



Zooplankton community structure and environmental conditions in a set of interconnected ponds

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Abstract

We studied the zooplankton community structure in a set of 33 interconnected shallow ponds that are restricted to a relatively small area ('De Maten', Genk, Belgium, 200 ha). As the ponds share the same water source, geology and history, and as the ponds are interconnected (reducing chance effects of dispersal with colonisation), differences in zooplankton community structure can be attributed to local biotic and abiotic interactions. We studied zooplankton community, biotic (phytoplankton, macrophyte cover, fish densities, macroinvertebrate densities), abiotic (turbidity, nutrient concentrations, pH, conductivity, iron concentration) and morphometric (depth, area, perimeter) characteristics of the different ponds. Our results indicate that the ponds differ substantially in their zooplankton community structure, and that these differences are strongly related to differences in trophic structure and biotic interactions, in concordance with the theory of alternative equilibria. Ponds in the clear-water state are characterised by large *Daphnia* species and species associated with the littoral zone, low chlorophyll-*a* concentrations, low fish densities and high macroinvertebrate densities. Ponds in the turbid-water state are characterised by high abundances of rotifers, cyclopoid copepods and the opposite environmental conditions. Some ponds show an intermediate pattern, with a dominance of small *Daphnia* species. Our results show that interconnected ponds may differ strongly in zooplankton community composition, and that these differences are related to differences in predation intensity (top-down) and habitat diversity (macrophyte cover).

Introduction

Several studies have investigated the relationships between environmental variables and zooplankton community structure in ponds or lakes situated in a large geographic area (e.g. Pinel-Alloul et al., 1995: area = 236 000 km²; Tittel et al., 1998: area = 15 300 km²; Keller & Conlon, 1994: area = 110 km²). These studies clearly indicated a hierarchy of ecological factors. However, such large-scale surveys will tend to reveal gross patterns determined by strong differences in water quality, or soil type, which interact with tolerance levels of the taxa at different trophic levels. This may impede the determination of the relative importance of specific factors that may act on a background of local conditions. In addition, the regional species pools that are the source of the zooplankton community of individual ponds in a large geographic area may differ among habitats because

of the limited geographic range of certain species and chance events associated with colonisation. Some species have even been shown to have different environmental preferences in different regions (Patalas, 1971; Sprules, 1975). Finally, even if the ecological context is very similar, the ponds may differ strongly in their history. Differences in fish stocking, recreational use, inundation frequency and egg banks may all have consequences for the actual community structure.

Part of the unexplained variance in zooplankton community structure may stem from local community dynamics and small-scale spatial variation. Many studies have, for instance, indicated the importance of biotic interactions in structuring local communities, both in relatively deep (Carpenter et al., 1985; Carpenter & Kitchell, 1993) and shallow (Scheffer et al., 1993; Scheffer, 1998) lakes. Scheffer et al. (1993) developed a model of two alternative stable states in shallow lakes. One equilibrium state, which predom-

inates at low nutrient concentrations, is characterised by abundant macrophytes and clear water. This state is stabilised by high zooplankton grazing rates, low planktivorous and benthivorous fish abundances and high piscivorous fish abundances. The other state is characterised by abundant phytoplankton and turbid water at relatively high nutrient concentrations. The turbid state is stabilised by light limitation due to algal blooms. At intermediate nutrient levels, both alternative stable states can occur. This illustrates that, within a given background of abiotic conditions, biotic interactions may strongly influence both function and community structure at different trophic levels, including the zooplankton. Irrespective of the importance of large-scale studies, there is a need of detailed studies on a small scale to determine how local interactions may determine zooplankton species composition.

To evaluate the relative importance of local biotic and abiotic interactions associated with zooplankton community structure in a system with a similar overall ecological background, we studied a set of 33 neighbouring and interconnected ponds. The ponds are all situated in a relatively small area (200 ha; 'De Maten', Genk, Belgium), receive water from the same sources and are interconnected, resulting in essentially the same regional species pool for the individual ponds. Hence, it reduces the possibility of geographic and climatic variability between the different ponds as an explanation of differences in species composition. Moreover, the network of connecting overflows and rivulets can easily transport individuals from one pond to the other, so chance effects are much reduced (Michels et al. 2001), unlike in the case of dispersal of resting stages via waterfowl (Proctor, 1964; Proctor & Malone, 1965). Finally, the history of the ponds is more or less similar. All ponds were used as fish ponds until 1990. Fish culture activities consisted of regular carp stockings, followed by drainage (Daniëls, 1998). Irrespective of their similar ecological background and history, the ponds still differ widely in ecological conditions, including water transparency. As it is likely that differences between the zooplankton communities of the different ponds are due to differences in internal ecological processes, we relate our observations on zooplankton communities to variation at the other trophic levels (fish and phytoplankton densities, macrophyte cover, macroinvertebrate diversity), as well as to abiotic characteristics (morphometric variables, turbidity, eutrophy, pH, conductivity). More specifically, it was our aim to test the hypothesis (1) that zooplankton communities in neighbouring and interconnected

ponds can differ strongly in species composition, and (2) that the observed differences are to an important extent related to biotic factors rather than abiotic factors.

Study area: 'De Maten' (Belgium)

The ponds studied are part of the nature reserve 'De Maten' (Genk, Belgium), and cover an area of 200 ha (Fig. 1). There is an altitude difference of 15 m between the highest pond (Pond 32, NE part of the nature reserve) and the lowest pond (Pond 1, SW part of the nature reserve). The soil consists essentially of sand. The marshes were converted to fish ponds around 1400 by peat-digging and the building of dikes (Daniëls, 1998). At present, there are 35 ponds in the area. 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 N–W 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 again diverted to the Stiemerbeek, the main rivulet.

