

## ZOOPLANKTON METACOMMUNITY STRUCTURE: REGIONAL VS. LOCAL PROCESSES IN HIGHLY INTERCONNECTED PONDS

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**Abstract.** Local communities can be structured by both local interactions (competition, predation, environmental variables, etc.) and by regional interactions (dispersal of individuals between habitats). Using data from a three-year study on 34 neighboring ponds in an interconnected pond system, we tested whether zooplankton communities show a metacommunity structure, how much variation in zooplankton community structure is related to local environmental factors vs. spatial configuration (taking into account the dispersal pathways), and what environmental variables are the locally structuring forces. In three different years, we found evidence for a metacommunity structure. We also found that spatial and environmental components act independently of each other due to the small geographic area and the high dispersal rates in this system. Despite these homogenizing forces, local environmental variables (associated with alternative equilibria in shallow lakes) were strongly related with zooplankton community structure in the studied years. This suggests that, even in this system of highly interconnected ponds, local environmental constraints can be strong enough to structure local communities.

**Key words:** *alternative equilibria in shallow ponds; dispersal; interconnected ponds; local vs. regional factors; metacommunity; spatial analysis; variance decomposition; zooplankton.*

### INTRODUCTION

The most fundamental structural properties of a local community are the number and relative abundances of its member species and the pattern of their dynamical interactions (Roughgarden and Diamond 1986, Tokeshi 1999). Much attention has been focused on local processes, such as competition, predation, environmental heterogeneity (resource diversity or disturbance regimes; Chesson 1986), direct and indirect interactions (e.g., dynamical constraints on food chain length; Wootton 1994), and historical contingency (priority effects in competition; Jenkins and Buikema 1998). Spatial dynamics can, however, influence all these interactions when individual (local) communities are directly connected to each other. The idea that colonization and extinction can determine local community structure through dispersal was first incorporated in ecology through the theory of island biogeography (MacArthur and Wilson 1967), in which habitat fragments are colonized from a large “mainland” source. Recently, some models have begun to extend the ideas of metapopulation dynamics (Gilpin and Hanski 1991, Hanski and Gilpin 1996) to explore the consequences of multiple habitat patches for species diversity where there is no mainland source of colonists (e.g., Tilman 1994, Tilman et al. 1994, Karieva and Wennergren 1995). Based on the concept of metapopulation, a “me-

tacommunity” can be defined as a set of local communities in different locations, coupled by dispersal of one or more of their constituent members (Gilpin and Hanski 1991). Ecological systems are thus best understood and studied in the context of where they are located in space (Legendre 1993, Turner 1998, Magnuson and Kratz 1999), particularly in relation to the dispersal pathways of the different species.

Zooplankton species inhabiting lentic freshwater habitats offer an excellent model system to study spatial interactions because the island-like nature of ponds and lakes creates well-defined habitat boundaries. In studies focusing on the population genetic structure of zooplankton, both the importance of local processes and regional processes could be documented. De Meester (1996) reviewed the available literature and concluded that zooplankton often show strong genetic differentiation and hypothesized that gene flow is reduced due to local interactions, especially through competition with locally superior resident genotypes. Thus, incipient local adaptation in an autocatalytic way offers opportunity for further local adaptation. Declerck et al. (2001) show a striking example with local adaptation in two *Daphnia* populations whose habitats are separated by only 5 m of land and in the presence of occasional water exchange between the two lakes during floods. Metapopulation dynamics are also active in several zooplankton species. Bengtsson (1989, 1991) showed local extinction (due to interspecific competition, predation, and variation in abiotic factors) and colonization events in three *Daphnia* species inhabiting rock pools. Bohonak (1998) showed that estimated dispersal rates of an anostracan through transport via sal-

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amanders were very similar to dispersal rates based on gene flow values (measured in individuals per generation). Brendonck et al. (2000) illustrated the effect of stochastic events and limited effective long-range wind dispersal in anostracans of desert rock pools. Finally, Michels et al. (2001a, b) mapped dispersal pathways in a system of interconnected ponds, measured dispersal rates, computed effective geographic distances between the different ponds taking into account these pathways, and found a positive correlation between this effective geographic distance and genetic differentiation of *Daphnia* between different ponds.

