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Spatio-temporal investigations on the planktonic organisms of the Middle Loire (France), during the low water period: biodiversity and community dynamics

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Abstract

The objective of this work was to analyse the distribution of the planktonic communities involved in the functioning of a 255-km river stretch and to get a better understanding of the influence of the river morphology on the diversity and dynamics of the micro-organisms. The planktonic communities (phytoplankton, bacterioplankton, proto- and metazooplankton) scarcely considered together in fluvial systems, were analysed at four sites of the Middle Loire during the low water period, in parallel to physical and chemical analyses. Physical and chemical variables such as turbidity, pH, suspended matter and chlorophyll *a* concentration were high, illustrating the classical, productive summer period. The algae played a major role in the water oxygenation until end-summer, then the algal drop concomitant to the bacterial sustained abundance appeared responsible for oxygen depletion. The downstream site enriched by nutrients inputs of two tributaries, carried the highest algal and bacterial densities. Situated in a meanders zone, the Middle Loire is characterised by a high habitat heterogeneity, the up- and downstream sites were wide and spread of vast standing zones and vegetated islands, whereas the two intermediate ones were narrower and more uniform. This morphological variability strongly impacted the micro-organisms diversity and distribution. Indeed, the algae and zooplankton composition were clearly influenced by the physical habitats of the river, the Cyanophyta were favoured by the lentic conditions and the Bacillariophyta by the turbulent ones, while the young stage of copepod and the large rotifer predators were indicator of a lentic origin. Thereafter, the river heterogeneity interfered with the zooplankton dynamics, the standing conditions enhancing the rotifer predation. In that way, we hypothesise that two opposite patterns characterised the wide sites spread of lentic water and the more uniform channels. In the first case, the zooplankton could prey on the ciliates protozoan, which in return favoured the flagellate ones; conversely in the second situation the zooplankton limited by the physical constraints did not impact the ciliates which could depress the flagellates. Thus, the similar geomorphology of the distant upstream and downstream sites (255-km apart) induced relatively close organisms distribution. Hence, disagreeing with the river continuum concept, this assertion shows the strong influence played by the local morphological characteristics of the Middle Loire in potamoplankton composition and dynamics.

Introduction

In recent years, hydrobiologists and stream ecologists have made considerable progress in quantifying the physical aspects of water flow (Morrice et al., 1997) but far less progress has been made in quantifying the longitudinal and lateral movements of the living organic matter. Studies focussed on the spatial and temporal distribution of riverine micro-organisms have essentially examined only the

phytoplankton and zooplankton communities (Rzoska, 1968; Saunders & Lewis, 1988; Brown et al., 1989; Hamilton et al., 1990; Rundle & Ormerod, 1991; Vranoský, 1995; Pourriot et al., 1997; Reckendorfer et al., 1999; Viroux, 1999) and, to our knowledge, bacteria, heterotrophic flagellates or ciliates have not been documented together with the other components of the plankton.

In the Middle Loire, which ranks among the more productive temperate rivers, during the low water period, the major part of the suspended matter consists of algae and, in parallel to their decrease, the end of summer is marked by a classic oxygen deficit (Lair & Sargos, 1981, 1993; Leitao & Lepretre, 1995; Lair & Reyes-Marchant, 1997). Following previous results illustrating the importance of the algae, protozoans and micro-metazoans at two sites (90-km apart) on this river (Lair et al., 1998, 1999), this study including changes in the density of the five planktonic communities (phytoplankton, bacterioplankton, flagellated and ciliated protozooplankton and metazooplankton, classically designated as 'zooplankton') was extended to four sites (255-km stretch) in order to establish the main items involved in the river functioning, and more particularly the impact of the potamoplankton on the physical and chemical composition of the water.

Thereafter, most lotic systems characterised by structural instability (Reynolds, 1984) are not hydrodynamically uniform and often contain areas of very low flow (Quang, 1991; Reckendorfer et al., 1999), which may act as refuges for riverine organisms as has been observed for algae, crustaceans and rotifers (Reynolds et al., 1991; Robertson et al., 1997; Reckendorfer et al., 1999). In that way, Lair & Reyes-Marchant (1997) deduced that the mobile littoral zone of the river Loire was responsible for the rapid increase in algae and rotifer densities observed over short distances in the main stream; hence our attention was focused on the river morphology which would impact the community distribution in terms of diversity and dynamics.

Materials and methods

The Loire has a drainage area covering 115.120 km^2 of central and western France, representing about 20% of the country, and reaches the Atlantic Ocean after 1012 km. According to the typology of Strahler (1957), the Middle Loire is an 8th- order river. Within the framework of a monitoring programme initiated by 'Electricité de France' (EDF), four sites were chosen 3–7 km downstream of their nuclear power plants. These sites: 1Bel (Belleville-sur-Loire), 2Dam (Dampierre-en-Burly), 3Slb (Saint Laurent-des-Eaux) and 4Ch (Chinon), respectively 505, 550, 640 and 760 km from the source, were sampled bimonthly through four months (Fig. 1). This section of the river, known as the Val de Loire, is characterised by meander zones. All samples were taken at 50 cm below the surface in the current close to the banks and they can be considered as representative of the whole channel. Indeed, a preliminary study held at 3Slb showed that sampling in the current, which favoured lower variability of density and biomass, remains a good compromise for gaining knowledge of the micro-organisms communities (see Picard, 2003). At the upstream site, 1Bel, where there are extensive zones of shallow water and the river is about 500 m wide, the samples were collected near the right bank, from a boat moored in the current. At the three downstream sites, the water was taken in the current from pontoons on the left bank. At 2Dam and 3Slb, the channel is more uniform and the river width is about 300 and 250 m, respectively. Finally at 4Ch, in a zone of large vegetated islands, it reaches 500 m again and there also, lentic areas are numerous during low water. Just upstream this last site, the Loire receives two important tributaries, the River Indre (265 km, drainage area 3 500 km^2) and the River Cher (350 km, drainage area 14 000 km^2).