Materials and methods

Sampling and sample processing

Quantitative zooplankton samples (cladocerans, copepods and large rotifers) were collected with a 12 l Schindler-Patalas sampler (Vanni et al., 1997) between 8 and 10 July 1996 in 33 different ponds. Four random samples were taken in the pelagic zone of each pond. The samples from a given pond were combined, filtered through a 64 μm mesh net and preserved in 5% formaldehyde (final concentration). Subsamples of 2 ml (total volume 60 ml) were taken using a 4 mm pipette (Edmondson & 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 species level because different species have different important impacts on the ecosystem (Scheffer, 1998), (2) copepods were divided into cyclopoid (mainly *Halicyclops neglectus*, *Paracyclops* sp., *Cyclops strenuus strenuus* and *Acanthocyclops vernalis*), calanoid (mainly *Eudiaptomus vulgaris*), harpacticoid copepods and nauplii, and (3) large rotifers were identified to the genus level. For the Cladocera, a second

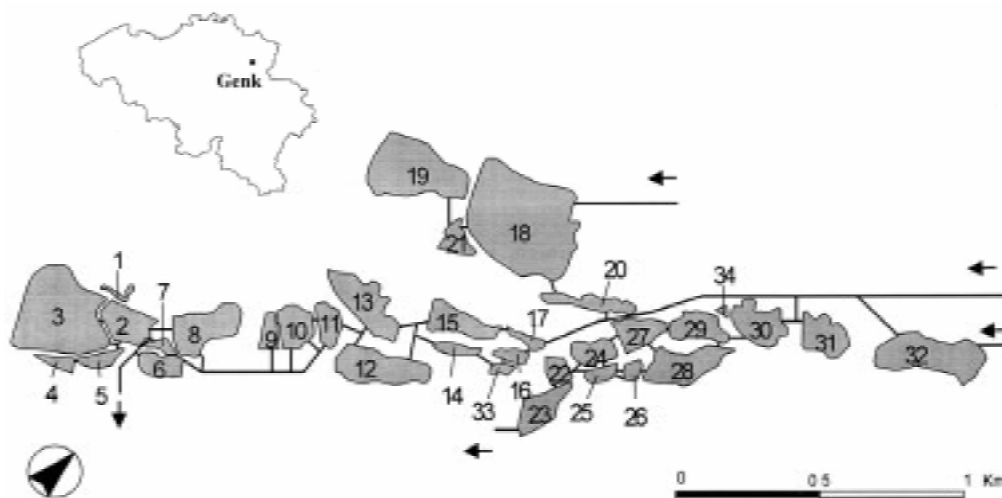


Figure 1. Geographical position of the study area, the nature reserve 'De Maten' ($50^{\circ} 57' N$, $5^{\circ} 27' E$; Genk, Province of Limburg, Belgium). Map of the pond complex showing pond numbers. Arrows indicate the in- and outflows, with the overall direction of water flow from Pond 32 to Ponds 3 and 5. The total altitudinal difference between the ponds is 15 m.

subsample of 3 ml was taken if the number of counted individuals was less than 50 for a particular species. For identification of the cladocerans, the following keys were used: Flößner (1972), Flößner & Kraus (1986) and Smirnov (1996).

Semi-quantitative samples of macroinvertebrates were taken between 10 and 12 July 1996. The macroinvertebrates were sampled during 8 min in each pond using a net with $500 \mu\text{m}$ mesh size (Sutherland, 1996). This time-effort method yields reliable data that are suitable to compare different ponds (Reid et al., 1995). The time allocated to sample different vegetation types in each pond was proportional to the percentage cover of the different vegetation types in the different ponds. The animals were identified and counted in the field. The following level of identification was used: Planorbidae, *Argyroneta aquatica*, Hydracarina, Ephemeroptera, Zygoptera, Anisoptera, Gerridae, Hydrometridae, *Nepa cinerea*, *Ranatra linearis*, Corixidae, *Ilyocoris*, *Notonecta*, Dytiscidae (adults and larvae), other Coleoptera larvae, Hydrophilidae (adults and larvae) and *Chaoborus* larvae (De Pauw & Vannevel, 1993). For each taxon and pond, the number of individuals was assessed using a score (0 = absent; 1 = 1 individual; 2 = 2–5; 3 = 6–10; 4 = 10–20; 5 = 20–50; 6 = > 50 individuals). We also sampled all the ponds once during the night (July 23, 1996) using a Schindler–Patalas trap to collect *Chaoborus* larvae, known to exhibit diel vertical mi-

gration behaviour in the presence of fish (La Row & Marzolf, 1970; Berendonk & O'Brien, 1996).

Fish were sampled between 20 and 30 September 1996, because in autumn there is less sampling stress on the animals, the young-of-the-year are included in the catches and stable population densities. Every pond was sampled twice with a fyke (semi-quantitative; catch per unit effort, CPUE) once for 2 days and once for 3 days. All individuals were counted and identified to species level. A random sample of 40 fish (if present) were measured and the total wet biomass for each species was determined. CPUE is the average biomass or number of individuals per species per fyke per day. For data analysis, we lumped the fish in three functional groups: planktivorous, benthivorous and piscivorous fish.

Phytoplankton samples were taken at the same time as the zooplankton samples. Phytoplankton abundance was measured as chlorophyll-*a* concentration. One 250 ml sample from each lake was filtered through glass-fiber filters (Whatman GF/C). 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 & Driver (1963).

