muller) but this taxa has been reclassified, following the work of DeMelo & Hebert (1994), as *Bosmina (Sinobosmina) freyi*. *Eurytemora* was the dominant crustacean in August samples, while *Bosmina* was more common in the October samples. Contrary to our original expectation, *Eurytemora* exhibited a reverse DVM pattern in both sample periods (Figs 2 & 3). During these sample dates, *Eurytemora* populations were consistently and significantly (August $P < 0.001$; October $P < 0.004$) congregated near the surface water during the afternoon sampling period (16:00 hours). Three-factorial analysis demonstrated that their migratory patterns did not vary significantly between August

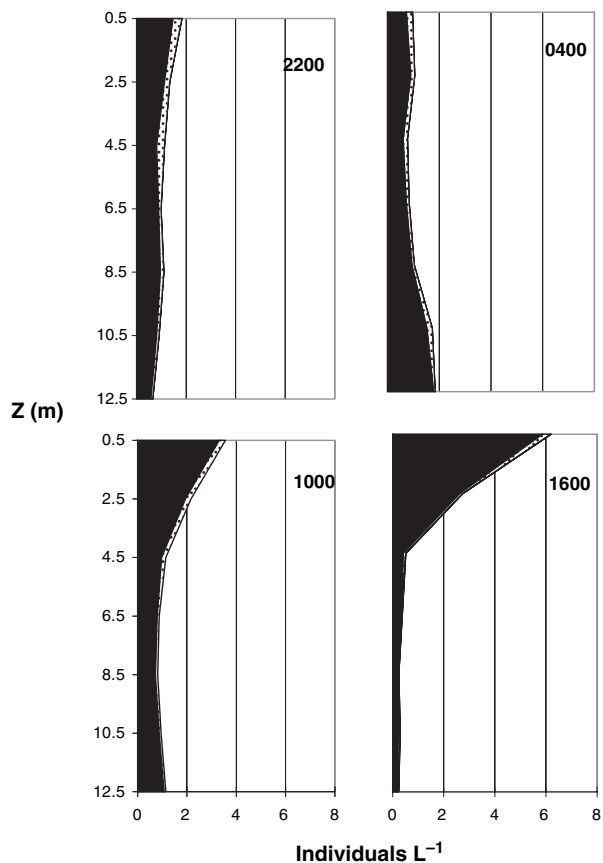


Fig. 2 Vertical distribution of *Eurytemora affinis* (black pattern) and *Bosmina* sp. (stippled pattern) over 6-h periods in August.

and October ($P > 0.27$). *Bosmina*'s migration pattern varied significantly between the sample periods in the vertical movement study ($P < 0.0001$; Figs 2 & 3). The diel vertical distribution of *Bosmina* in October ($P < 0.0001$) was similar to that exhibited by *Eurytemora*, but the pattern was not significant in August ($P > 0.77$) when densities of this zooplankter were considerably lower. In the July drift study, both *Eurytemora* and *Bosmina* showed the reverse DVM pattern observed for the vertical migration study (Fig. 4; $P < 0.001$ and $P < 0.003$).

In the lateral movement study, *E. affinis* densities were higher during both sampling periods in the shoreline areas at night than during daytime (Fig. 5; $P < 0.03$). The densities of *Bosmina* and the microzooplankton collected (primarily rotifers, which were numerically dominated by *Keratella cochlearis* Gosse, *Polyarthra* sp. and *Brachionus* spp.) were not significantly different among the three positions over the course of the study ($P > 0.25$).