Water sampling, physical and chemical analyses

To cover the period of low water flow, sampling was carried out fortnightly from 28 June to 6 October 1999, on three or four consecutive days. At every site, the flow rate was monitored continuously by EDF, as were the diel variations in oxygen concentration. Temperature, pH, dissolved oxygen, conductivity and Secchi disk transparency were measured at each site using portable equipment (WTW 196). Samples were taken in the flow with a 10-l Van Dorn bottle, at approximately 50 cm below the water surface. Three samples were gently mixed in a 30-l vessel before

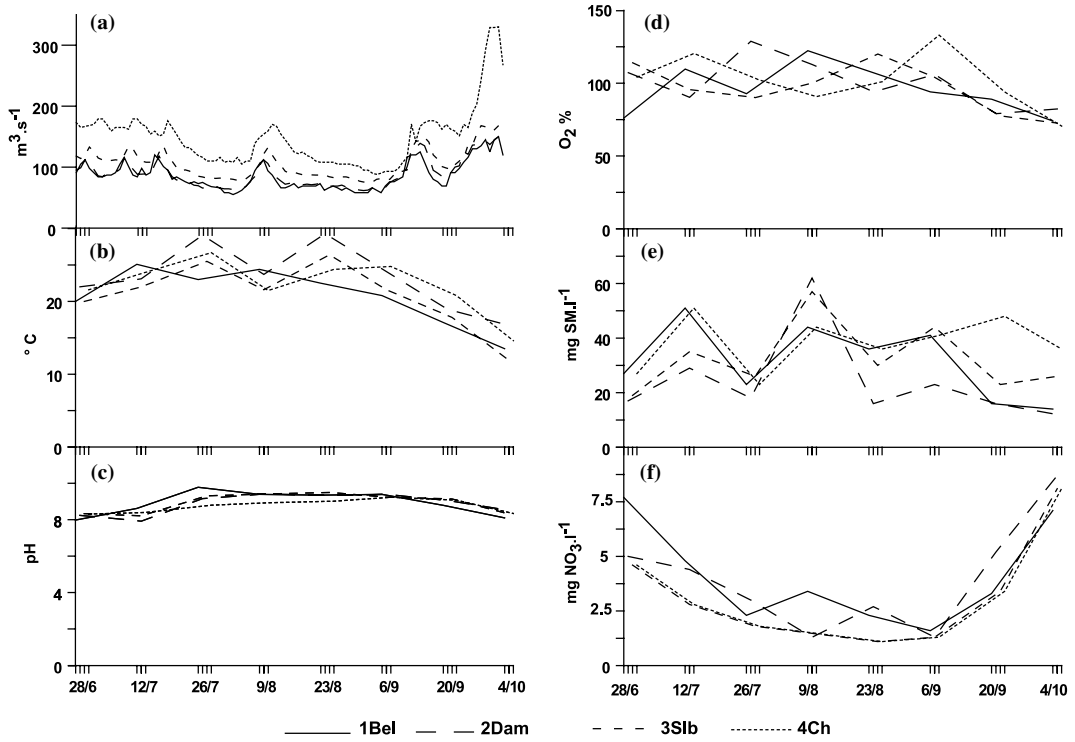

Figure 1. Variations of flow rate (a), water temperature (b), pH (c), oxygen saturation (d), suspended matter (e) and nitrates (f) at the four sampling sites: 1Bel, 2Dam, 3Slb & 4Ch.

sub-sampling for chemical analysis and study of the organisms. The chlorophyll *a* concentration was measured spectrophotometrically, after 6 h extraction in 90% ethanol, using SCOR-UNESCO (1966) equations. The suspended matter (SM), nitrates (NO_3) and phosphates (PO_4) were measured at the Municipal Laboratory of Clermont-Ferrand and the dissolved (DOC) and total organic carbon (TOC) were analysed by high temperature catalytic oxidation (samples filtered through 0.22 μm filters) at the Analytical Institute Louise Blanquet of Clermont-Ferrand, both accredited COFRAC.

In addition, monthly measures of O_2, BOD_5, DOC, NH_4, NO_2, NO_3 and P total from the rivers Loire (up- and downstream of 4Ch), Cher and Indre (just before the confluence), produced by the 'Agence de l'Eau Loire-Bretagne' during the sampling period, were used to estimate the possible impact of the tributaries. The methods used for these analyses conformed to the procedures registered by the French ministry of Health.

Treatment and analysis of the micro-organisms

A 200-ml aliquot was fixed with Lugol's solution for phytoplankton study (Bourelly, 1966), 100-ml was fixed with formalin (2% final concentration) for counting heterotrophic bacteria (HB) (Porter & Feig, 1980), a 200-ml fraction was fixed with glutaraldehyde at 1% final concentration for observation of heterotrophic flagellates (HF) (Bloem et al., 1986) and another 200-ml was fixed with mercury chloride at 2.5% final concentration for study of the ciliates (Sime-Ngando & Grolière, 1991). For observations of the zooplankton, 5-l of water were filtered through 35 μm sieves and the rest was fixed with formalin (4% final concentration). Algae, ciliates and zooplankton, were counted using an inverted microscope, and were determined to genus or species wherever possible. The bacteria and heterotrophic flagellates, stained with DAPI (Porter & Feig, 1980) and primulin (Bloem et al., 1986), respectively, were assigned to morphotypes and

enumerated using an Olympus HBS, equipped for epifluorescence microscopy.

Graphics and statistical analysis

A polynomial curve (order 5) was fitted to the density data of the five communities, using Grapher 3.0, to emphasize the principal variations. The coefficient of determination (R^2) was computed to illustrate the accuracy of the observed abundances. Using SPSS 10.0, a correlation matrix was performed on the abiotic and biotic data, to determine which combinations of variables best characterise the dynamics of this stretch. In addition, through tests of statistical significance, regression analysis was used for assessing which environmental variables contributed most to the community response and which appeared to be unimportant. MDS ordination from Bray-Curtis similarities, on square root transformed taxa abundances, were performed with PRIMER 5.0, to specify the inter-site differences during the sampling period. Moreover, in reference to the continuum pattern (Vannote et al., 1980), the data were processed according to Cody's measure of beta-diversity (species turnover among sites) to evaluate how species richness changes along the habitat gradient (Cody, 1975).