Vegetation cover was studied between 10 and 12 July 1996. We distinguished among three groups of macrophytes: emergent vegetation (dominated by *Typha* species and *Phragmites australis*), submerged macrophytes (mainly *Utricularia* and *Potamogeton*

species) and species with floating leaves (mainly *Nuphar*). We used the following scores to quantify the occurrence and abundance of the different macrophyte types: (1) emergent species: 0 = absent, 1 = almost none, 2 = poorly developed littoral zone, 3 = reasonably developed littoral zone, 4 = well developed littoral zone with high abundances but low diversity, 5 = well developed littoral zone with high abundances and high diversity. We distinguished between score 4 and 5 because it was judged that a high diversity in emergent macrophytes creates a higher structural diversity. This problem does not occur with the other two macrophyte types; (2) submerged macrophytes: 0 = absent, 1 = not abundant, 2 = abundant; (3) floating vegetation: 0 = absent, 1 = less than 3% coverage, 2 = 3–5%, 3 = 5–10%, 4 = 10–20%, 5 = 20–50%, 6 = 50–100%.

Total phosphorus concentration was measured following the procedure of Murphy & Riley (1962), adjusted to Watanabe & Olsen (1965). N-NO₃ was measured semi-automatically with a Technicon AutoAnalyzer III (Technicon corporation, 1966), after reduction to NO₂. Fe was measured with a Perkin Elmer 2260 Atomic Absorption Spectrometer (Perkin Elmer Corporation, 1982). Conductivity, pH and O₂ concentration were measured *in situ* with a DATA SONDE 3 (Hydrolab). Water transparency was determined as Secchi disk depth (diameter 25 cm). If the Secchi disk depth could not be measured accurately because of the disk was still visible at the bottom of the pond, an arbitrary Secchi disk depth of 100 cm was used as input.

Morphometric variables of the lake were measured in the field (depth) or using the GIS environment of IDRISI (Version 2.0; Clark lab, 1997) after digitising maps of the different ponds (area [module AREA] and perimeter [module PERIM]; Michels et al., 2001).

Statistical analysis

Outliers (>3 standard deviations from the mean) in the zooplankton data were set to values just slightly higher than the highest value in the rest of the data set. This 'winsorizing' (Sokal & Rohlf, 1981) allowed us to work with the complete data set rather than to have to delete outliers, and needed to be applied to approximately 3% of the data. Zooplankton species with a total abundance less than 0.1% of the total zooplankton individuals or occurring in only one pond were not included in the multivariate analysis. All zooplankton densities were square-root transformed to minimize

the effect of high densities (ter Braak & Smilauer, 1998), and following the suggestion of Downing et al. (1987) with respect to sampling variability in zooplankton.

The general strategy in treating the environmental variables was an *a priori* reduction in the number of variables. In order to have a reliable redundancy analysis (RDA), the number of environmental variables should be less than the number of ponds included in the analysis (ter Braak & Smilauer, 1998). We screened for significant correlations among variables derived from the same trophic level, and correlated variables were substituted by compound variables. All the biotic variables were square-root transformed, unless scores were used.

The macroinvertebrate data were reduced to two compound variables: the exponent of the Shannon–Wiener diversity index (giving the number of taxa, but taking into account the rareness of some taxa; Hill, 1973) and the total number of individuals in each sample (adding the average number of individuals for each scoring class over all taxa for each sample).

No piscivore fish species were caught in the fykes. There was a highly significant correlation between the planktivorous and benthivorous fish densities (both biomass and abundances) with total fish densities (square-root transformation; biomass total fish-planktivorous fish: $r=0.82$, $p<0.001$; biomass total fish-benthivorous fish: $r=0.97$, $p<0.001$; densities total fish-planktivores: $r=0.83$, $p=0.001$; densities total fish-benthivorous fish: $r=0.89$, $p<0.001$; total densities-total biomass: $r=0.91$, $p<0.001$). We therefore used only the square-root transformed total densities as input. The ratio of square-root transformed planktivorous fish densities on the square-root transformed benthivorous fish densities was not correlated with total fish density, and was included to differentiate the effects of planktivory from turbidity caused by benthivory. The three different macrophyte types were used as independent variables.

Water transparency (Secchi disk depth), total phosphorus, N-nitrate, chlorophyll-*a* concentrations were square-root transformed. pH, conductivity, oxygen and Fe were not transformed. We used the square-root transformed area as a measure of size of the pond. Depth is not correlated with any of these variables, and was used as an independent variable.

A hierarchical clustering method (Ward's method; Ward, 1963), based on the euclidean distances computed with standardised zooplankton densities, constructed different groups of ponds (Statistica; Stat-

Soft inc., 1997). Redundancy analysis (ter Braak & Smilauer, 1998) was used to describe the relationships between the zooplankton species (dependent matrix) and the environmental variables (independent matrix) (CANOCO program; ter Braak & Smilauer, 1998). Because of interference with sampling gear (Pond 1) and partial drainage (Ponds 4 and 5), no reliable fish density estimates could be obtained. These ponds were hence not included in the RDA analysis.

The automatic forward selection procedure (CANOCO, ter Braak & Smilauer, 1998) was used to select those environmental variables that contribute most to the explanation of the species data set. The automatic forward selection procedure computes the significance of the addition of a given variable and the stepwise cumulative variance explained with all the selected variables in the model.

