

**SEASONAL SUCCESSION  
AND SPATIAL DISTRIBUTION  
OF THE ZOOPLANKTON COMMUNITY  
IN THE RESERVOIR OF ESCH-SUR-SÛRE  
(LUXEMBOURG)**

by

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**ABSTRACT**

During three years (1990, 1992 and 1993), the zooplankton community of the Esch-sur-Sûre reservoir was investigated. A total of 75 taxa, dominated by rotifers, was observed. Zooplankton densities increased from the damsite towards the headwaters of the reservoir ; they peaked in spring and at the end of summer. Despite quantitative differences, the same species succession was observed during the three years and at all the lake sampling stations. Thus the zooplankton community shifted from rotifers in early spring to small-bodied cladocerans (*Bosmina* spp.), and, finally, to larger cladocerans (*Daphnia* spp.) in early summer. Shifts in zooplankton composition have also frequently been observed in midsummer, when the cladoceran assemblage of *Daphnia-Bosmina* was generally replaced by a combination of *Ceriodaphnia-Diaphanosoma*. These species successions are discussed in relation to size-selective predation, resource limitation and interspecific competition.

*Key words* : competition, community structure, predation, reservoir, seasonal succession, zooplankton.

**INTRODUCTION**

In early studies, zooplankton species succession was usually considered to be the result of differences in ecological tolerance to various abiotic environmental factors,

such as light intensity and water density or viscosity (e.g. EDMONDSON, 1965; MIRACLE, 1977). More recently, descriptive field studies and laboratory experiments have implicated competition (e.g. SMITH and COOPER, 1982; EDMONDSON, 1985; KERFOOT *et al.*, 1985; LAMPERT and MUCK, 1985; TAYLOR, 1985; THRELKELD, 1985; VANNI, 1986; GILBERT, 1988; LAMPERT and ROTHHAUPT, 1991; WICKHAM and GILBERT, 1991; CONDE-PORCUNA *et al.*, 1994) or predation (e.g. ZARET, 1978; LANE, 1979; STENSON, 1982; RIESSEN, 1985; GULATI, 1990; ARCIFA *et al.*, 1992; RONNEBERGER *et al.*, 1993; KASPRZAK *et al.*, 1993) as factors which may alternately favour one species over another in successional events. In their publication of the « size-efficiency hypothesis », BROOKS and DODSON (1965) popularised the general belief that the coexistence of large — and small-bodied zooplankton species could be explained by a balance between predatory forces and competition. These authors postulated that all planktonic herbivores compete for the « fine particulate matter (1-15  $\mu\text{m}$ ) of the open water », but that large-bodied species are superior competitors, because of their assumed increased filtering efficiency and ability to ingest larger particles. It is presumed that competition forces communities towards larger-bodied species (e.g. *Daphnia*), while fish predation forces them towards smaller-bodied species (e.g. *Bosmina*, rotifers) by selectively removing the larger-bodied forms. In this way, both factors, competition and predation, are believed to interact to cause species replacements in seasonal successions (NEILL, 1975; LYNCH, 1979; GLIWICZ *et al.*, 1981; DEMOTT and KERFOOT, 1982; DEMOTT, 1983; BENDORF and HORN, 1985; GLIWICZ, 1985; GOPHEN and POLLINGER, 1985). At the same time, the role of abiotic factors cannot be ignored because they are well synchronised with changes in the magnitude of food limitation and predation intensity (GLIWICZ and PIJANOWSKA, 1989; SCHMID-ARAYA and ZUÑIGA, 1992).

Until now, there was virtually no work published on the zooplankton of the reservoir of Esch-sur-Sûre. This first paper briefly presents the field data of a three-year study (1990, 1992, 1993) on the zooplankton structure, i.e. vertical and longitudinal distribution, composition and abundance, in the reservoir. The seasonal successions of rotifers and cladocerans during these three years of investigations are described and discussed in relation to predation and competition as explaining factors.

## MATERIAL AND METHODS

### Study area

The Esch-sur-Sûre reservoir (Fig. 1) lies in the Northern part of the G.-D. of Luxembourg and is the result of a dam built on the Sûre river in 1960. The reservoir, located at an altitude of 320 m, has an area of 3.2 km<sup>2</sup> and a length of 18 km

from the major influent river to the dam. The reservoir has a volume of  $55.10^6$  m<sup>3</sup>, a mean depth of 17 m and a maximum depth of 46 m. The watershed has a surface of about 430 km<sup>2</sup>. The maximum water flow occurs in the winter period (December-February); the annual mean retention time amounts to about 3 months.