Results

Physical and chemical features

Throughout the sampling period, the flow rate, which ranged from 87 to 150 $m^3 s^{-1}$ on average, remained low at every site, except in early October, when the maxima occurred {values up to 150 $m^3 s^{-1}$ (1Bel)–330 $m^3 s^{-1}$ (4Ch)}. The water temperatures similar at all four sites reached its highest values from late July to early September (Table 1, Fig. 1). The pH was high at every site illustrating the classically productive summer period. Its lowest values occurred at the beginning and end of the sampling period. The Secchi disk depth was low revealing the high turbidity of the water. At the two intermediate sites, the transparency increased from early September onwards, reaching values >100 cm whereas the other two sites were less transparent at that time (no more than 65 and 75 cm, at 1Bel and 4Ch, respectively). Except at 1Bel in late June, the water remained well oxygenated until September. It then decreased at the first three sites (down to 74.0, 79.0, 73.0%) in early September and two weeks later at 4Ch (down to 70.5%). Overall, the mean values of conductivity, SM and NO_3 were higher at the downstream site, where the NO_3 concentrations could punctually reach 17 mg l^{-1}. The low PO_4 levels were at the limit of detection by the standardised method throughout the sampling period. The TOC concentrations were on average lower at the upstream site, 1Bel, than downstream. At the four sites, it reached minimum values by the end of September, before increasing in parallel to the flow. Overall, the DOC consisting of 80% of TOC, followed the same pattern. The chlorophyll *a* concentrations were high and at all four sites, the lowest values occurring at the beginning and end of the sampling period. At the three upstream sites, chlorophyll decreased from the end of September, and two weeks later at 4Ch, in parallel with the decline in oxygen.

Impact of the main tributaries

The physical and chemical conditions of the Loire upstream and downstream the confluences differed under the influence of inputs from two rivers, the Indre and the Cher. The Cher had occasional oxygen deficits and carried DOC, NH_4, NO_2, NO_3 and total P in concentrations higher than those encountered in the Loire upstream of the confluence (Table 2). The Indre was also responsible for inputs of NO_3.

Phytoplankton structure

The algal community consisted of 116 taxa, belonging mainly to three phyla: Chlorophyta, Bacillariophyta and Cyanophyta with 80, 19 and 13 taxa, respectively. The number of taxa observed throughout the sampling period was 87 at 1Bel, 96 at 2Dam, 91 at 3Slb and 92 at 4Ch, and only 38 taxa were observed along the entire stretch (Tables 3 & 4). On average, the Cody index was largely lower between 2Dam and 3Slb (with 89 common taxa) than for the first and last stretches, illustrating that the two intermediate sites carried a very similar community (Table 5).

Table 1. Physical and chemical features of the four stations: 1Bel, 2Dam, 3Slb and 4Ch of the Middle Loire

	1Bel	2Dam	3Slb	4Ch
Flow rate	86.5 ± 23.1	90.0 ± 23.9	106.3 ± 25.0	149.6 ± 50.1
(m^3 s^{-1})	(55.0 < *F* < 150.0)	(61.5 < *F* < 150.0)	(75.3 < *F* < 168.0)	(88.0 < *F* < 330.0)
T °C	20.8 ± 3.9	23.4 ± 4.4	20.9 ± 4.6	22.3 ± 3.7
	(13.5 < *T* °C < 25.1)	(16.7 < *T* °C < 29.3)	(11.9 < *T* °C < 26.4)	(14.6 < *T* °C < 26.7)
PH	8.9 ± 0.7	8.9 ± 0.6	8.9 ± 0.5	8.8 ± 0.4
	(8.0 < pH < 9.8)	(7.9 < pH < 9.4)	(8.2 < pH < 9.5)	(8.3 < pH < 9.2)
Secchi (cm)	65.0 ± 8.3	77.6 ± 17.6	63.4 ± 18.5	60.3 ± 12.3
	(58.0 < S < 83.0)	(55.0 < S < 110.0)	(48.0 < S < 105.0)	(48.0 < S < 79.0)
O_2 (mg l^{-1})	8.9 ± 1.4	8.4 ± 1.1	9.4 ± 2.0	8.8 ± 1.1
	(7.0 < O_2 < 10.7)	(7.0 < O_2 < 9.7)	(7.2 < O_2 < 12.8)	(7.3 < O_2 < 10.4)
O_2 (%)	95.8 ± 16.8	100.1 ± 16.7	96.7 ± 16.5	102.0 ± 18.9
	(74.0 < O_2% < 122.3)	(79.1 < O_2% < 128.8)	(72.6 < O_2% < 120.0)	(70.5 < O_2% < 133.0)
Conductivity	277 ± 18	285 ± 27	260 ± 28	325 ± 20
(μS cm^{-1})	(256 < *C* < 304)	(245 < *C* < 323)	(220 < *C* < 307)	(295 < *C* < 353)
SM (mg l^{-1})	31.5 ± 13.6	24.1 ± 16.2	32.5 ± 12.5	38.3 ± 9.8
	(14.0 < SM < 51.0)	(12.0 < SM < 62.0)	(19.0 < SM < 57.0)	(23.0 < SM < 51.0)
NO_3 (mg l^{-1})	4.1 ± 2.3	4.0 ± 2.4	3.3 ± 2.5	5.5 ± 5.2
	(1.6 < N < 7.7)	(1.3 < N < 8.7)	(1.1 < N < 8.1)	(1.6 < N < 17.3)
PO_4 (mg l^{-1})	< 0.02	< 0.02	< 0.02	< 0.02
TOC (mg C l^{-1})	4.7 ± 0.9	6.0 ± 2.1	5.5 ± 1.2	5.8 ± 1.1
	(3.6 < TOC < 6.4)	(3.8 < TOC < 10.4)	(3.8 < TOC < 7.2)	(4.1 < TOC < 7.4)
DOC (mg C l^{-1})	3.9 ± 0.9	5.0 ± 1.7	4.4 ± 0.8	4.8 ± 0.9
	(2.8 < DOC < 5.8)	(3.6 < DOC < 8.8)	(3.0 < DOC < 5.3)	(3.7 < DOC < 6.8)
Chl a (μg l^{-1})	93.4 ± 36.7	100.5 ± 63.8	158.1 ± 62.3	135.1 ± 36.8
	(50.9 < Chl a < 162.4)	(30.9 < Chl a < 177.7)	(69.3 < Chl a < 260.5)	(77.9 < Chl a < 188.2)

Average ± standard deviation (minimum < variable < maximum) *T* = water temperature; SM = suspended matter; TOC = total organic carbon; DOC = dissolved organic oxygen.