Results and discussion

Pond characteristics

The ponds studied are very shallow (mean depth of 0.5 m) and eutrophied (Table 1). Total P was in the range of very eutrophic waters for all the ponds, whereas chlorophyll-*a* concentration and secchi-disk depths covered the spectrum from meso- to eutrophy (Carlson, 1977). Most of the ponds had the potential to be in both the turbid and clear-water equilibrium state, given the threshold value of 350 $\mu\text{g TP l}^{-1}$ set by Jeppesen et al. (1990) for lakes smaller than 3 ha.

Zooplankton species richness and composition

The number of pelagic cladoceran species (following Keller & Conlon, 1994: *Daphnia* species, *Ceriodaphnia* species, *Diaphanosoma* species, *Scapholeberis mucronata*, *Bosmina longirostris* and *Chydorus sphaericus*) was comparable to the number of species found in ponds with comparable area and depth in other studies. In our study, an average of 5 cladoceran species per pond was found. Dodson (1991) found an average of 4.5 cladoceran species for ponds with an area of less than 6 ha, and Keller & Conlon (1994) found an average of 9 species for ponds with a depth of less than 2 m, approximately half were cladocerans. Within the limited range in habitat sizes of the ponds studied, there was no relationship between the number of species and pond area ($r = -0.007$, $p = 0.96$).

The cluster analysis of the zooplankton data yielded three groups (Fig. 2). Figure 3 shows the densi-

ties of the different zooplankton taxa in the different ponds, grouped according to the results of the cluster analysis (Fig. 2). When the results of the clustering are used as a second labeling variable in the results of the RDA (Figs 4 and 5), it can be seen that there is a tendency for a gradient of Group 1, via Group 2 to Group 3. The moderate length of the species arrows and the blurred differences between the different groups on the graph suggest, however, that the ponds cannot be divided into clearly distinctive groups. If we combine the results of this analysis with the original species data (Fig. 3), some overall distinctions between the different groups can be observed. Ponds in Group 1 are characterised by the presence of *Daphnia pulex*, *Polyphemus pediculus*, *Simocephalus vetulus* and the poor representation of *Bosmina longirostris*, *Daphnia ambigua*, cyclopoid copepods and rotifers. Ponds in Group 2 are characterised by the presence of cyclopoid copepods, *Chydorus sphaericus*, *Ceriodaphnia pulchella*, *Daphnia ambigua*, *Daphnia galeata* and *Bosmina longirostris*. Ponds of Group 3 are mainly characterised by a high abundance of rotifers and cyclopoid copepods.

Alternative equilibria

Figure 4 and Table 1 shows that ponds of Group 1 were characterised by clear water, low chlorophyll-*a* concentrations, low fish densities, and high diversities of macroinvertebrates. Ponds of Group 3 were turbid, whereas ponds of Group 2 had intermediate characteristics.

Figure 6 presents the results of the automatic selection procedure. A sharp decline in significance after the fish densities, and the fact that half of the total variance explained with the full model (30% compared to 60%) is already explained by the first five selected variables (depth, turbidity, submerged vegetation, diversity of macroinvertebrates and fish density), suggests the importance of those variables. Four of these variables (excluding depth) are factors that play a role in the feedback loops determining whether a shallow water body occurs in the clear-water or turbid state (Scheffer et al., 1993).

Substantial variation in ecological conditions was observed among ponds, and this variation was mainly associated with the state (clear-water or turbid state) of the ponds studied (cf. Secchi-disk depth, phytoplankton concentration, fish abundance). It is striking that clear-water and turbid ponds co-occurred in a system in which the ponds were so strongly connected

Table 1. Environmental variables of the different ponds. The following abbreviations were used: O₂=oxygen concentration, cond=conductivity, Fe=Fe concentration, secchi=Secchi-disk depth, N=N-NO₃ concentration, TP= total phosphorus concentration, Chl_a=chlorophyll-*a* concentration, EM=emergent macrophyte cover, FM=floating macrophyte cover, SM=submerged macrophyte cover, DenMI=total density of macroinvertebrates, DivMI=diversity macroinvertebrates, PF/BF=ratio planktivorous versus benthivorous fish densities, DenF=total density of fish. - = fish densities not available. * = for the different scoring systems, see 'Materials and methods'. §= Exponent of the Shannon-Wiener diversity index