Studies on the relative importance of local control vs. regional influence in structuring zooplankton community structure are strikingly scarce. A lot of research has focused on local factors that structure zooplankton community, resulting in a rich body of literature identifying, among others, the presence of macrophytes and fish as major factors that determine zooplankton community structure (for a review of interactions in shallow lakes, see Scheffer 1998). Few studies have, however, incorporated both local and regional factors simultaneously into their design or observations. Moreover, the results show opposite conclusions. Shurin et al. (2000) found observational evidence for the importance of regional factors. Unsaturated local communities are evident through linear local vs. regional species richness curves, suggesting the importance of dispersal limitation in structuring local zooplankton communities. Yet, Lukaszewski et al. (1999) and Shurin (2000) found communities to be very resistant to invading species through biotic interactions in an experimental setup. Using observational data and multivariate data analysis, Pinel-Alloul et al. (1995) were the first to incorporate both local environmental variables and the regional (the spatial configuration of the different lakes) factors in a study on zooplankton community structure. They could decompose the zooplankton variation in independent local and spatial components. Due to the large geographic extent of the study (an area of  $\sim 3 \times 10^5 \text{ km}^2$ ), however, the spatial gradient was completely confounded in the important abiotic gradient, thus not discriminating between abiotic factors and dispersal phenomena. Their results suggest that zooplankton dispersal is fairly uniform among lakes within a geographic area of  $\sim 3 \times 10^5 \text{ km}^2$ .

Studies incorporating dispersal in relation to zooplankton species living in discrete habitat patches (lakes, ponds, reservoirs, rock pools; Pinel-Alloul et al. 1995, Shurin 2000) suppose dispersal with bird vectors (Proctor 1964, Proctor and Malone 1965, Proctor et al. 1967), human movement (Duffy et al. 2000), or wind (Brendonck and Riddoch 1999). These pathways are mostly long-distance transportation and/or low-probability events (Jenkins and Underwood 1998). A second mode of dispersal, the movement of adult individuals and resting stages through connecting elements (Thorpe et al. 1994, Stoeckel et al. 1996, Michels

et al. 2001b), may exert a much greater and continuous influence on local interactions. The set of interconnected ponds "De Maten" (Belgium) can be considered a model system to study the latter type of interactions. The connected and neighboring ponds potentially harbor a metacommunity of local zooplankton communities, since dispersal between the different ponds through the connecting elements was found to be substantial (Michels et al. 2001b). Cottenie et al. (2001) discussed differences in local community structure in different ponds of the system in terms of local biotic and abiotic environmental factors. The current study integrates both the local environmental variables and the spatial configuration of the interconnected ponds in order to (1) look for direct observational evidence of metacommunity structure in the zooplankton communities of the ponds in this pond complex, (2) identify the contributions of both local and regional (spatial) processes in the variation of zooplankton community structure, and (3) verify interannual variation in these contributions by comparing the patterns obtained in three different study years.

#### MATERIALS AND METHODS

The studied ponds are part of the nature reserve "De Maten" in Genk, Belgium, and cover an area of  $\sim 200 \text{ ha}$  (Fig. 1). There is an altitude difference of 15 m between the highest pond (Pond 32, northeast part of the nature reserve) and the lowest pond (Pond 1, southwest part of the nature reserve). The soil is essentially made up of sand. The former marshes were converted to fish ponds around 1400 through the digging of peat and the building of dikes (Daniels 1998). At present, there are 35 ponds in the area, of which 34 were regularly sampled. Fish farming stopped in 1991. The ponds are connected with each other through a system of overflows and rivulets. The main sources of water are two rivulets, one of which mainly feeds a subset of ponds located in the northwest corner of the area (Ponds 18, 19, 21). The ponds are also fed by groundwater. At the other end of the nature reserve, the outflow of water is diverted back to the Stiemerbeek, the main rivulet.

Quantitative zooplankton samples (cladocerans, copepods, and large rotifers) were collected with a 12-L Schindler-Patalas sampler (Wildlife Supply Company, Buffalo, New York, USA). Data for three consecutive years were obtained: 1996 (8 to 10 July; Cottenie et al. 2001), 1997 (22 to 24 July), and 1998 (26 to 28 June). Four random samples were taken in the pelagic zone of each pond. The samples from a given pond and date were combined, filtered through a  $64\text{-}\mu\text{m}$  mesh net, and preserved in 5% formaldehyde (final concentration). Subsamples of 2 mL were taken using a 4-mm pipette (Edmondson and Winberg 1971). All individuals present in the subsample were identified and counted under a stereomicroscope. Different levels of identification were used: (1) cladocerans were identified to