Table 2. Physical and chemical characteristics of the Middle Loire and its two major tributaries (monthly data of the Loire-Bretagne Water Agency) during the sampling period

	Loire upstream the confluences (upstream 4Ch)	Cher	Indre	Loire downstream the confluences (downstream 4Ch)
O_2 (mg l^{-1})	10.2 ± 1.4	8.0 ± 1.5	10.3 ± 1.5	8.4 ± 0.9
O_2 (%)	117.4 ± 18.8	91.3 ± 18.9	115.3 ± 22.4	94.8 ± 6.0
BOD_5 (mg O_2 l^{-1})	4.5 ± 2.3	4.1 ± 1.4	3.8 ± 1.3	5.6 ± 1.4
DOC (mg C l^{-1})	4.9 ± 0.5	5.7 ± 0.9	4.9 ± 0.4	4.6 ± 0.8
NH_4 (mg l^{-1})	0.04 ± 0.01	0.18 ± 0.13	0.06 ± 0.04	0.08 ± 0.02
NO_2 (mg l^{-1})	0.06 ± 0.01	0.13 ± 0.03	0.05 ± 0.01	0.06 ± 0.01
NO_3 (mg l^{-1})	5.2 ± 2.7	10.9 ± 7.1	15.8 ± 4.3	5.6 ± 5.6
P tot (mg l^{-1})	0.11 ± 0.03	0.16 ± 0.02	0.13 ± 0.09	0.13 ± 0.10

Average ± standard deviation.

Table 3. Number of taxa encountered in the Middle Loire, at each site and observed at the four sites

	Total	1Bel	2Dam	3Slb	4Ch
Algae	116	87	96	91	92
Ciliates	22	20	17	19	17
Rotifers	44	23	30	30	27

Table 4. Cody index of the algal, ciliate and rotifer community (between parentheses: number of common taxa observed during the sampling period)

	1Bel-2Dam	2Dam-3Slb	3Slb-4Ch
Algae	26.5 ± 3.8 (44)	13.0 ± 7.6 (89)	25.0 ± 6.5 (43)
Ciliates	5.1 ± 0.9 (14)	4.9 ± 0.8 (14)	4.3 ± 0.9 (13)
Rotifers	10.1 ± 1.7 (19)	3.4 ± 1.5 (30)	9.0 ± 2.5 (17)

The algae growth extended from early-July to end-September and the high densities (ranging from 7.2 to 53.4×10^6 cell l^{-1}) reflected the summer photosynthetic activity (Fig. 2). The mean algal density was slightly higher at 1Bel, quite similar at the two intermediate sites and highest downstream. Throughout the sampling period, the Chlorophyta remained dominant at the four sites, accounting on average for 60 to 75% of the total density. With a stress value of 0.09, the MDS ordination performed with the taxa abundance, gave a good representation of the inter-site similarities (Fig. 3a). The plot divided into two parts, the 2Dam and 3Slb data pooled together on the left and those of 1Bel and 4Ch on the right. On the left, the pattern was governed by the Bacillariophyta, more abundant at these two sites than at 1Bel and 4Ch, and more particularly by a single taxon, *Cyclotella* sp., which dominated the community. Conversely on the right, the 1Bel and 4Ch data were mainly structured by the presence of Cyanophyta, which occurred in higher density than at the intermediate sites.

During the productive summer period, the algal density was positively correlated with water temperature ($p = 0.05$) and pH ($p = 0.01$) while the Secchi disk transparency was negatively correlated with total algal density ($p = 0.01$). The algae density was also positively related to SM concentrations ($p = 0.01$) and the maxima of SM coincided with the highest algal densities at all four sites. In addition, algal abundance was, classically, positively correlated with oxygen concentration ($p = 0.05$) and the oxygen deficit observed from mid-September at the three upstream sites and from early-October at 4Ch, evolved in parallel to the decrease in algae. When algal density was maximal, daily variations in dissolved oxygen (derived from the continuous monitoring at each site) could reach up to 10 mg l^{-1}. Finally, the algae density was negatively related to the nitrates ($p = 0.01$).

Table 5. Number and list of algal, ciliate and rotifer taxa

	1Bel-2Dam-3Slb-4Ch	1Bel-2Dam-3Slb	2Dam-3Slb-4Ch	1Bel-2Dam	2Dam-3Slb	3Slb-4Ch	Isolated sites
Algae	38	3	4	3	44	1	23
	Actinastrum hantzschii	*Gomphonema parvulum*	*Acanthosphaera zachariasi*	*Closterium* sp.	*Achnanthes minutissima*	*Rhodomonas* sp.	*Amphora* sp.
	Anabaena sp.	*Microcystis* sp.		*Selenastrum gracili*	*Anabaenopsis circulari*		*Chlamydocapsa* sp.
	Ankistrodesmus falcatus	*Pediastrum boryanum*	*Gloeocystis* sp.	*Staurastrum* sp.	*Ankistrodesmus braunii*		*Chodatella ciliata*
	Chlamydomonas sp.		*Kirchneriella lunaris*		*Ankistrodesmus gracilis*		*Chodatella quadriseta*
	Chlorella vulgaris		*Monoraphidium* sp.		*Ankistrodesmus mirabilis*		*Closterium luna*
	Chroococcus minutus				*Aphanothece* sp.		*Coconeis* sp.
	Coelastrum microporum				*Asterionella formosa*		*Crucigenia tetrapediaz*
	Cosmarium reniforme				*Closterium acutum*		*Cymbella* sp.
	Crucigenia quadrata				*Closterium gracile*		*Eudorina elegans*
	Crucigenia rectangularis				*Coelastrum cambricum*		*Gyrosigma* sp.
	Cryptomonas sp.				*Coelastrum reticulatum*		*Kirchnerellia luna*
	Cyclotella sp.				*Coelosphaerium*		*Micrasteria* sp.
	Diatoma vulgaris				*kuetzingianum Coelastrum*		*Nephrocytium* sp.
	Dictyosphaerium pulchellum				*sphaericum Coenococcus*		*Peridinium* sp.
	Fragilaria sp.				*planctonicus*		*Polyedriopsis* sp.
	Kirchneriella obesa				*Coenocystis planctonica*		*Quadrigula closteroides*
	Melosira sp.				*Crucigenia apiculata*		*Rhoicophenia abbreviata*
	Merismopedia sp.				*Crucigenia fenestrata*		*Scenesdesmus crassus*
	Microcystis bothrys				*Dicellula planctonica*		*Scenesdesmus flexuosus*
	Navicula spp.				*Dictyosphaerium*		*Scenesdesmus*
	Nitzschia				*ehrenbergianum*		*rostratopinous*
	Oocystis sp.				*Errerella bornhemiensis*		*Surirella* sp.
	Pandorina morum				*Gomphosphaeria lacustris*		*Tabellaria* sp.
	Pediastrum clathratum				*Kirchneriella contorta*		*Trochiscia obtusa*
	Pediastrum duplex				*Meridion circulari*		
	Pediastrum simplex				*Oscillatoria* sp.		
	Pediastrum tetras				*Pseudoanabaena* sp.		
	Scenedesmus acuminatus				*Pseudosphaerocystes*		