Pond	Depth (cm)	Area (ha)	O ₂ (mg l ⁻¹)	Cond (μS cm ⁻¹)	pH	Fe (mg l ⁻¹)	Secchi (cm)	N (μg l ⁻¹)	TP (μg l ⁻¹)	Chl _a (μg l ⁻¹)	EM (score*)	FM (score*)	SM (score*)	DenMI (ind 8 ⁻¹)	DivMI §	PF/BF	DenF (CPUE)		
Group 1	1	4	0.3	9.15	14	5.4	0.17	100	211	198	15	1	1	2	22	4.1	—	—	
	2	10	1.3	6.8	34	7.4	1.9	55	550	280	5	3	5	1	62	3.8	0.0	690.0	
	13	7	2.9	7.8	16	7.7	1.0	100	200	266	4	1	2	2	35	7.3	0.6	6.6	
	14	8	0.6	7.5	39	7.7	2.0	77	197	248	5	1	1	1	60	7.2	1.6	14.5	
	15	7	1.4	9.1	39	8.6	0.4	100	200	235	1	4	0	0	15	5.7	2.0	22.9	
	18	3	9.5	6.1	36	6.7	0.0	100	200	253	2	1	0	0	93	4.1	11.7	50.8	
	21	1	0.3	9.6	12	4.1	0.0	100	167	221	1	5	3	0	15	5.7	0.0	0.6	
	33	6	0.2	6.9	48	7.4	1.0	38	200	321	5	2	6	0	24	3.6	0.7	159.3	
	34	6	0.1	2.6	43	6.9	0.5	100	150	339	5	4	0	0	55	7.6	0.0	5.2	
	Group 2	4	4	0.4	5.7	17	7.4	3.0	100	397	289	1	3	0	0	57	4.8	—	—
		5	2	0.5	5.2	49	7.5	1.9	100	337	235	3	5	0	0	105	6.8	—	—
		6	6	1.1	6.3	11	7.3	0.4	100	550	229	11	5	1	0	10	3.8	5.0	169.4
		16	9	0.4	7.8	39	7.7	0.6	56	183	248	5	3	5	0	35	1.0	2.9	182.2
		19	5	5.2	8.1	34	7.1	0.1	35	187	221	4	1	0	0	26	5.5	0.1	621.2
24		7	1.3	6.2	25	7.2	1.5	53	187	231	5	2	5	0	107	4.1	0.1	31.8	
25		5	0.7	4.8	48	7.3	1.6	100	167	325	1	5	0	0	32	3.6	5.2	6.2	
26		6	0.2	6.4	41	6.9	1.0	100	150	361	1	4	0	0	22	4.5	0.0	0.2	
27		7	1.4	5.8	49	7.5	1.8	40	183	388	4	2	5	0	9	2.9	1.0	644.9	
28		3	1.9	7.5	44	8.0	0.6	100	150	411	1	2	0	0	88	3.3	7.2	70.7	
30		8	1.3	4.4	43	7.2	0.3	50	173	461	3	2	0	2	95	5.1	19.4	364.9	
31		7	1.8	3.7	44	7.2	0.2	67	160	361	2	4	0	0	95	3.3	8.4	61.3	
32		4	2.8	7.9	37	7.7	0.2	30	437	235	20	1	0	0	5	1.9	0.6	92.8	
Group 3		3	7	7.4	6.6	58	7.6	1.4	60	513	488	3	3	0	1	88	3.3	2.1	558.7
	7	4	0.3	6.4	34	7.4	0.3	100	550	280	4	2	0	1	9	1.8	2.7	347.5	
	8	6	2.6	8.6	52	7.9	0.9	32	333	289	13	3	2	1	69	3.8	1.0	249.5	
	9	3	0.6	7.2	73	7.8	4.7	100	277	325	5	1	0	0	1	1.0	24.0	241.7	
	10	3	1.6	7.3	66	7.6	4.8	25	373	226	6	1	0	0	6	2.8	1.1	349.6	
	11	2	0.5	6.8	21	7.7	3.6	20	263	501	30	4	0	0	8	1.0	21.8	85.7	
	12	4	3.0	6.0	21	7.4	6.0	25	260	506	11	2	4	0	4	1.0	0.1	376.3	
	17	3	0.4	7.7	37	7.9	0.3	22	273	334	14	4	0	0	95	3.3	3.4	78.7	
	22	7	0.5	4.9	65	7.5	1.6	30	173	271	1	5	4	0	27	6.3	0.8	441.5	
	23	5	1.3	4.3	60	7.3	1.9	38	200	289	3	4	0	0	13	2.7	0.7	620.7	
	29	4	1.7	6.3	47	7.5	2.2	37	167	316	5	3	4	1	110	7.2	2.8	412.9	

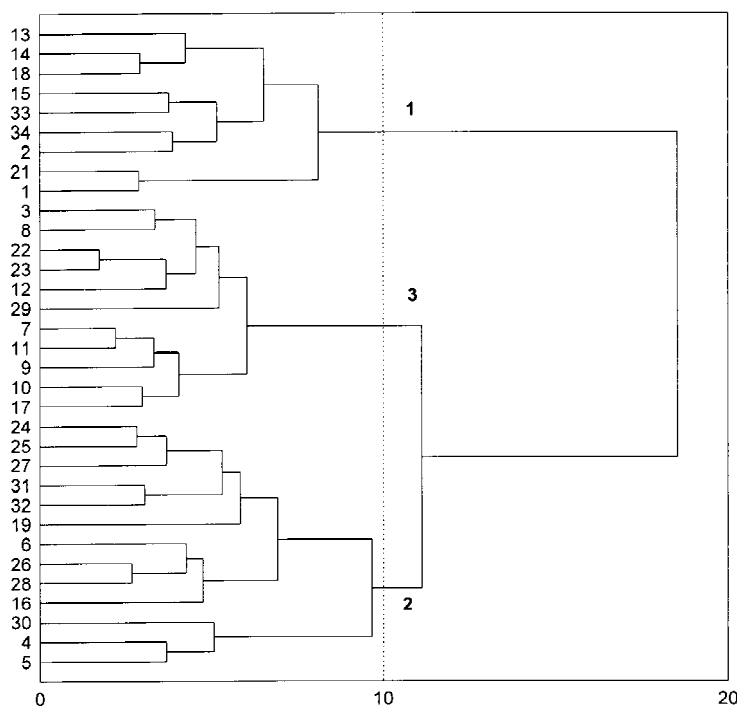


Figure 2. Result of hierarchical clustering analysis (Ward's method), using the Euclidean distance of the square-root transformed 'winsorized' zooplankton data as dissimilarity measure. The numbering of the different clusters is obtained from the results of the multivariate analysis (Figs 4 and 5).