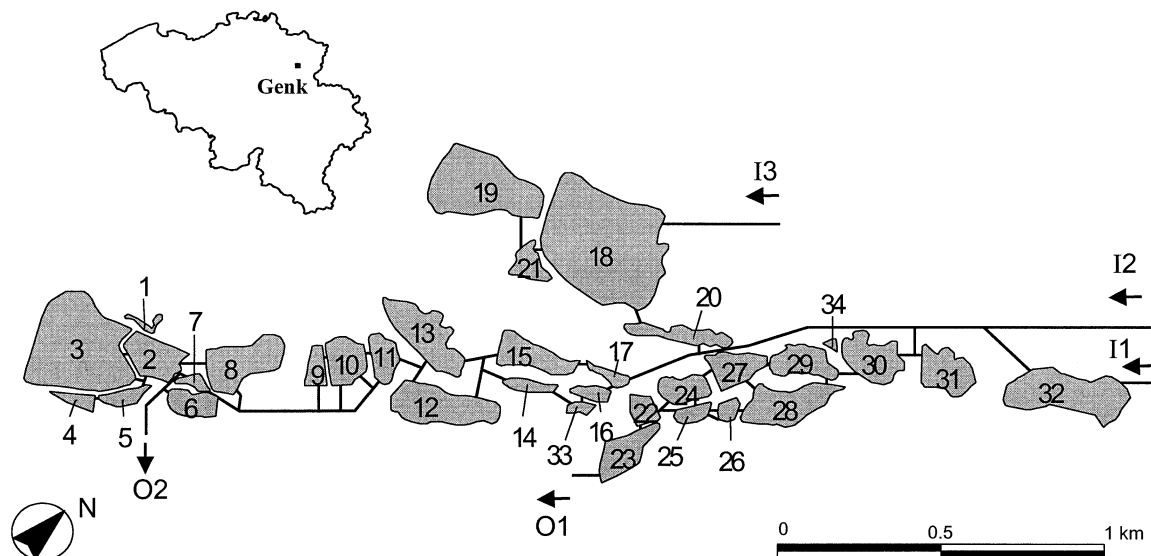


FIG. 1. Location of the nature reserve "De Maten," Genk, Belgium, and the spatial configuration of the different ponds and the connecting elements (overflows and rivulets). There are two different input sources (I1 and I2 come from the Stiemerbeek, and I3 from the Heiweyerbeek), and two output sources (O1 and O2).

species level because different species of the same genus may show important differences in impact on the ecosystem (Gilbert 1988, Gliwicz 1990, Rudstam et al. 1993); (2) copepods were divided into cyclopoid (mainly *Halicyclops neglectus*, *Paracyclops* sp., *Cyclops strenuus strenuus*, and *Acanthocyclops* (*Acanthocyclops*) *vernalis*), calanoid (mainly *Eudiaptomus vulgaris*), harpacticoid copepods, and nauplii; and (3) large rotifers were identified to the genus level. Thus, our study focuses primarily on cladocerans. Filtering the sample through 64- $\mu$ m mesh results in the loss of a large part of the rotifer community. Yet, differences in the rotifer taxonomic composition that were sampled remain informative, and the data were thus included in our analysis. For the Cladocera, a second subsample of 3 mL was taken if there were <50 counted individuals of a particular species. For identification of the cladocerans, the following keys were used: Flöbner (1972), Flöbner and Kraus (1986), and Smirnov (1996).

Outliers (extremely high densities in a few ponds for some species that completely dominated the results, i.e., >200 individuals/L) in the zooplankton data were set to values just slightly higher than the highest value in the rest of the data set ("winsorizing"; Sokal and Rohlf 1981, Cottenie et al. 2001). The species used in Cottenie et al. (2001), selected because they represent >0.1% of the total density, were also used for the other two years (*Bosmina longirostris*, *Ceriodaphnia pulchella*, *Daphnia pulex*, *Daphnia galeata*, *Daphnia ambigua*, *Simocephalus vetulus*, *Scapholeberis mucronata*, *Alona excigua*, *Alona quadrangula*, *Graptoleberis testudinaria*, *Disparalona rostrata*, *Pleuroxus truncatus*, *Pleuroxus trigonellus*, *Chydorus sphaericus*, *Polphemus pediculus*, Cyclopoids, Calanoids, nauplii,

*Brachionus*, *Polyarthra*, *Asplachna*, *Keratella quadrata*, *Keratella cochlearis*). All zooplankton densities were square-root transformed to minimize the effect of high densities (ter Braak and Smilauer 1998). Due to management practices, some ponds were empty during some periods. As a result, no complete data sets are available for these ponds. These ponds were removed from the analysis (1996: Ponds 1, 4, 5, 20; 1997: Ponds 1, 2, 3, 4, 5, 21; 1998: Ponds 1, 5, 11, 14, 20, 29), with a total number of 30, 28, and 28 ponds, respectively.