Continued on p. 76

Table 5. (Continued)

	1Bel-2Dam-3Slb-4Ch	1Bel-2Dam-3Slb	2Dam-3Slb-4Ch	1Bel-2Dam	2Dam-3Slb	3Slb-4Ch	Isolated sites
Algae							
	Scenedesmus acutus			*lacustris*			
	Scenedesmus armatus			*Scenedesmus carinatus*			
	Scenedesmus bicaudatus			*Scenedesmus denticulatus*			
	Scenedesmus ecornis			*Scenedesmus dispar*			
	Scenedesmus opoliensis			*Scenedesmus falcatus*			
	Scenedesmus ovalternus			*Scenedesmus spinosus*			
	Scenedesmus quadricauda			*Sphaerocystis schroeteri*			
	Stephanodiscus hantzschii			*Stichococcus* sp.			
	Synedra acus			*Synechocystis* sp.			
	Tetraedron minimum			*Tetrachlorella* sp.			
				Tetraedron caudatum			
				Tetraedron incus			
				Tetraedron longispina			
				Tetraedron trigonum			
				Tetrastrum sp.			
				Treubaria triappendiculata			
				Treubaria trigonium			
				Ulothrix sp.			
				Westella botryoides			
Ciliates	9	4		1	1	4	3
	Cyclidium sp.	*Acineta* sp.		*Nassula* sp.	*Chilodonella* sp.	*Codonella* sp.	*Amphileptus* sp.
	Didinium sp.	*Litonotus* sp.				*Podophrya* sp.	*Coleps hirtus*
	Euplotes sp.	*Phascolodon vorticella*				*Stentor* sp.	*Tintinnidium* sp.
	Holophrya sp.	*Vorticella* sp.1				*Vorticella* sp.2	
	Monodinium sp.						
	Strobilidium sp.						
	Strombidium sp.						
	Uronema sp.						
	Urotricha sp.						

Rotifers	16	3	1	10	14
	Anuraeopsis fissa	*Brachionus nilsoni*	*Brachionus urceolaris*	*Ascomorpha ovalis*	*Asplanchna ovalis*
	Asplanchna priodonta	*Cephalodella gibba*		*Ascomorpha saltans*	*Brachionus budapestinensis*
	Brachionus angularis	*Synchaeta pectinata*		*Brachionus bennini*	*Conochilus unicornis*
	Brachionus calyciflorus			*Gastropus* sp.	*Colurella adriatica*
	Brachionus leydigi			*Lecane closterocerca*	*Filinia terminalis*
	Brachionus quadridentatus			*Notholca acuminata*	*Gastropus stylifer*
	Epiphanes macrourus			*Polyarthra major*	*Hexarthra* sp.
	Keratella cochlearis			*Polyarthra vulgaris*	*Keratella valga*
	Keratella cochlearis v tecta			*Rhinoglena* sp.	*Lepadella ovalis*
	Lecane bulla			*Trichocerca similis*	*Polyarthra remata*
	Lecane luna				*Sinantherina socialis*
	Lecane lunaris				*Testudinella* sp.
	Polyarthra dolichoptera				*Trichocerca longiseta*
	Trichocerca brachyura				*Trichotria* sp.
	Trichocerca elongata				
	Trichocerca pusilla				

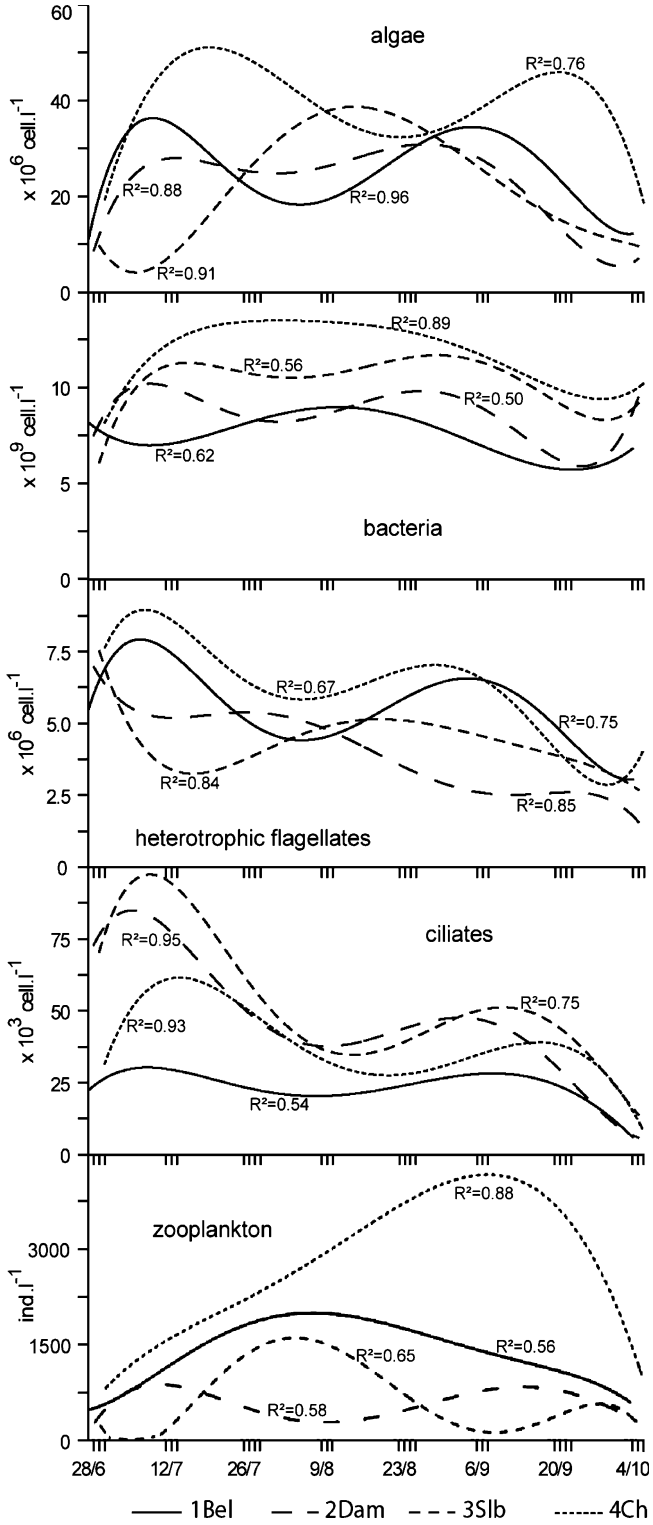

Figure 2. Density of the five planktonic communities at the four sampling sites: 1Bel, 2Dam, 3Slb & 4Ch.