and shared the same water source. Timms & Moss (1984) described a similar situation for the Norfolk Broads in eastern England, with two ponds in a series that were fed by the same river and approximately the same nutrient loadings, were characterised by a very different food web structure. Although our data on zooplankton species composition are largely in agreement with the theory on alternative states developed by Scheffer et al. (1993), it should be noted that our results also suggest that there are three different types of ponds in 'De Maten': clear-water and turbid ponds, and ponds that have characteristics of both types. The ponds in the clear-water state are characterized by large *Daphnia* species (*Daphnia pulex*), species that are associated with macrophytes-species (chydorids, *Simocephalus vetulus* and *Scapholeberis mucronata*) and species that typically occur in clear waters (*Polypheumus pediculus*). Although samples were taken in the pelagic zone of the ponds, they typically also revealed species that are associated with the littoral zone. Timms & Moss (1984) and Irvine et al. (1989) also observed that when macrophytes were present, macrophyte-associated animals also occurred in the pelagic zone of the pond. The dominance of *D. pulex*

and the low relative abundance of other *Daphnia* species suggest the absence of effective fish predation, even though all ponds contained fish. Low fish predation leads to the dominance of large cladocerans either through competitive superiority of large species (size-efficiency theory, Hall et al., 1976; Gliwicz, 1990) and/or size-selective predation by macroinvertebrates (Gliwicz & Pijanowska, 1986; Lampert, 1987). The ponds of Group 1 had the highest macroinvertebrate densities and diversities of all ponds. Only in four ponds, however, were negatively size-selective predators observed in the pelagic zone: Ponds 3 and 9 (both belong to Group 3) harboured some *Leptodora kindtii*, whereas *Chaoborus* larvae occurred in Ponds 13 and 14. The only other predatory macroinvertebrate species that is not strictly associated with vegetation is *Notonecta*, found in Ponds 4, 13, 14, 15 and 34. *Notonecta*, however, is a positively size-selective predator (Murdoch & Scott, 1984). Our results therefore suggest that the size-efficiency relationship plays a role in determining zooplankton community structure in the studied system. The high diversity and densities of macroinvertebrates in ponds of Group 1 can itself be attributed to a combination of two factors: absence

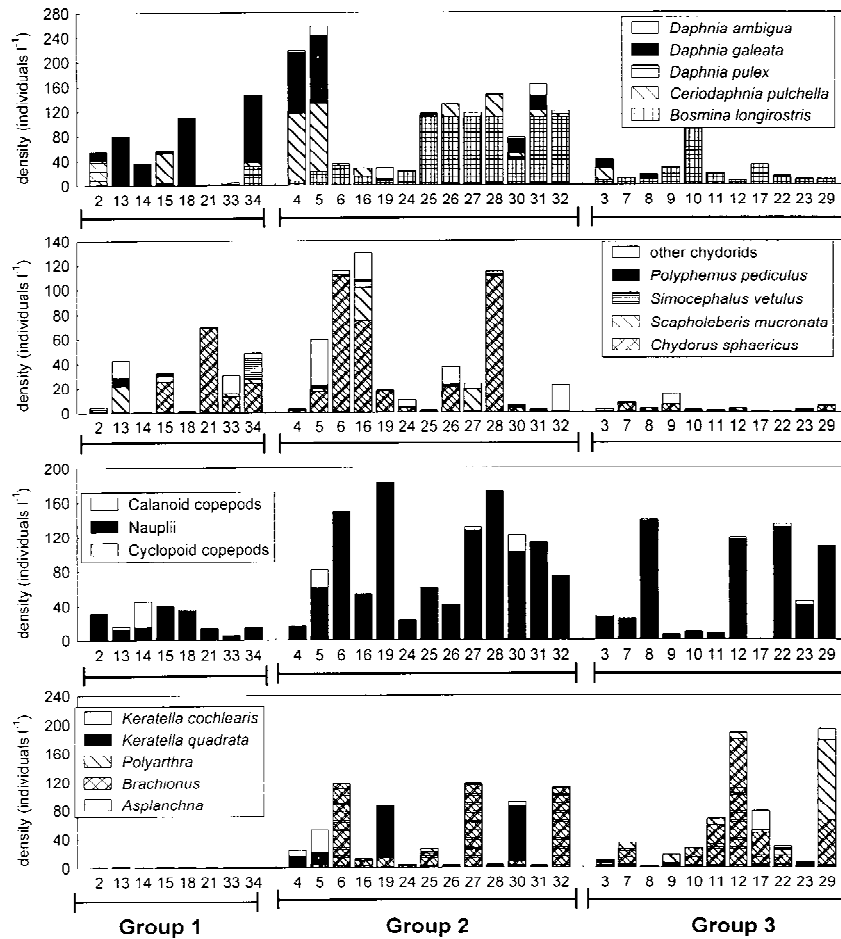


Figure 3. Univariate representation of the 'winsorized' zooplankton densities (individuals l⁻¹). 'Other chydorids' is the sum of *Pleuroxus truncatus*, *Pleuroxus trigonellus*, *Alona quadrangula*, *Alonella excisa*, *Disparalona rostrata*, *Graptoleberis testudinaria*. The ponds are grouped following the results of the cluster analysis (Fig. 2).

of predation by fish and/or the presence of macrophytes, resulting in a more diverse habitat (Crowder & Cooper, 1982; Gilinsky, 1984; Diehl, 1992; van den Berg et al., 1997). Group 3 encompasses ponds in the turbid state, with a dominance of rotifers (*Asplanchna*, *Polyarthra*, *Brachionus* and some *Keratella* species). The negative relation between the presence of *Daphnia* and rotifers has been well documented (Fussmann, 1996). A similar difference in community structure between clear-water ponds with large herbivores and turbid ponds with rotifers has also been found by Reintertsen et al. (1990, 1997). The abundance of cyclopoid copepods in the turbid ponds can be explained by the fact that copepods are relatively efficient at escaping fish attacks (Drenner et al., 1978).