Although this is a mensurative study, we used inferential statistics to test the different hypotheses. However, the associated *P* values (and the common 5% significance level) should be mainly viewed as the strength of the observational evidence for a certain process to occur (Hurlbert 1984). As we did not use the statistics in an inferential way, there was no need to correct for multiple comparisons when (1) testing the different hypotheses, (2) testing different subsections of a hypothesis, (3) executing the variable selection procedure, and (4) repeating the analyses for the three different years.

If the zooplankton communities show a metacommunity structure (i.e., communities in different locations are coupled through the dispersal of individuals), we expect local communities to be more similar to neighboring communities than to non-neighboring communities. Since overflows and rivulets are very effective dispersal routes (Michels et al. 2001b), we defined "neighboring" as being connected through overflows and rivulets. We consequently constructed a neighboring matrix (Thioulouse et al. 1995). This square and diagonally symmetrical matrix, **D**, has the individual ponds in the rows and columns. If pond *i*

and  $j$  ( $i \neq j$ ) are connected, the cell entry at row  $i$  and column  $j$  ( $d_{ij}$ ) is one, and zero otherwise. The diagonal of the matrix contains zeros (if  $i = j$ ,  $d_{ij}$  is zero) following graph theory (Thioulouse et al. 1995, Urban and Keitt 2001), but does not influence the Mantel test, since only the upper (or lower) diagonal elements are used. The Bray-Curtis dissimilarity measure (Legendre and Legendre 1998) was used to construct the zooplankton dissimilarity matrix based on the zooplankton species composition. If our hypothesis was correct, we expected neighboring ponds to be less dissimilar than non-neighboring ponds, i.e., a negative relationship between the lower triangular elements of the dissimilarity matrix and the neighboring matrix. We used the Mantel test to test the significance of this relationship (Mantel 1967, Legendre and Legendre 1998). The Mantel correlation was computed and its significance was obtained through permutation of the ponds (20 000 times). We used the freeware function `mantel.fcn` (J. H. Reynolds and B. Bolker, available online)<sup>2</sup> for use in S-Plus (MathSoft 1999).

To compute the relative importance of environmental and spatial factors, the spatial configuration of the ponds was used as input, taking into account the connecting elements (flow rate model; Michels et al. 2001a). Within a Geographic Information System (GIS) environment, we computed effective geographic distances between all the ponds in the system, taking into account the connecting elements, the flow rates in those elements, and the current direction (see the Appendix). The matrix of spatial variables (**S**, three final variables) was then constructed in the following way (Pinel-Alloul et al. 1995): (1) the effective geographic distances were transformed into  $xy$  coordinates with principal coordinate analysis, which Michels et al. (2001a) showed to correspond to three different hydrological subgroups of ponds, (2) the coordinates were centered, and (3) a third-degree polynomial was constructed and used in a forward-selection Redundancy Analysis (RDA) procedure with the zooplankton abundances as the dependent matrix. In 1996, the first three variables had significant conditional effects, in 1997 the first two, and in 1998 the first four. The first three elements were used (1996— $y$ ,  $xy^2$ , and  $x$ ; 1997— $y^2$ ,  $xy$ , and  $x^2$ ; 1998— $y^2$ ,  $y$ , and  $x^2y$ ) to avoid differences in explained variance caused by the number of variables in the matrix when comparing the three different years with each other.

The following environmental variables (matrix **E**) were included in the analysis: depth, phytoplankton abundance, total fish density, macroinvertebrate diversity, submerged macrophytes, turbidity, pH, conductivity, oxygen, total phosphorus, and nitrate concentration. Phytoplankton samples were taken at the same time as the zooplankton samples. Phytoplankton abun-