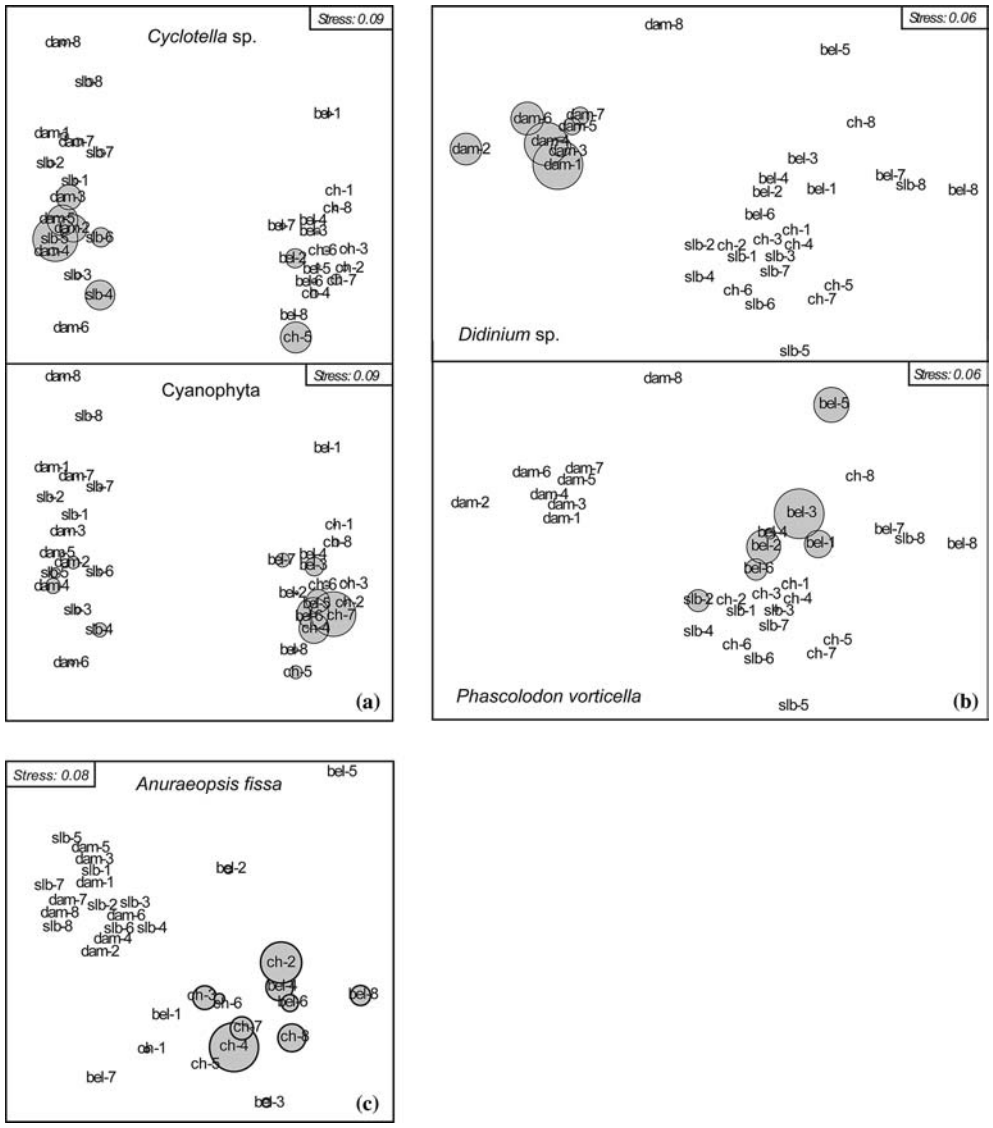

Figure 3. MDS ordination of Bray-Curtis similarities from square root transformed density data of the four sites (1Bel, 2Dam, 3Slb and 4Ch) at the 8 sampling dates: (a) The algal community (with superimposed circles of *Cyclotella* sp. and Cyanophyta density). (b) the ciliate community (with superimposed circles of *Dididinium* sp. and *Phascolodon vorticella* density). (c) the rotifer community (with superimposed circles of *Anuaeropsis fissa* density).

Bacterioplankton structure

The bacteria were described according to the shapes (cocci, rods or filament) and sizes (0.7–3.5 μm) of the cells, and classified as single or colonial (in chains of two cells or more) forms. Among the sixteen morphotypes observed, 9 were generally dominant (> 95% of the density) and, except at 1Bel in early-October where only 4 morphotypes were observed, on average, the bacterial community was composed of 6 of the main morphotypes.

The bacterial densities ranged between 5.6 and 14.4×10^9 cell l^{-1}, increasing regularly from up- to downstream (Fig. 2). Overall at the four sites, the density was lowest at the start of the summer and in late-September, before a recovery on the last sampling date. Along this river stretch, the majority of the cells was cocci-shaped, representing

on average 49% of total density, and this morphotype occurred in higher proportions at 1Bel and 4Ch. Rods represented, on average, 35% of the bacterial community, while colonies and filaments were less abundant, comprising, on average, 12 and 4% respectively. At all four sites the small forms (~1 μm) dominated and no spatial distribution was clearly defined within the morphotype data (Table 6). Finally, a negative correlation was observed between bacteria and oxygen concentration ($p = 0.05$).

Protozooplankton structure

The heterotrophic flagellates were described according to the shape (spherical or ovoid) and size (1–18 μm) of their cells, and the number of flagellae. Twenty-two morphotypes were distinguished, 14 of which were generally dominant (>98% of the density). Except at 2Dam in late-August when only 5 morphotypes were observed, on average, 12 of the main morphotypes comprised the community.

The heterotrophic flagellates densities ranged from 1.5 to 9.4 × 10^6 cell l^{-1}, the maxima being observed at the beginning of the summer (Fig. 2). On average, their abundance was lower at the two intermediate sites than at the extremes where a similar distribution occurred. Along the river stretch, the majority of the cells was spherical, representing on average 70% of total density, and this morphotype occurred in higher proportions at 2Dam. The <5 μm size-class of HF was the most abundant at all sites and dates and throughout the sampling period, comprising 88% of the HF density (Table 6) and no spatial distribution was clearly defined within the morphotype data.