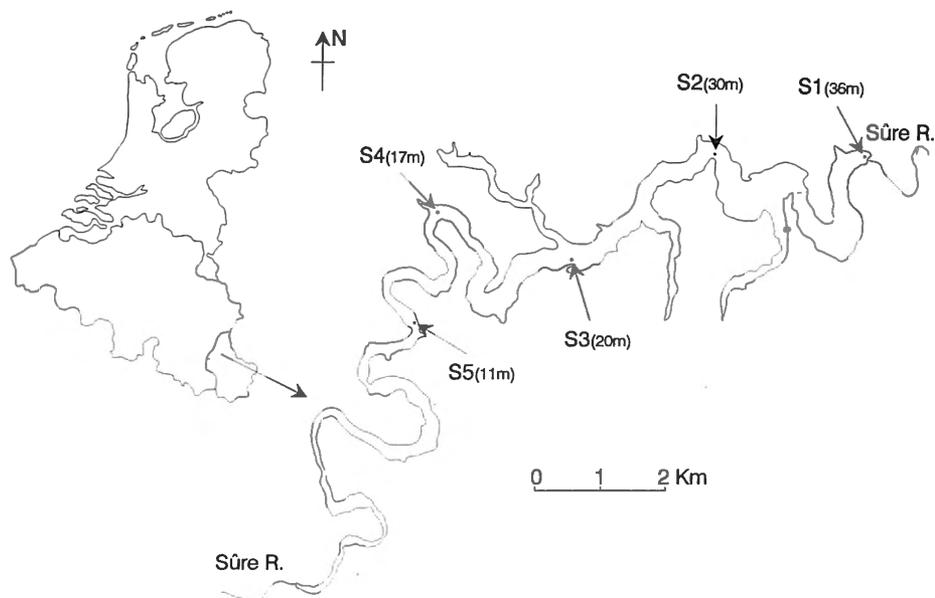


Fig. 1. — Map of the Esch-sur-Sûre reservoir showing the locations of sampling stations. Numbers in parentheses show the mean depth of the station.

According to the OECD classification (1982), the reservoir is considered as a meso-eutrophic waterbody (annual mean chlorophyll a concentration in the euphotic zone : 5.0-8.8 µg/l; annual maximum total chlorophyll concentration : 16.3-34.9 µg/l; annual mean Secchi transparency 4.2-4.7 m; annual minimum transparency : 1.8-2.5 m; data for the sampling station near the dam from 1990 to 1993). In winter the reservoir may be partly ice-covered, but this was only the case in 1992. During the study period, the water temperature remained below 10° C until the beginning of April when it rapidly increased in the epilimnion. From mid-June until the end of August, the surface water temperature was higher than 17° C. From the beginning of September, water temperature decreased reaching 8° C by November. During the whole period the temperature of the hypolimnion always remained below 10° C at station 1. The stratification of the reservoir generally starts at the end of April-beginning of May and the fall destratification begins in September. The metalimnion occurs in summer between 10 and 15 m. The hypolimnion remains oxic throughout the year. Most dominant fish species in the reservoir are planktivorous (roach : *Rutilus rutilus* ; bleak : *Alburnus alburnus* ; perch : *Perca*

*fluviatilis*; coregone : *Coregonus nasus*...). The spring algal bloom is dominated by small centric diatoms and Cryptophyceae; it is followed by a clear water phase in June and then by a summer phytoplankton bloom dominated by large species that are inedible for most zooplankton species (e.g. *Aphanizomenon flos-aquae*, *Anabaena* spp., *Ceratium hirundinella*, *Peridinium* gr. *cinctum*).

### Zooplankton analysis

Samples were collected weekly from January to November in 1990 and twice a month from April to November in 1992 and 1993. In 1991, the reservoir was emptied in order to repair the main dam wall. Zooplankton was sampled every 2.5 metres in the epilimnion and every 5 metres in the meta- and hypolimnion at 5 stations (S 1-S 5) between the dam and the influent river. The samples were taken between 9 and 11 o'clock with a 10-litre sampling bottle.

The zooplankton was concentrated by gently filtering 2 litres of lake water through a 55  $\mu\text{m}$  sieve; the sieve was thoroughly rinsed and its content preserved with a 4 % formalin solution. In the laboratory, the organisms contained in a 100 ml sample were allowed to settle down for at least one day. The water was then removed with a vacuum pump until only 10 ml remained.

Species in the zooplankton were counted at a magnification of 63 with an inverted microscope (Leitz Labovert); depending on the zooplankton densities, either an entire or half a settling chamber was examined.