dance was measured as chlorophyll *a* concentration. One 250-mL sample from each lake was filtered through glass-fiber filters (Whatman GF/C; Whatman Incorporated, Clifton, New Jersey, USA). Pigments were extracted in methanol in the dark at 6°C for 24 h. Pigment concentration was measured spectrophotometrically and corrected for degradation products, following the procedure of Talling and Driver (1963). Fish were sampled between 20 and 30 September 1996, between 29 September and 10 October 1997, and between 19 September and 2 October 1998. We sampled in autumn because there is less sampling stress on the animals than in summer, the young-of-the-year are included in the catches, and population densities are stable. During each of the sampling periods, every pond was sampled twice with a fyke (semiquantitative; catch per unit effort, CPUE), once for two days and once for three days (Cottenie et al. 2001). All individuals were counted and identified to species level. The total number of individuals per fyke per day was used as the fish predation pressure. Semiquantitative samples of macroinvertebrates were taken between 10 and 12 July 1996, between 4 and 12 October 1997, and between 29 July and 7 August 1998. The macroinvertebrates were sampled for a fixed time (8–15 min, standardized to CPUE per minute) in each pond using a net with 500- $\mu$ m mesh size (Sutherland 1996). This time-effort method yields reliable data that are suitable for comparing different ponds (Reid et al. 1995). The time allocated to sample macroinvertebrates in different vegetation types in each pond was proportional to the percentage of cover of the different vegetation types in the different ponds. In 1996, the animals were identified and counted in the field using a score (0, absent; 1, one individual; 2, 2–5 individuals; 3, 6–10 individuals; 4, 11–20 individuals; 5, 21–50 individuals; 6, 51 or more individuals). In 1997 and 1998, the samples were preserved in formaldehyde (final concentration 7%), and identified and counted in the laboratory. The following level of identification was used: Planorbidae, Zygoptera, Anisoptera, *Argyroneta aquatica*, Hydracarina, Ephemeroptera, Corixidae, *Ilyocoris*, *Chaoborus* larvae, *Notonecta*, Gerridae, Nepidae, Dytiscidae (adults and larvae), other Coleoptera larvae, Hydro-metridae, *Ranatra linearis*, and Hydrophilidae (adults and larvae) (De Pauw and Vannevel 1993). The exponent of the Shannon-Wiener diversity index (giving the number of taxa, but taking into account the rareness of some taxa; Hill 1973) was used as the measure of the macroinvertebrate diversity. Submerged macrophytes were scored in July 1996, 1997, and 1998 with a three-point score: 0 = absent, 1 = not abundant, 2 = abundant. Water transparency was determined as Secchi disk depth (diameter 25 cm). If the Secchi disk depth could not be measured accurately because the disk was still visible at the bottom of the pond, an arbitrary Secchi disk depth of 100 cm was used as input. Phosphorus concentration was measured follow-

<sup>2</sup> URL: <http://www.biostat.wustl.edu/maillinglists/s-news/200103/msg00154.html>

ing the procedure of Murphy and Riley (1962), adjusted to Watanabe and Olsen (1965). N-NO<sub>3</sub> was measured semiautomatically with a Technicon AutoAnalyzer III (Technicon Instruments Corporation 1966), after reduction to NO<sub>2</sub>. Conductivity, pH, and oxygen concentration were measured in situ with a DataSonde 3 (Hydrolab Corporation, Austin, Texas, USA) in 1996, and with a WTW pH 325 and WTW Oxi 325 (WTW Measurement Systems, Incorporated, Fort Myers, Florida, USA) in 1997 and 1998.

We used these 11 environmental variables as explanatory variables in a forward selection Redundancy Analysis (RDA) procedure, with the zooplankton abundances as the dependent matrix, in order to find a set of parsimonious environmental variables. In 1996, the first three variables had significant conditional contributions; in 1997, the first variable; and in 1998, the first three variables. We used the first three variables selected (1996: depth, turbidity, submerged macrophytes; 1997: turbidity, conductivity, diversity of macroinvertebrates; 1998: pH, nitrate concentration, submerged macrophytes) to compare the different years and the variances obtained with the spatial variables.

To divide the variance in the zooplankton species into local and global components, the procedure of Borcard et al. (1992) and Pinel-Alloul et al. (1995) was used. The total variation in the dependent matrix (zooplankton species abundances) was broken down in different components: total explained variation (corresponds in the univariate case to a multiple regression procedure)  $[E + S]$ , environmental variation  $[E]$ , the fraction of species variation that can be explained by the environmental factors independently of any spatial structure (corresponds in the univariate case to a partial linear regression procedure)  $[E|S]$ , the fraction of species variation that can be explained by the spatial factors independently of any environmental factor  $[S|E]$ . Monte Carlo permutation test (999 new values under the null hypothesis) computed the significance for all these different components. We used permutations under the reduced model (this permutes the raw data in the  $[E + S]$ ,  $[E]$ , and  $[S]$  analyses, and the residuals from the covariables in the  $[E|S]$  and  $[S|E]$  analyses) since this better maintains the Type I error in small data sets (ter Braak and Smilauer 1998). We derived two other fractions (without significance testing): (1) the unexplained variation ( $= 1 - [E + S]$ ) and (2) the spatial structuring in the species data that is shared by the environmental data ( $[E \cap S] = [E] - [E|S] = [S] - [S|E]$ ). We used the linear direct gradient analysis method Redundancy Analysis since a preliminary Detrended Canonical Correspondence Analysis showed that the species respond linearly to gradients (gradient lengths of 1.943, 2.331, and 1.497 standard deviation units of species turnover  $[SD]$  for 1996, 1997, and 1998, respectively [all smaller than 3  $SD$ ]; ter Braak and Smilauer 1998). All the analyses were done with CANOCO

for Windows, version 4.0 (ter Braak and Smilauer 1998).