The ciliates community consisted of 22 taxa, belonging to five classes: the Litostomatea, Nassophorea, Oligohymenophorea, Phyllopharyngea, Prostomatea and Spirotrichea. The number of taxa observed throughout the sampling period was 20 at 1Bel, versus 17 at 2Dam and 4Ch, and 19 at 3Slb, and only 9 taxa were observed along the entire stretch (Tables 3 & 4). On average, the Cody index was similar for the three stretches (Table 5).

The ciliates densities ranged from 5.5 to 99.1 × 10^3 cell l^{-1} (Fig. 2) and, except at 1Bel, the maxima were observed in early-July. Conversely to the flagellate distribution, the ciliate values were higher at the two intermediate sites. The density was twice as high at 2Dam as at 1Bel, and their decrease between 3Slb and 4Ch was 44%. With a stress value of 0.06, the MDS ordination performed with the abundance of ciliates taxa, allowed an accurate representation of the similarities between sites (Fig. 3b). The plot divided into two parts, with the 2Dam data grouped on the left, and on the right those of 1Bel, 3Slb and 4Ch. On the left, the high proportion of *Didinium* sp. caused the isolation of the 2Dam data. On the right, the 1Bel data essentially governed by the presence of *Phascolodon*

Table 6. Percentage density of the size and shape classes of bacteria and heterotrophic flagellates

% density	1Bel	2Dam	3Slb	4Ch
Bacteria				
<1.3 μm	78.1 ± 15.0	79.8 ± 12.1	74.8 ± 8.9	71.8 ± 16.1
1.3–2.5 μm	18.8 ± 14.1	14.8 ± 8.1	23.0 ± 8.5	22.9 ± 16.1
>2.5 μm	3.2 ± 1.5	5.4 ± 5.2	2.2 ± 1.4	5.2 ± 4.5
Cocci	55.9 ± 21.0	48.7 ± 16.1	41.8 ± 12.1	49.6 ± 17.8
Rods	28.1 ± 13.0	37.3 ± 20.3	34.3 ± 18.0	39.3 ± 16.1
Filament	3.0 ± 1.8	2.2 ± 1.4	5.2 ± 4.5	6.2 ± 6.5
Colony	13.0 ± 14.1	11.8 ± 4.8	18.7 ± 16.9	5.0 ± 6.4
Heterotrophic flagellates				
<5 μm	91.9 ± 3.8	78.8 ± 8.3	93.0 ± 3.6	86.8 ± 6.0
5–10 μm	7.4 ± 4.1	20.4 ± 8.4	6.2 ± 4.1	12.4 ± 5.8
>10 μm	0.7 ± 1.0	0.8 ± 0.8	0.8 ± 1.4	0.8 ± 1.1
Ovoid	29.8 ± 15.6	23.6 ± 11.3	30.2 ± 11.4	35.9 ± 19.0
spherical	70.2 ± 15.6	76.4 ± 11.3	69.8 ± 11.4	64.1 ± 19.0

Average ± standard deviation.

vorticella were differentiated from the 3Slb and 4Ch data more inter-mingled.

Metazooplankton structure

The metazooplankton was restricted to rotifers at the three downstream sites (2Dam, 3Slb and 4Ch), while at the upstream site, 1Bel, some young naupliar instars of Cyclopoïds (68 ± 89 ind l^{-1} on average) were also recorded sporadically. Some typically benthic *Alona* sp. were very scarcely encountered during counting and not included. The number of rotifers taxa observed throughout the sampling period was 23 at 1Bel, versus 30 at 2Dam and 3Slb, and 27 at 4Ch, and only 16 taxa were observed along the entire stretch (Tables 3 & 4). On average, the Cody index was largely lower between 2Dam and 3Slb (with 30 common taxa) than for the first and last stretches, illustrating again that the two intermediates sites carried a similar community (Table 5).

The abundance of rotifers ranged from 104 to 4151 ind l^{-1} and the highest values were observed in early-September at 4Ch and in early-August à 1Bel (Fig. 2). The similar mean densities at the two intermediate sites, were a half or quarter of those at 1Bel and 4Ch, respectively. With a stress value of 0.08, the MDS ordination carried out with the abundance of rotifer taxa, gave a good representation of the inter-site similarities (Fig. 3c). The plot divided again into two parts, the data from 2Dam and 3Slb were pooled together in the top left sector, and at lower right were those of 1Bel and 4Ch. The data from the intermediate sites were strongly intermingled and grouped together by date. On the right, the data of the two sites were more dispersed, the 1Bel data being at the periphery and those of 4Ch more central. Among the 44 taxa used in this analysis, *Anuraeopsis fissa* was the one which most clearly differentiated the intermediates from the extreme sites.

Discussion

Water composition and potamoplankton

The sampling period extended from June to October 1999, during the low water period, simultaneously to the monitorifsng programs dedicated to the nuclear power plants of the Loire in relation with eutrophication processes. Overall, illustrating the classical productive summer period, the phytoplankton supported by the temperature, induced high pH values and the drop of nitrates concentrations, while the PO_4 were always depleted, as previously observed in this eutrophic river (Lair & Reyes-Marchant, 1997; Lair et al., 1998, 1999). Considering the flow rate of the Indre, the Cher and the Loire, the concentrations of DOC and NO_3 should respectively reach 5.1 and 6.5 mg l^{-1} downstream of the confluences. However, these two elements were less concentrated suggesting that the micro-organisms had consumed the tributaries input. In addition, the oxygen concentration was still good, but lower than upstream and the BOD_5 values increased, which certainly resulted from the decomposer development. Furthermore, the abundant algae community was responsible for high SM concentrations and low Secchi depth, especially at the extreme sites.

Throughout the 255-km stretch, the water remained well oxygenated during the summer period, then diurnal oxygen deficits occurred from mid-September onwards. This process, which generally follows a decrease in numbers of algae (Lair et al., 1999), has been shown to be also typical of several other temperate European rivers: the Mosel (Gosselain et al., 1998; Garnier et al., 1999), Rhine (Admiraal et al., 1990, 1994; de Ruyter van Steveninck et al., 1992), Seine (Garnier et al., 1995) and the Spree (Köhler, 1993). In the Middle Loire, the appearance of this oxygen deficit was linked to the decrease of the algal density (associated with the increasing flow and the temperature drop) and the maintainence of abundant bacteria, which confirms the responsibility of the primary producers on the water oxygenation during the low water period (Lair & Reyes-Marchant, 2000; Lair, 2002). At the level of 4Ch, the oxygen deficit appeared two weeks later than at the three upstream sites, owing to tributaries fertilizer inputs and higher water temperature (20 °C), which would preserve the algal development.