In addition, samples were taken with a plankton net towed vertically from the bottom to the surface. This sampling technique was used to obtain a large number of living organisms for the estimation of the biomass and for the identification of some species difficult to recognize after preservation with formalin.

In order to compare seasonal successions of zooplankton species between years and between different sampling stations, the densities recorded at each depth (expressed in individuals per litre) were converted to values per  $\text{m}^2$  of surface area. Since the volume of water at different depths is not the same, conversion to  $\text{m}^2$  was weighted by a depth factor.

## RESULTS AND DISCUSSION

### Zooplankton composition

Zooplankton species and indication of their frequency of occurrence throughout the study period are shown in Table 1. A total of 75 taxa, comprising 49 rotifers,

TABLE 1

*Zooplankton species and indication of their frequency of occurrence among the samples taken from 1990 to 1993 at 5 stations in the reservoir of Esch-sur-Sûre : ... dominant species, ... common species, ... sporadic species, ... one or two observations*

<b>Rotifers</b>	<i>Proales</i> sp. •
<i>Anuraeopsis fissa</i> (Gosse, 1851) •	<i>Scaridium</i> sp. ✕
<i>Ascomorpha ecaudis</i> (Perty, 1850) ••	<i>Synchaeta pectinata</i> Ehrenberg, 1832 ••
<i>Ascomorpha saltans</i> Bartsch, 1870 •	<i>Synchaeta tremula</i> O.F. Müller, 1786 ••
<i>Ascomorpha</i> sp. •	<i>Trichocerca bicristata</i> (Gosse, 1887) ✕
<i>Asplanchna priodonta</i> Gosse, 1850 ••	<i>Trichocerca pusilla</i> (Lauterborn, 1898) ••
<i>Brachionus angularis</i> Gosse, 1851 ••	<i>Trichocerca rousseleti</i> (Voigt, 1902) •
<i>Brachionus calyciflorus</i> (Pallas, 1766) ••	<i>Trichocerca similis</i> (Wierzejski, 1893) ••
<i>Brachionus quadridentatus</i> (Hermann, 1783) ••	<i>Trichocerca</i> sp. •
<i>Brachionus</i> sp. •	<i>vTrichotria</i> sp. •
<i>Cephalodella gibba</i> (Ehrenberg, 1838) •	<b>Cladocerans</b>
<i>Cephalodella</i> sp. •	<i>Alona quadrangularis</i> (O.F. Müller, 1785) ••
<i>Colurella adriatica</i> (Ehrenberg, 1831) •	<i>Alona rectangula</i> Sars, 1862 •
<i>Colurella</i> sp. •	<i>Alona</i> sp. •
<i>Conochilus unicornis</i> (Rousselet, 1892) •••	<i>Biapertura affinis</i> (Leydig, 1860) •
<i>Epiphanes senta</i> (O.F. Müller, 1773) ✕	<i>Bosmina (Eubosmina) coregoni</i> Baird, 1857 •••
<i>Euchlanis dilatata</i> (Ehrenberg, 1832) ••	<i>Bosmina (Bosmina) longirostris</i> (O.F. Müller, 1785) ••
<i>Filinia longiseta</i> (Ehrenberg, 1834) ••	<i>Ceriodaphnia pulchella</i> Sars, 1862 ••
<i>Filinia</i> sp. •	<i>Ceriodaphnia</i> sp. •
<i>Gastropus hyptopus</i> (Ehrenberg, 1838) ✕	<i>Chydorus brevilabris</i> (Frey, 1980) •
<i>Kellicottia longispina</i> (Kellicott, 1879) ••	<i>Chydorus sphaericus</i> (O.F. Müller, 1785) ••
<i>Keratella cochlearis</i> (Gosse, 1851) •••	<i>Chydorus</i> sp. •
<i>Keratella cochlearis tecta</i> (Lauterborn, 1900) ••	<i>Daphnia cucullata</i> Sars, 1862 ••
<i>Keratella hiemalis</i> (Carlin, 1943) ••	<i>Daphnia galeata</i> Sars, 1864 •••
<i>Keratella quadrata</i> (O.F. Müller, 1786) ••	<i>Daphnia longispina</i> O.F. Müller, 1785 •
<i>Keratella ticinensis</i> (Callieris, 1920) ✕	<i>Daphnia</i> sp. •
<i>Keratella valga</i> (Ehrenberg, 1834) ✕	<i>Diaphanosoma brachyurum</i> (Liévin, 1848) •••
<i>Lecane (Monostyla)</i> sp. ••	<i>Eurycercus lamellatus</i> (O.F. Müller, 1785) ✕
<i>Lecane (Lecane)</i> sp. ••	<i>Holopedium gibberum</i> Zaddach, 1855 ✕
<i>Lepadella ovalis</i> (O.F. Müller, 1786) •	<i>Leptodora kindtii</i> (Focke, 1844) ••
<i>Mytilina mucronata</i> (O.F. Müller, 1773) ✕	<i>Polyphemus pediculus</i> Linnaeus, 1761 •
<i>Notholca acuminata</i> (Ehrenberg, 1832) ••	<i>Simocephalus</i> sp. ✕
<i>Notholca squamula</i> (O.F. Müller, 1786) ••	<b>Copepods</b>
<i>Notholca</i> sp. •	<i>Cyclops venustus</i> (Norman and Scott, 1906) •
<i>Ploesoma hudsoni</i> (Imhof, 1891) ••	<i>Cyclops vernalis americanus</i> (Marsh, 1893) •
<i>Polyarthra dolichoptera</i> (Idelson, 1985) ••	<i>Cyclops vicinus</i> (Ulianine, 1875) •••
<i>Polyarthra major</i> (Burckhart, 1900) ••	<i>Eudiaptomus gracilis</i> (Sars, 1862) •••
<i>Polyarthra vulgaris</i> (Carlin, 1943) ••	<i>Halicyclops christianensis</i> (Boeck, 1872) •••
<i>Polyarthra « vulgaris x dolichoptera »</i> •••	
<i>Pompholyx sulcata</i> (Hudson, 1845) ••	