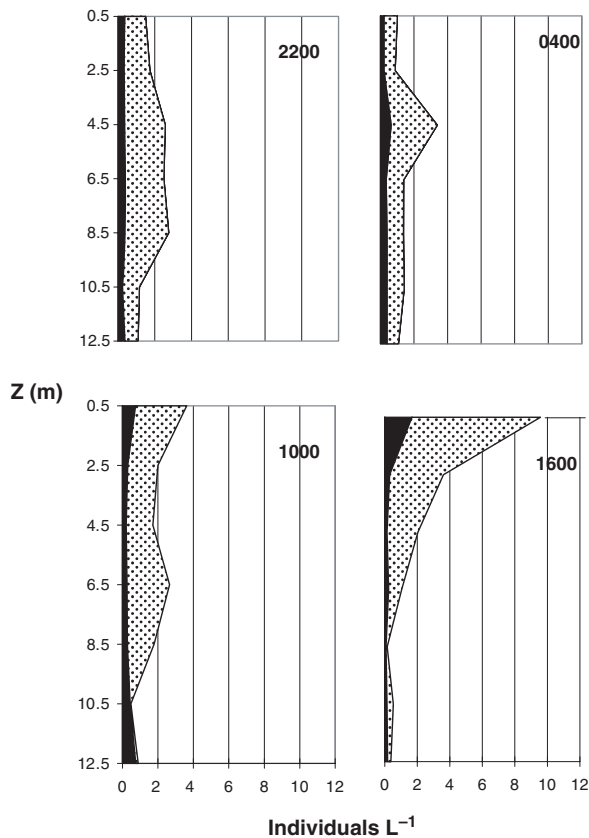


Fig. 3 Vertical distribution of *Eurytemora affinis* (black pattern) and *Bosmina* sp. (stippled pattern) over 6-h periods in October.

Discussion

Our results indicate that zooplankton distributions can vary spatially and temporally in the Ohio River and that the species-specific migration patterns observed in the Ohio River are similar to those seen in some lentic systems (Stich & Lampert, 1984; Watt & Young, 1992; Kelso, Rutherford & Davidson, 2003; Wojtal *et al.*, 2003). *Eurytemora affinis* consistently showed reverse DVM in the river channel and lateral migration on and off the river-bank area. The different migration patterns detected for *Bosmina* in August and October could have been the result of a difference in densities (Figs 2 & 3); reverse DVM may have been difficult to detect when *Bosmina* densities were so low in August. The ability of copepods to position themselves in specific patches of a flowing waterbody may seem unusual but studies in Lake Kinneret have shown that copepods can position themselves favourably in the presence of seiche waves (Easton & Gophen, 2003). While we are not aware of any studies

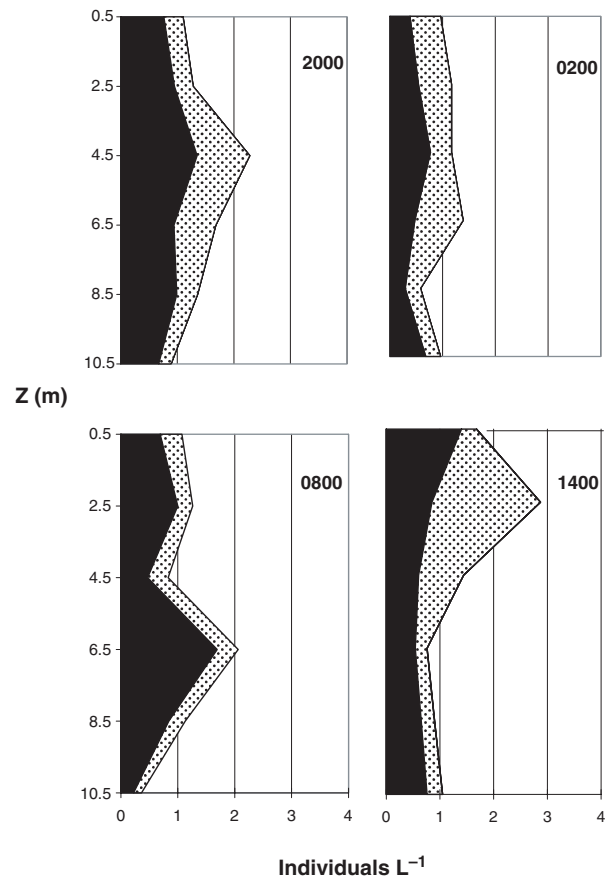


Fig. 4 Vertical distribution of *Eurytemora affinis* (black pattern) and *Bosmina* sp. (stippled pattern) during the longitudinal drift study in July.

on the swimming speeds of adult *Eurytemora*, the calanoid copepod *Temora longicornis* Muller can maintain foraging speeds of 6 mm s^{-1} , with escape bursts of up to 80 mm s^{-1} (Van Duren & Videler, 2003) and the marine copepod *Metridia pacifica* Brodsky can reach and maintain upward migration speeds of 90 m h^{-1} (Enright, 1977.) While *Eurytemora* may not be swim directly against river current, during low flow periods it may be able to move on and offshore in a diagonal fashion with the river current. *Bosmina* has a maximum recorded speed of 10 mm s^{-1} during its power stroke (Zaret & Kerfoot, 1980), but it may not be able to maintain this velocity for extended periods necessary to successfully migrate in the river.