The intermediate zooplankton community structure could be explained in two ways: (1) it could

be a transition phase between the two stable states, or (2) a result of continuous dispersal in this highly interconnected pond system.

A potential problem with the zooplankton data is the fact that the ponds were sampled only once during the seasonal succession of the different ponds. If the seasonal succession between the different ponds is not synchronised, it is possible that 'different' communities were sampled in the different ponds, especially with respect to macrophyte development. We tried to minimize this effect as much as possible by sampling in July, which is the period during which macrophyte vegetation is fully developed. Timms & Moss (1984) observed that the macrophyte cover was quite constant from the end of May to the beginning of August, for three consecutive years, and it was during this period

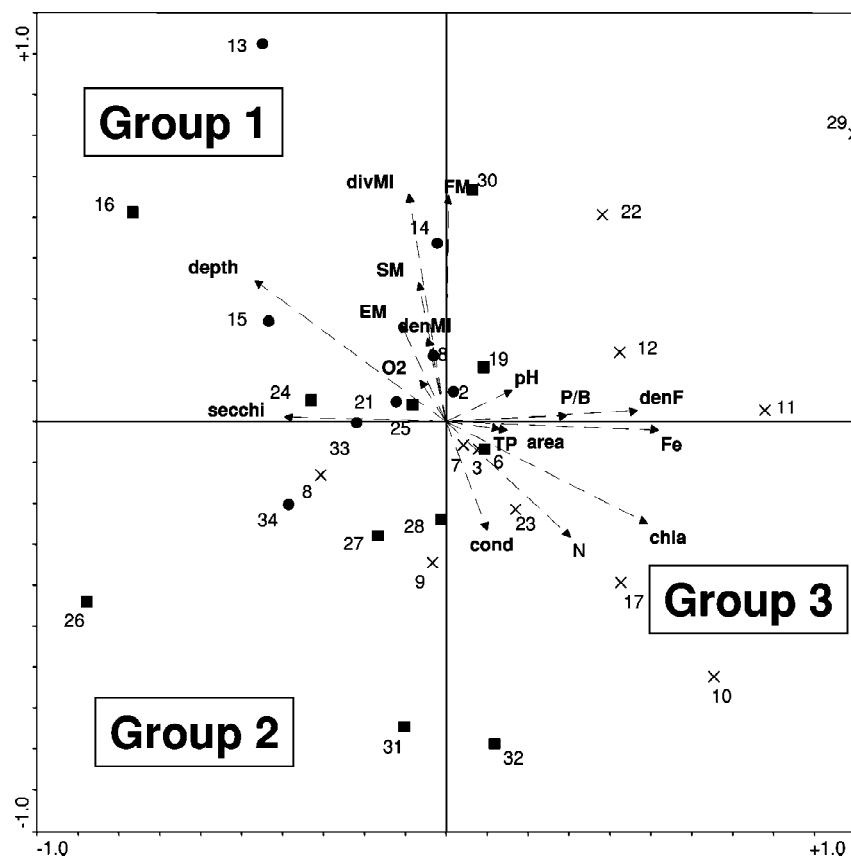


Figure 4. Results of the Redundancy Analysis. Pattern of environmental (independent) variables and ponds. For abbreviations of the environmental variables, see legend Table 1. The position of the ponds is indicated by the number of the pond (see Fig. 1) and the group membership (see Fig. 3): ●=Group 1, ■=Group 2, ×=Group 3.

that the effect of zooplankton on phytoplankton was most noticeable.

We observed no correlation between total phosphorus and chlorophyll-*a*, as one would suspect in a basically three-level trophic system (phytoplankton-zooplankton-planktivores; we observed no piscivorous fish in 'De Maten'). A three level trophic structure should reduce the predation pressure of the zooplankton on the phytoplankton and let bottom-up factors rule. The absence of the relation between total phosphorus and chlorophyll-*a*, however, suggests that other forces control the densities of the phytoplankton. Macrophyte vegetation probably plays an important role (Scheffer et al., 1993). It is, for instance, possible that the zooplankton escapes predation by fish through vertical or horizontal migration (Irvine et al., 1990; Lauridsen & Lodge, 1996).

Our results indicate that neighbouring and even interconnected ponds may differ substantially in their zooplankton community structure, and that these dif-

ferences are strongly related to differences in trophic structure and biotic interactions. Indeed, our analysis indicates that most of the variation in zooplankton community structure is correlated to factors such as fish abundance, macroinvertebrate densities and turbidity. We conclude that in the type of ponds studied (shallow, eutrophied waters), differences in zooplankton community structure may be understood quite well within the framework of alternative stable states developed by Scheffer et al. (1993) and Scheffer (1998). Our results, however, indicate the possibility of a zooplankton community structure which is intermediate to that typical of clear-water and turbid ponds.