## RESULTS

Fig. 2 shows the results of the Mantel analysis for the relation of Bray-Curtis dissimilarities in zooplankton abundances and the neighboring-pond matrix. In the three consecutive years, the zooplankton community structure in connected ponds was more similar than in non-connected ponds.

As can be seen in Table 1 and Fig. 3, there is a significant effect of spatial configuration  $[S]$  on the zooplankton species composition in all three years. The spatial component explains ~20% of the variation. The spatial effect is still significant after partialling out the environmental effects  $[S|E]$  over the three years (16.6%, 14.3%, and 13.4%, respectively). The environmental variables also had a significant effect on zooplankton species composition ( $[E]$ : on average 22.5%,  $[E|S]$ : on average 17.3%, and significant in the three studied years).

## DISCUSSION

Our results clearly show that the spatial configuration of the ponds in the pond system of "De Maten" correlates with zooplankton community structure in the local ponds. Both the Mantel test and the variance decomposition showed a significant relationship between the spatial configuration through the connecting elements and species composition. Two alternative interpretations are possible for this pattern: (1) the dispersal of individuals making two directly connected ponds more similar (thus, observational evidence for a metacommunity structure in the zooplankton communities of "De Maten"), or (2) connected ponds have similar environmental conditions. The results of the variance decomposition, however, show that the spatial variation is clearly not correlated with the measured environmental variables, since the fractions explained by correlations between the environmental and spatial variables ( $[E \cap S]$ ) are small (on average 5.2%), in comparison with the pure spatial and pure environmental variation (on average 14.8% and 17.3%, respectively). The only other similar study on zooplankton community structure in relation to spatial and environmental variables is the study by Pinel-Alloul et al. (1995). Their study showed a distinctly different pattern, with a much stronger correlation between spatial configuration and (abiotic) environmental conditions (~13%). The difference between our study and the study by Pinel-Alloul et al. (1995) is likely to be due to the different spatial scales of the two studies. The confounded explanation of the zooplankton variation by the spatial structure and the environmental variables found in the Pinel-Alloul et al. (1995) was caused by the large sampling area ( $3 \times 10^5$  km<sup>2</sup>), which resulted in broad-scale spatial structuring of the physical and chemical lake conditions. Both geomorphological and

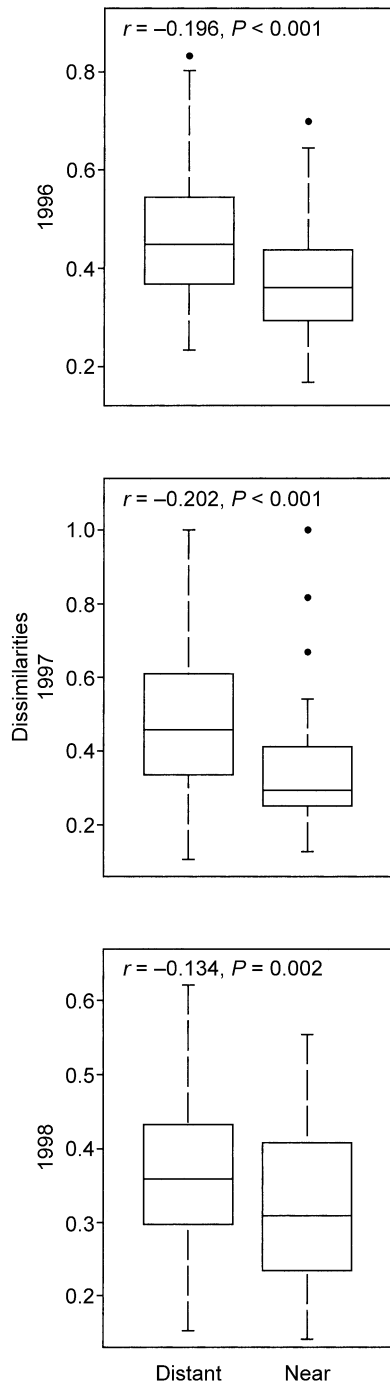


FIG. 2. Boxplots of Bray-Curtis dissimilarities in zooplankton species composition between neighboring ponds (directly connected through overflows; near) and not directly connected to each other (distant) in the three different years. Boxes represent the interquartile range, the central bar represents the median, the whiskers represent the range of the data, and the outliers are points lying outside 1.5 times the interquartile range. The reported  $r$  value is the Mantel correlation coefficient between the Bray-Curtis dissimilarities and the neighboring-pond matrix, and the  $P$  value is the Mantel  $P$  value, computed with 20 000 permutations.