While this study did not focus on causative factors for zooplankton movements, we can examine zooplankton distributions in the light of factors that have been proposed to be significant drivers of DVM in lakes. DVM appears to be a inducible

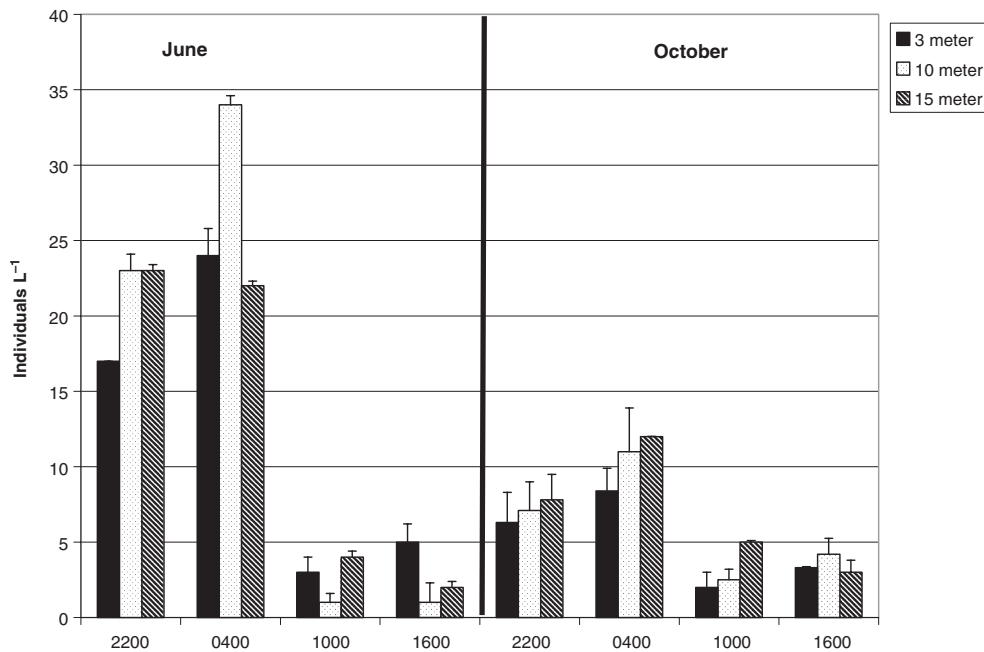


Fig. 5 Mean densities of *Eurytemora affinis* in the 0–2 m water column of the littoral zone of the Ohio River in June and October. Dark bars are 3 m, stippled 10 m and cross hatched 15 m distances off shore. Error bars show standard errors.

behaviour in that many zooplankton only undertake DVM when certain environmental conditions are present, such as a chemical cue associated with a predator. Other factors such as temperature and dissolved oxygen (Hanazato, 1992) or food resource availability may also play a role. During the study period, temperatures were not greatly different between the upper and lower parts of the water column in this vertically mixed river, so it is unlikely that differences in temperature regime would be important factor in driving zooplankton DVM or lateral movements in the river. Although data on the vertical profile of phytoplankton were not collected during this study, the substantial mixing and lack of a thermal stratification in the river make it unlikely that phytoplankton distribution could have affected DVM even during the low flow period. It also seems unlikely that UV radiation would be a major driver of migration in turbid systems such as the Ohio.

Predation pressure is the most likely factor driving the various migrational movements we observed for the larger zooplankton in the Ohio River but the reverse DVM behaviours seen in the vertical and longitudinal studies suggest that avoidance of visu-

ally feeding predators in this system may not be the main impetus for these migrations. Reverse DVM has been seen in systems where the zooplankton are escaping invertebrate predation (Ohman, Frost & Cohen, 1983; Neill, 1990). However, very few large invertebrate predators, such as the phantom midge *Chaoborus*, were found in the samples collected in the Ohio River during this study. Other invertebrate predators are present in the benthos of the Ohio River, notably the zebra mussel *Dreissena polymorpha*, which can prey directly on small zooplankton in the river (Jack & Thorp, 2000). However, it does not seem likely that their presence would be a major driver of DVM behaviour in the zooplankton. This suggests that avoidance of invertebrate predators was probably not the immediate cause of the observed reverse DVM but we cannot rule out the possibility that some other invertebrate species or group may be influencing the movements of these zooplankton.