21 cladocerans and 5 copepods, were identified. However, about half of them were only sporadically found and their density was very low. This species number is similar to that found in some other lakes of the temperate zone (e.g. GULATI, 1990; ARNDT *et al.*, 1993), but considerably higher than the diversity observed in other reservoirs (e.g. ADALSTEINSSON, 1979; SELIN and HAKKARI, 1982; URABE and MURANO, 1986; ARCIFA *et al.*, 1992; SCHMID-ARAYA and ZUÑIGA, 1992). Among the rotifers, *Keratella cochlearis*, *Polyarthra vulgaris-dolichoptera* and *Conochilus unicornis* were the dominant species throughout the year. *Synchaeta tremula* was very abundant only in early spring. Among the cladocerans, the most abundant species were *Daphnia galeata*, *D. cucullata* and hybrids (from the end of April to the beginning of October) and *Diaphanosoma brachyurum* (during summer). *Bosmina (Eubosmina) coregoni* and *Bosmina longirostris* were common in spring. Among the copepods, *Eudiaptomus gracilis*, *Halicyclops christianensis* and *Cyclops vicinus* were abundantly and frequently found throughout the year. The species diversity assessed by the Shannon index (RICHARD *et al.*, 1985) did not significantly differ between the downlake and the uplake stations (Table 2).

TABLE 2

*Annual mean Shannon diversity index at 5 stations  
in the reservoir of Esch-sur-Sûre*

	Station 1	Station 2	Station 3	Station 4	Station 5
1992	1.84	1.76	2.09	2.33	2.35
1993	1.70	2.19	2.16	2.25	2.44

### Vertical and longitudinal distribution

Except for quantitative differences, the zooplankton showed the same vertical and longitudinal distribution patterns during the three investigated years. Fig. 2 shows, as an example, the vertical and temporal distribution of the zooplankton at the 5 sampling stations in the reservoir in 1993. The zooplankton was concentrated in the top 15 m at the times of sampling; in the parts with the greatest depth (stations 1, 2 and 3), a distinct vertical gradient in zooplankton density was thus observed whereas in the shallower parts of the reservoir (stations 4 and 5), the zooplankton was as a result distributed more uniformly over the whole water column. With the exception of *Ceriodaphnia pulchella* which appeared preferentially in the hypo or metalimnion of the reservoir, this vertical distribution was quite similar for all the species and was also observed by URABE (1990) in the Ogochi reservoir (Tokyo).