TABLE 1. Variance partitioning and associated  $P$  values of the zooplankton data matrix for the three different study years at the ponds of "De Maten" nature reserve in Genk, Belgium, into different components.

Variation	1996		1997		1998	
	Variance explained (%)	$P$	Variance explained (%)	$P$	Variance explained (%)	$P$
[E+S]	38.6	0.001	37.6	0.001	35.4	0.001
[E]	22.0	0.001	23.3	0.001	22.1	0.001
[S]	18.9	0.001	20.4	0.003	20.4	0.001
[E S]	19.7	0.001	17.2	0.005	15.5	0.017
[S E]	16.6	0.003	14.3	0.031	13.4	0.049
[E∩S]	2.3		6.1		7.1	
1 - [E+S]	61.4		62.4		64.6	

Notes: The components are: [E+S] = total variation explained by all environmental and spatial variables together, [E] = variation explained by environmental variables, [S] = variation explained by spatial variables, [E|S] = pure environmental variation, [S|E] = pure spatial variation, [E∩S] = the spatial structuring in the species data that is shared by the environmental data, and 1 - [E+S] = unexplained variation.

geological processes (hardness, alkalinity, acidity, and metal contamination) and climatic processes (wind dispersion of pollutants and sulfate deposition by acid precipitation) resulted in important northeast to southwest gradients of alkalinity, hardness, and sulphate; and southwest to northeast gradients of acidity and metal contamination that influence zooplankton community composition. Contrastingly, our study area comprised an area of 2 km<sup>2</sup> with all ponds belonging to the same functional unit (all ponds share the same main rivulet as source of water). This diminishes the probability of the occurrence of important abiotic (or biotic) spatial gradients, which could structure the zooplankton community structure, and enables us to disentangle the impact of spatial and environmental variables nicely.

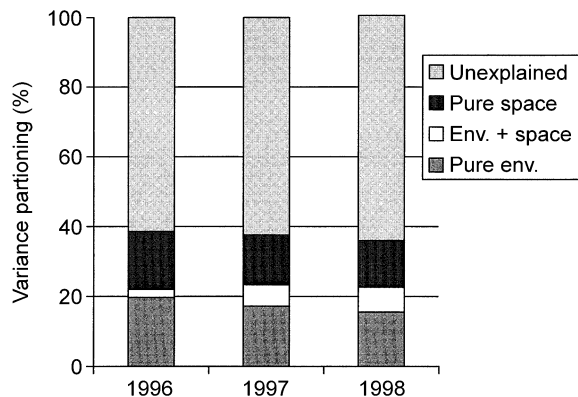


FIG. 3. Variance partitioning (%) of the zooplankton data matrix in the three different years of study. Four different components are given: pure environmental variation, pure spatial variation, the spatial structuring in the species data that is shared by the environmental data, and the unexplained variation.

The regional process of dispersal that we have incorporated into our study is fundamentally different in its effect from earlier studies (e.g., Shurin et al. 2000), due to the difference in geographic scale and/or degree of continuous connectivity of our model system. Shurin et al. (2000) start from the assumption that regional processes (i.e., dispersal) may act as a limiting factor, preventing species from colonizing certain lakes just because they can not get that far. This can, for instance, result in unsaturation patterns of local and regional species diversity. The ponds in our study area, however, are very closely situated to one another and are highly interconnected through overflows and rivulets. Michels et al. (2001*b*) measured average dispersal rates of 3600 zooplankton individuals/h in connecting elements. Thus, the probability of dispersal limitation in our system is very low. Rather, dispersal is likely to act as an homogenizing force, and the spatial factors singled out in our variance decomposition analysis can be viewed to quantify the degree to which dispersal directly influences community structure of neighboring ponds, providing evidence for a metacommunity structure. Thus, dispersal is not a limiting, but a structuring force. This is an interesting perspective, given that dispersal rates are so high in the pond system (Michels et al. 2001*b*).