Another possibility is that the vertical and lateral movements of the *Eurytemora* were linked. In some lentic systems, 'shoreline avoidance', that is zooplankton densities that dramatically increase from the shallow nearshore water to the pelagic zone, is a

well-established phenomenon (Burks *et al.*, 2002). However, horizontal migration between littoral and pelagic zones has also been associated with DVM. Franke (1983, 1987) studied the diurnal migrations of larvae and pupae of *Chaoborus* in Lake Heilingensee and concluded that the migration of this phantom midge had vertical and horizontal components, which he called transversal migration. He maintained that transversal migrations are also characteristic of other zooplankton species and suggested that a possible relation exists between these migrations and the phenomenon of shoreline avoidance.

The lateral movements of *Eurytemora* and perhaps even reverse migration pattern (i.e. near surface during day and closer to bottom at night) shown for *Eurytemora* and sometimes for *Bosmina* could be linked in response to the distribution of fish predators. Compared with lentic systems, there has been comparatively little work carried out on fish planktivory in large rivers. Work conducted using *in situ* mesocosms in the Ohio River established that increasing fish biomass of emerald shiners (*Notropis atherinodes* Rafinesque) and bluntnose minnows (*Pimephales notatus* Rafinesque) was inversely correlated with the population growth rates of the larger planktonic crustaceans, in that case, *Diatylops thomasi* Forbes (Jack & Thorp, 2002). Similar effects of yellow perch (*Perca flavescens* Mitchell) predators were noted for crustaceans in an *in situ* enclosure experiment in the St Lawrence River (Thorp & Casper, 2003). In addition, there are data that suggest that the movements of *Eurytemora* may be influenced by some of their likely fish predators. Sanders (1992) reported that abundances of two major planktivorous fish, gizzard shad (*Dorosoma cepedianum* LeSueur) and emerald shiner were significantly higher during daytime than at night in nearshore waters of the Ohio and Muskingum Rivers. Kessler (1999) surveyed fish populations near our sampling site and found that gizzard shad and emerald shiners densities increased along the shoreline cobble beds during the day but decreased in these same habitats during the night. Therefore, during the day the littoral zones may be an area of higher predation pressure for zooplankton than open water areas. If this is true, moving to the open water can be viewed as a mechanism to allow zooplankton to avoid heavy predation in the littoral zones. The zooplankton aggregation in the surface water of mid-channel during daytime seen in the DVM studies could be

the result of the horizontal movement of zooplankton from shallow littoral zone to the surface areas of pelagic zone in a manner analogous to that seen in Franke's studies. Unfortunately, little is known about the role of *Eurytemora* in riverine foodwebs. *Eurytemora* is a relatively new invader in this portion of the Ohio River; it was not reported as a member of the plankton until the 1990s (Thorp *et al.*, 1994). In marine systems, this copepod is preyed upon by a variety of fish and large invertebrates such as mysids (Hostens & Mees, 1999; Viitasalo, Flinkman & Viherluoto, 2001), so it is likely to be vulnerable to the planktivores in the Ohio River as well.

River plankton communities have been the focus of an increasing number of studies over the past two decades but few sampling programmes seem to consider that the distribution of the larger taxa may not be uniform in the river (but see Viroux, 1999.) Such 'patchiness' is acknowledged in lakes and needs to be considered as river monitoring and experimental projects are conducted. Many rivers are numerically dominated by rotifers and smaller zooplankton like *Bosmina* that may not be capable of such directed movements, but larger zooplankton species like *Eurytemora* may account for a large percentage of zooplankton biomass particularly during low flow periods (D. Guelda & P.A. Bukaveckas, unpublished data). As regulatory agencies begin to consider zooplankton as candidates for metric development in large river systems, such sampling considerations will be important. As more studies are performed in large rivers, investigators need to consider spatial and temporal variation in the zooplankton communities so that sampling and experimental work accurately reflects the community structure and biomass of these important members of the riverine plankton assemblage.

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