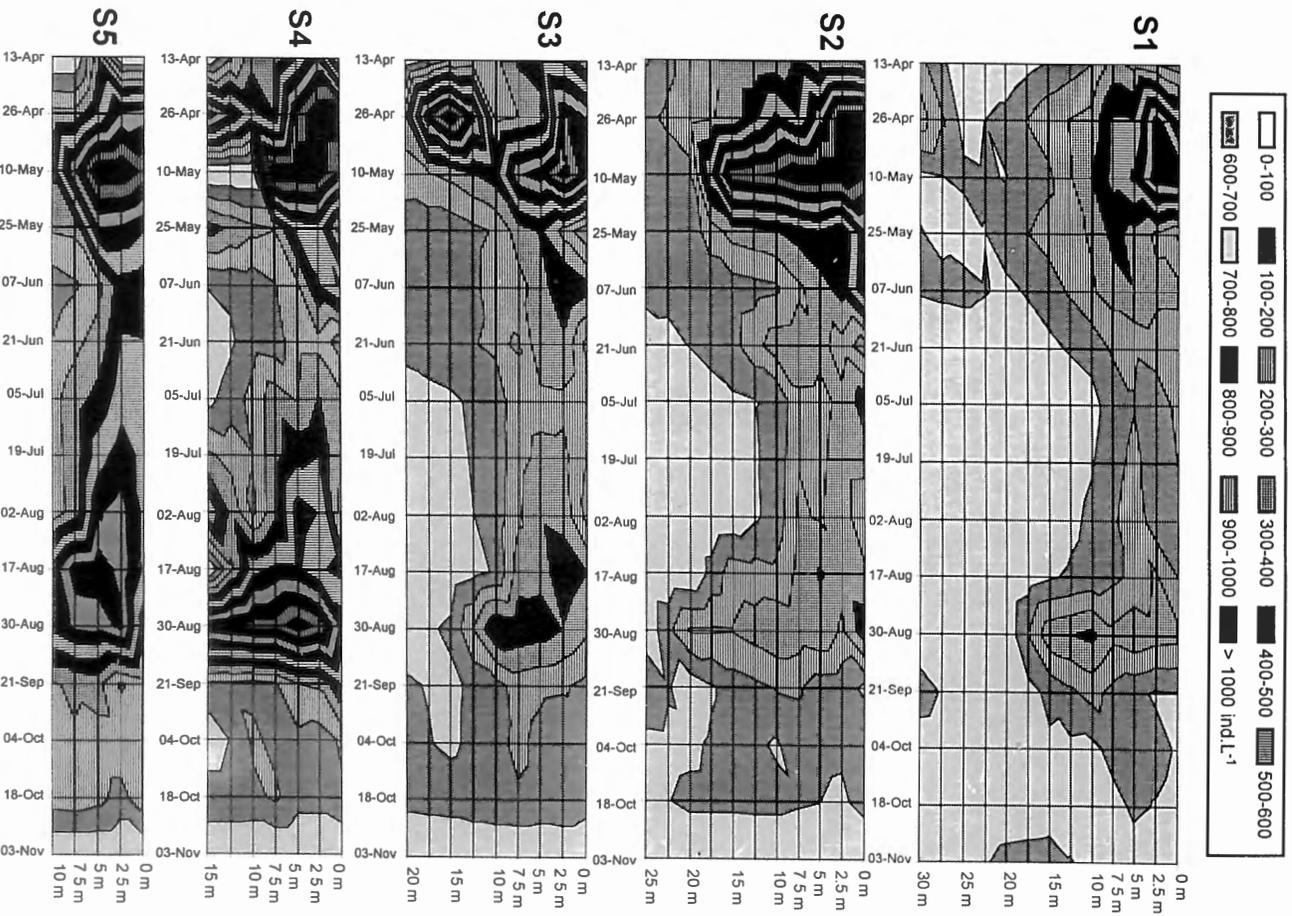


Fig. 2. — Temporal and vertical distribution of the zooplankton at the five sampling stations in the reservoir of Esch-sur-Sûre during 1993.

The highest zooplankton densities (> 800 ind/l) were observed in all the stations during spring; a second peak occurred at the end of the summer. During spring, total zooplankton density was quite similar in all the stations whereas, from July to September, zooplankton density increased from the damsite (station 1) to the headwaters with a maximum at station 4. This gradual uplake increase was commonly found for most of the dominant species (Table 3). This was the case for

TABLE 3

*Longitudinal variation in the mean density ( $10^3 \text{ ind.m}^{-2}$ ) of dominant species in 1993. Dgr : Eudiaptomus gracilis ; C : Cyclops spp. ; Dg : Daphnia galeata ; Db : Diaphanosoma brachyurum ; Kc : Keratella cochlearis ; P : Polyarthra spp.*

	Dgr	C	Dg	Db	Kc	P
S1	285	475	179	157	1.887	1.390
S2	235	636	159	328	2.027	1.133
S3	239	720	224	385	2.004	1.744
S4	233	1.025	312	466	2.445	1.934
S5	276	632	183	465	1.672	1.430

*Keratella cochlearis* and *Polyarthra* spp. among the rotifers and for *Cyclops* spp., *Daphnia galeata* and *Diaphanosoma brachyurum* among the crustaceans. On the contrary, mean densities of *Eudiaptomus gracilis* did not appreciably differ. Some rotifers, like *Brachionus* spp., *Filinia longiseta* and *Pompholyx sulcata*, species which are commonly used as indicators of eutrophic conditions (GANNON and STEMBERGER, 1978 ; PEJLER, 1983), also increased from the damsite to the uplake region.