Environmental variables explained a significant portion of zooplankton community structure during the three years. In all three years, environmental variables associated with clear water–turbid alternative equilibria in shallow lakes as outlined by Scheffer (1998), were selected (turbidity, submerged macrophytes, diversity of macroinvertebrates, and nitrate concentration) as contributing significantly to community structure. For 1996, Cottenie et al. (2001) could divide the different ponds of the study system as being in the clear water phase, the turbid phase, or in an intermediate phase, with each state being characterized by their specific zooplankton species composition and set of environmental variables. In that study, we gave two alternative explanations for the intermediate phase: it could either be a true transition phase between the two stable states or be the result of continuous dispersal. This second explanation can be tested by quantifying for every pond in 1996 if it was downstream from both a clear and a turbid pond or from an intermediate pond (“success”), or from only clear or turbid ponds (“failure”). If intermediate ponds are a result of the dispersal from both clear and turbid ponds or intermediate ponds, we expect the relative proportion of “successes” to “failures” to be significantly higher in intermediate ponds (proportion = 1.2) than in clear or turbid ponds together (proportion = 0.36). Fisher’s exact test cannot reject the hypothesis of no relation between the state of the pond and the success rates ( $P = 0.24$ ). Therefore, it is not likely that the intermediate zooplankton community type is the mere result of a mixed community

caused by the continuous dispersal from both a clear and turbid zooplankton community.

Two methodological limitations should be taken into account when interpreting our results. First, similar to most studies considering a larger number of populations (e.g., Pinel-Alloul et al. 1995, Shurin et al. 2000), the present study considered only a yearly snapshot of zooplankton community structure, since we did not take any seasonal dynamics into account. A silent assumption in correlating zooplankton community structure to environmental variables in such multi-pond observational studies is that all the ponds studied show temporal coherence (i.e., synchronous fluctuations in one or more parameters among locations within a geographic region; Magnuson et al. 1990). The literature, however, shows conflicting evidence: both no correlation and positive correlations among lakes were observed by Kratz et al. (1987) and Rusak et al. (1999) for some species, on a yearly scale, and by George et al. (2000) for total summer zooplankton abundances on a seasonal scale.

A second methodological limitation is a classical structural problem in any observational multivariate community analysis. As we did not measure all possible environmental variables, it is possible that some variables not measured affect the zooplankton community structure in connecting ponds. This limitation makes our interpretation with respect to the importance of local ecological conditions in determining zooplankton community structure conservative, and would further reduce the importance of the spatial component. Moreover, the environmental factors that we incorporated in our study are known to be important structuring variables in shallow lakes (Scheffer 1998), and were also found to be important in our study system (Cottenie et al. 2001).

Our study is the first that estimates the independent components of local and regional factors to variation in (zooplankton) community structure in strongly interconnected bodies of water. There are a few other studies in interconnected systems that take into account the spatial configuration and/or the connections between different water bodies. Lewis and Magnuson (2000) found a combination of both local and regional factors affecting local snail assemblages. Lakes with more connections to other lakes (high lake order) had higher species diversity than isolated lakes (low lake order). Riera et al. (2000) found, among other things, a relation between lake order and crayfish abundance, levels of chlorophyll *a*, and fish richness. Nevertheless, no relation between plankton dry mass and lake order was found. None of these studies included a variance decomposition or partial regression model to determine the individual importance of local and regional factors. This is important since other local environmental variables showed the same dependence to connectivity, and could be responsible for this pattern. Three other studies in very different systems present causal models

to explain local community structure based on interactions between local and regional factors. Magnuson et al. (1998) estimated the relative importance of local (extinction) variables vs. isolation (regional) variables in structuring fish assemblages in small northern forest lakes. They found the extinction parameters collectively to be more important than the regional variables, probably due to the temporal scale involved in the two different processes. Hershey et al. (1999) illustrated the importance of effective colonization routes, together with lake depth and area, in determining local fish community in arctic lakes with a geomorphic-trophic model. The lake trout community only occurs in deep, large, and easily accessible lakes, which in turn control local trophic structure. Bornette et al. (1998) showed that aquatic plant community structure in riverine wetlands are structured through the interplay of the nature of connectivity, its intensity, and the geomorphological characteristics of the channels.

Based on our results, we propose the following model for the community dynamics in the ponds of "De Maten," which effectively integrates both local and regional processes in this system. Because of the small geographic area, the existence of different species pools for the different ponds is very unlikely. Dispersal limitation can be considered nonexistent. Local biotic and/or abiotic and/or random factors regulate zooplankton community structure in a specific pond. In addition to this local structuring, continuous dispersal of individuals through connecting elements (overflows and rivulets) reduces the local differences between the different ponds, resulting in communities that are more similar. This is, however, limited to directly connected ponds, because the downstream pond acts as a buffer to the further dispersal of individuals from the upstream pond. Given this scenario, the striking differences in zooplankton community structure that remain among the ponds are intriguing (Cotténie et al. 2001), and suggest that local environmental factors can be very powerful in structuring zooplankton community in the face of high dispersal rates (Michels et al. 2001b).

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#### APPENDIX

A construction of the effective geographic distance matrix is available in ESA's Electronic Data Archive: *Ecological Archives* E084-021-A1.