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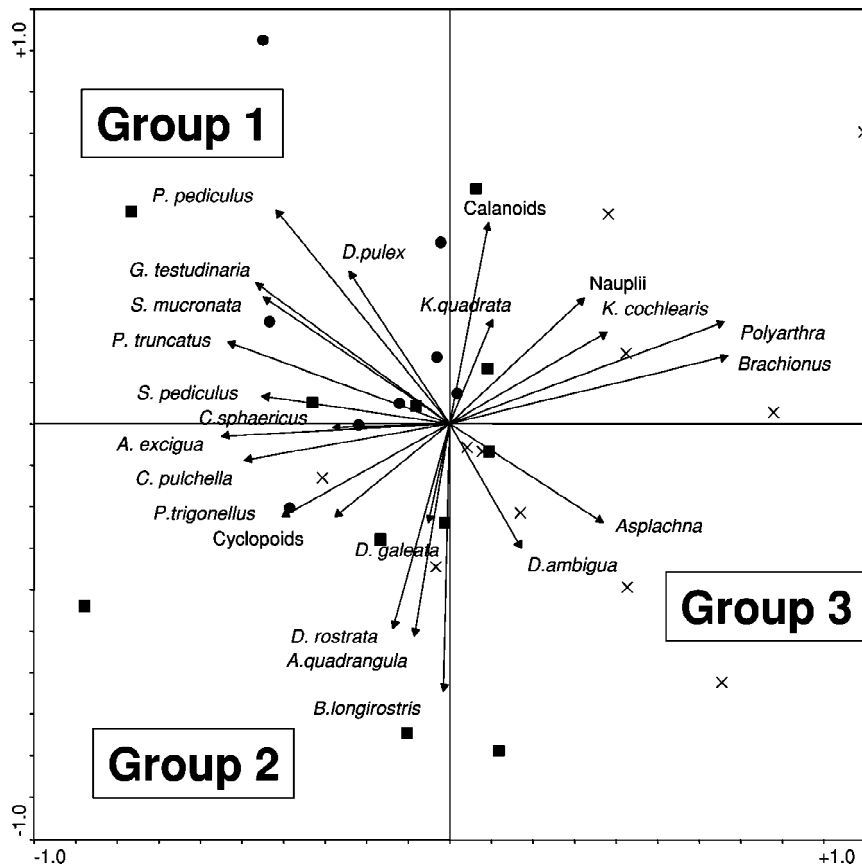


Figure 5. Results of the Redundancy Analysis. Representation of the zooplankton (dependent variables) taxa. The following abbreviations were used: *A. excisa*=*Alonella excisa*, *A. quadrangula*=*Alona quadrangula*, *Asplanchna*=*Asplanchna*, *B. longirostris*=*Bosmina longirostris*, *Brachionus*=*Brachionus*, *Calanoids*=calanoid copepods, *C. pulchella*=*Ceriodaphnia pulchella*, *C. sphaericus*=*Chydorus sphaericus*, *Cyclopoids*=cyclopoid copepods, *D. ambigua*=*Daphnia ambigua*, *D. galeata*=*Daphnia galeata*, *D. pulex*=*Daphnia pulex*, *D. rostrata*=*Disparalona rostrata*, *G. testudinaria*=*Graptoleberis testudinaria*, *K. cochlearis*=*Keratella cochlearis*, *K. quadrata*=*Keratella quadrata*, *Polyarthra*=*Polyarthra*, *P. pediculus*=*Polyphemus pediculus*, *P. trigonellus*=*Pleuroxus trigonellus*, *P. truncatus*=*Pleuroxus truncatus*, *S. mucronata*=*Scapholeberis mucronata*, *S. vetulus*=*Simocephalus vetulus*. Only the symbols representing the group a pond belongs to are shown (see Fig. 4).

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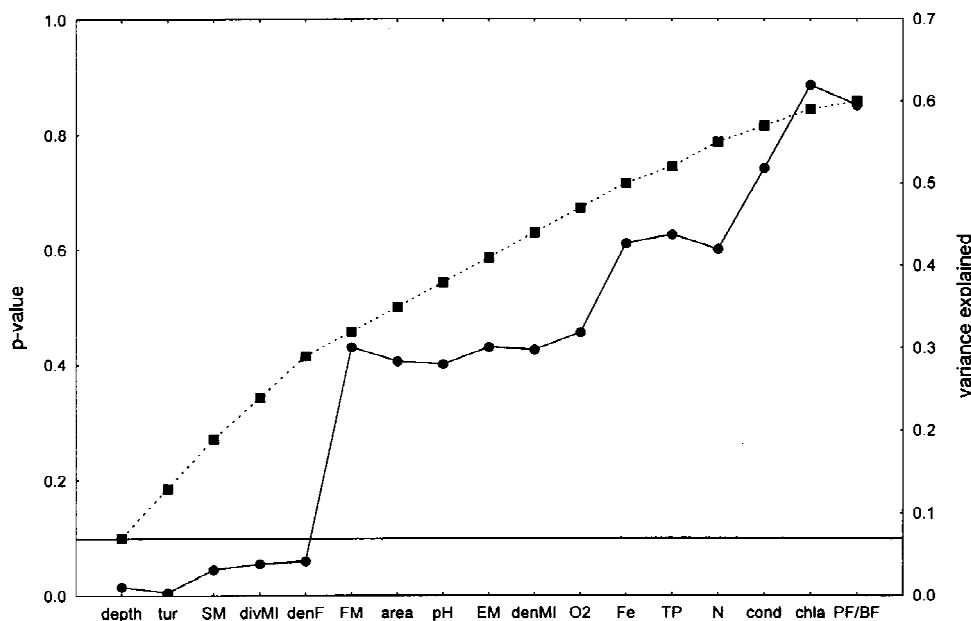


Figure 6. Results of the automatic variable selection procedure. Both the significance of the addition of a certain variable (left Y-axis, ● and solid line) as the variance explained by the selected variables (right Y-axis, ■ and dashed line) are shown. For the list of abbreviations of the environmental variables, see legend Table 1.

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