Gradual uplake increase in the abundance of the zooplankton has been observed in some other lakes or reservoirs (e.g. GANNON and STEMBERGER, 1978 ; URABE and MURANO, 1986). This longitudinal zooplankton density gradient is probably the result of high nutrient conditions near the river mouth which stimulate an increase in primary production resulting in a higher food availability. The algal biomass showed indeed a similar horizontal gradient to the zooplankton densities (for example, the annual mean chlorophyll concentrations in the epilimnion increased from 5.3  $\mu\text{g/l}$  at station 1 to 7.0  $\mu\text{g/l}$  at station 5 in 1993). This higher algal biomass can support an increase in secondary production, as was shown by GANNON and STEMBERGER (1978) for lake Michigan.

On the other hand, it is known that the hydrological regime, such as the flushing and dilution effects of inflowing water, sometimes affects the horizontal planktonic populations, decreasing their abundances, especially for stations nearest to the river (SOTO *et al.*, 1984 ; HAYWARD and VAN DEN AVYLE, 1986). The facts that the highest values of zooplankton density were observed at station 4 in the reservoir of Esch-sur-Sûre, would indicate that this station represents the optimal conditions for the zooplankton development, influenced by the dilution impact

of the inflowing water on one hand and high nutrient conditions on the other hand.

### Seasonal succession

Seasonal variations in the density of rotifers and dominant species of cladocerans at station 1, in 1990, 1992 and 1993 are shown in Fig. 3. Large interannual differences were observed in the dominance of the species. Thus for example, *Bosmina* reached by far the highest densities among the crustaceans in 1992, whereas in 1990 and 1993, its densities were comparable to or lower than those of *Daphnia*. Furthermore, there were considerable annual differences in total zooplankton biomass (52 kg.ha<sup>-1</sup> in 1990, 67 kg.ha<sup>-1</sup> in 1992 and 45 kg.ha<sup>-1</sup> in 1993). Despite these quantitative differences, the seasonal succession of zooplankton species remained the same during the three years of investigations, at all the sampling stations (example of 1993, Fig. 4). Thus, after the spring phytoplankton bloom formed by fast growing algae such as Cryptophyceae and small centric diatoms, a peak in rotifer species (in order of appearance : *Synchaeta tremula*, *Polyarthra vulgaris-dolichoptera*, *Keratella cochlearis* and *Conochilus unicornis*) occurred which was followed by a peak of *Bosmina* spp., and then by a peak of *Daphnia* spp. This early spring sequence of the peaks in densities from small to large zooplankton species has been observed in many lakes of the temperate zone (ELORANTA, 1982 ; DEMOTT, 1983 ; LEHTOVAARA and SARVALA, 1984 ; SOMMER *et al.*, 1986 ; ARNDT *et al.*, 1993).

The smallest species, which also have the shortest generation time, thus appear first and are subsequently replaced by larger species with longer generation time. The species sequence can thus be understood as a typical successional replacement of populations caused by resource limitation or interspecific competition alone. Indeed, each subsequent species can be assumed to be a more effective competitor for resources than the one before it since competitive advantage is believed to increase with increasing body size (BROOKS and DODSON, 1965). According to GLIWICZ and PIJANOWSKA (1989), the possibility cannot be excluded, however, that other forces are involved. First, the sequence may be produced by temperature-cued successive hatching of resting eggs. Second it may be caused by predation ; during this period (end of April to beginning of June), indeed, when temperature is increasing, planktivorous fish hatch (GLIWICZ and PIJANOWSKA, 1989). Juvenile fish thus appear as a synchronised cohort of gape-limited predators that grow and switch their feeding mode from smaller to larger prey (WONG and WARD, 1972 ; ZARET, 1978), and may cause the observed sequence from small to large zooplankton species (*e.g.* case of juvenile roach, CRYER *et al.* 1986).

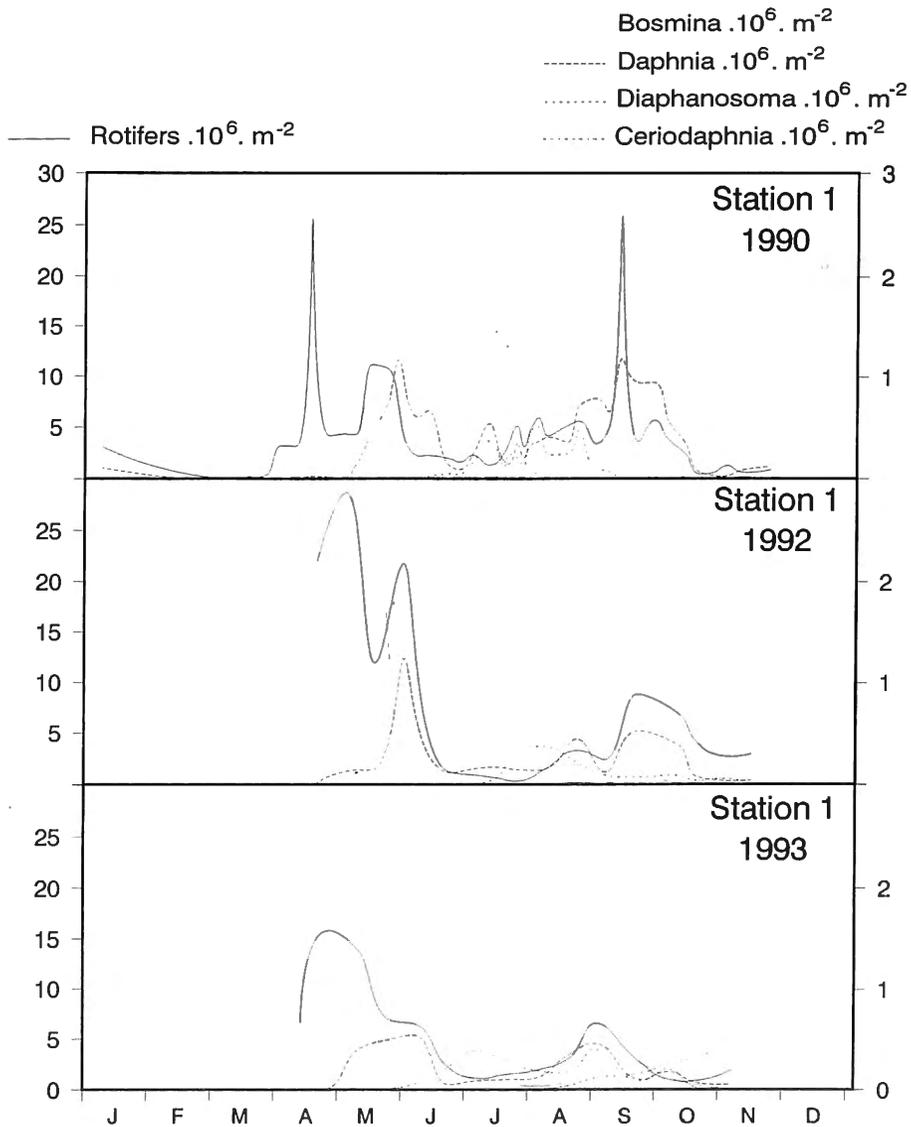


Fig. 3. — Seasonal changes in the abundance of rotifers, *Bosmina* spp., *Daphnia* spp., *Diaphanosoma brachyurum* and *Ceriodaphnia pulchella* in the reservoir of Esch-sur-Sûre from 1990 to 1993 (station 1).

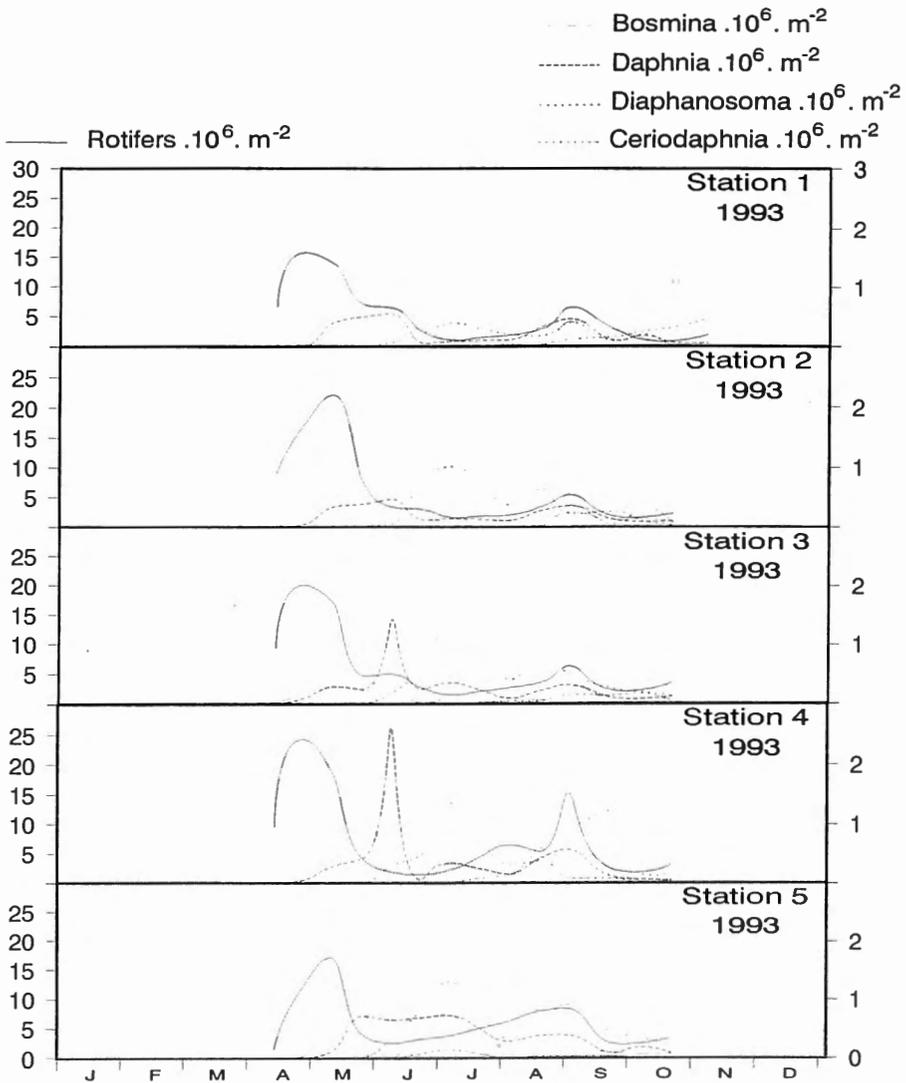


Fig. 4. — Seasonal changes in the abundance of rotifers, *Bosmina* spp., *Daphnia* spp., *Diaphanosoma brachyurum* and *Ceriodaphnia pulchella* in the reservoir of Esch-sur-Sûre from station 1 to station 5 in 1993.

Another common phenomenon observed in the Esch-sur-Sûre reservoir, is the midsummer replacement of the cladoceran assemblage of *Bosmina* spp. and *Daphnia galeata* by *Diaphanosoma brachyurum* or by a combination of *Diaphanosoma brachyurum* and *Ceriodaphnia pulchella*. The latter species showed indeed a significant peak in the hypolimnion during the end of summer 1993. These shifts in zooplankton composition were also frequently observed in other temperate

lakes (BEATTIE *et al.*, 1978 ; SOMMER *et al.*, 1986 ; GLIWICZ and PIJANOWSKA, 1989) and are often attributed to fish predation, especially when a large or less evasive species (like *Daphnia galeata*) is replaced by a smaller, less conspicuous one or by a species that has developed antipredator defences such as the escape ability of *Diaphanosoma brachyurum* (DRENNER and MCCOMAS, 1980 ; GLIWICZ and PIJANOWSKA, 1989). However, midsummer declines in *Daphnia* in eutrophic lakes and subsequent increases in *Diaphanosoma* have also been attributed to the greater tolerance of *Diaphanosoma* to interference from filamentous cyanobacteria (GLIWICZ, 1977). Radiotracer studies have indeed confirmed that *Diaphanosoma*'s feeding rate on small edible algae is less affected than *Daphnia*'s by the presence of cyanobacteria (FULTON and PAERL, 1987 ; FULTON, 1988). Because *Diaphanosoma brachyurum* exhibits midsummer peaks even in years without significant densities of cyanobacteria, greater tolerance to interfering particles cannot be the sole reason for *Diaphanosoma*'s success during midsummer in the Esch-sur-Sûre reservoir. Furthermore, DEMOTT and KERFOOT (1982) and DEMOTT (1985) have demonstrated the ability of *Diaphanosoma* to feed very effectively on bacteria ; this could explain the success of *Diaphanosoma* during midsummer minima in edible algae. However, despite correlations, it is often difficult to be sure which factor leads to the midsummer decline in *Daphnia* (DEMOTT, 1989).

## CONCLUSIONS

The early spring sequence of the peaks in densities from small to large zooplankton species and the midsummer declines in *Daphnia* were the only phenomena observed in all years. Predation and food limitation are two possible factors to explain the zooplankton species replacements in the Esch-sur-Sûre reservoir. An experimental approach and demographic analyses (birth and death rates, average clutch size) are needed to determine the respective impacts of predation, competition, various environmental factors and their interactions.

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