Community diversity and influence of the river morphology (see Table 7)

Composed of 116 taxa, the algal community remained very diversified. As usual in this river,

Table 7. Up- to downstream dissimilarities of the qualitative and quantitative distributions of the planktonic communities

	Distribution	1Bel	2Dam	3Slb	4Ch	Invoked reasons
Algae	qualitative	≠	=	=	≠	input of lentic zones at 1Bel and 4Ch
	quantitative	+(+)	+	+	+++	id. + input of the tributaries at 4Ch
Bacteria	qualitative	=	=	=	=	
	quantitative	+	++	+++	++++	input of the tributaries at 4Ch
Heterotrophic	qualitative	=	=	=	=	
flagellates	quantitative	++	+	+	+++	ciliates predation at 2Dam & 3Slb/fewer ciliates at 1Bel & 4Ch
Ciliates	qualitative	≠	≠	~	~	
	quantitative	+	+++	+++	++	rotifers predation at 1Bel & 4Ch
Zooplankton	qualitative	≠	=	=	≠	input of lentic water at 1Bel & 4Ch/fewer standing zones at 2Dam & 3Slb
	quantitative	++	+	+	+++	id.

Qualitative distribution: (≠) different, (~) similar or (=) equal; quantitative distribution : from low (+) to very high (++++) density.

the chlorophytes were numerically dominant, a scenario typical of several European rivers: Danube (Schmidt, 1994), Meuse (Descy et al., 1987; Descy & Gosselain, 1994) and Seine (Garnier et al., 1995), at this period of the year. Along the 255-km stretch, the algal community was structured in two different patterns, associating 1Bel with 4Ch, and 2Dam with 3Slb. The algal community of the intermediates sites, where the channel is relatively narrower and less sinuous, was composed of numerous diatoms, classically well-adapted to turbulent water (Köhler, 1997; Gervais et al., 1997). Conversely at the extreme sites, where the river is larger and spread of zones of standing water, sand banks and vegetated islands, the Cyanophyta favoured by the standing conditions, were observed in high proportion, suggesting the influence of the morphological context on the community composition.

In terms of morphotypes, the bacterial community was very close at the four sampling sites and, similarly, the flagellate community consisted of the same morphotypes throughout the 255-km stretch. Among the ciliate community, the inter-site differences were governed by the predominance of a few taxa: *Didinium* sp. at 2Dam and *Phascolodon vorticella* at 1Bel. With a relatively small number of taxa, the turnover of the ciliate community was low between the sites, which means that the species continuum was masked by the importance of local species, highlighted by the MDS ordination in the community structuring.

Finally, the zooplankton distribution showed again that morphological differences between sites induced differences in biotic diversity on account of habitat heterogeneity. Indeed, this assumption was illustrated by the presence of young nauplii instars of Cyclopoïds only at 1Bel. Compared with the rotifers, these young copepod stages do not survive within the constraints imposed by the current, nevertheless, it is not rare to encounter such organisms in rivers, which have drifted from lentic areas (Vranovský, 1995). Thus, the origin of the zooplankton at 1Bel would result from local processes, the principal channel being bordered by vast areas of standing water where the current velocity was nil. Thereafter, among the 44 rotifer taxa identified in the river, only 16 species were common at the four sites while the intermediate sites sheltered 30 common taxa, illustrating again that the inter-sites similarities were governed by analogous river morphology, resulting in similar specific composition.

Community dynamics and influence of the river morphology (*see Table 7*)

On average, the algal density was slightly higher at 1Bel, than at the two intermediate sites where it was quite similar, and clearly highest at 4Ch. As observed by Grobois et al. (2001), the downstream

site remained the most productive zone of this stretch all along the sampling period, owing to the tributaries input.

The bacterial density increased up- to downstream as observed in the Meuse (Servais, 1989) and in the Danube (Kasimir, 1992). At 4Ch, the very high numbers of bacteria, certainly supported by the carbon inputs of the tributaries, were in the upper range of the values observed in rivers (Servais,1989; Kasimir, 1992; Hoch et al., 1995; Basu & Pick, 1997; Meybeck et al., 1998).

The protozoan densities were similar to the values observed in rivers (Carlough & Meyer, 1989; Iriberri et al., 1993; Hoch et al., 1995; Basu & Pick, 1997; Bereczsky, 1998; Karrasch et al., 2001). The heterotrophic flagellates were less abundant at the intermediates site where conversely, the ciliates were more numerous than at the extreme sites. In that way, the geomorphological conditions did not affect directly the community dynamics, which seemed to be regulated by the trophic relationships. This leads to suppose that the abundant ciliates of the intermediate sites regulated the flagellates. Indeed, planktonic nanoflagellates can clearly suffer heavy predation losses to other protozoa (Dolan & Coats, 1991; Weisse & Scheffel-Möser, 1991). In contrast, at the extreme sites, the few abundant ciliates seemed to be consumed by the rotifers predators (details in Picard (2003)), which in return would favour the flagellates' growth. This supports the results obtained in experiments by McCormick & Cairns (1991), in which the input of rotifers caused a decrease in abundance of ciliates, conversely to an increase in heterotrophic nanoflagellates. In fact, the rotifer predation upon the ciliates was favoured by the lentic conditions encountered at the extreme sites. Indeed, experimental analysis performed with the rotifers of the Middle Loire grown in lentic and lotic conditions (Picard & Lair, 2003) showed that the predation of *Asplanchna priodonta* (the dominant rotifer predator of the Middle Loire) was only observed in standing waters (Picard & Lair, 2003). Thus, the river heterogeneity influenced the rotifers dynamics and, by cascading effects, the protozoan distribution.

In comparison with lakes of similar trophic levels, the zooplankton remained not very abundant, which is general in river systems (Pourriot et al., 1991; Van Dijk & van Zanten, 1995; Lair et al., 1996; Akopian et al., 1999), while large edible feeding resources consisting of nano- auto and heterotrophic unicellular organisms were available. In fact, flow rate and turbulence in lotic systems are known to influence the filtration rate and development of rotifers (Koste, 1978; Rzoska, 1978; Sanders et al., 1989; Viroux, 1997; Miquelis et al., 1998), especially those without lorica (Picard & Lair, 2003). Thus, the origin of the numerous rotifers at 1Bel and 4Ch could essentially result from local processes, the channel being bordered by large lentic zones. Nevertheless, the export of zooplankton from lentic area probably represents only a small fraction of the real production because most zooplankton biomass is undoubtedly lost to higher trophic levels within the lentic habitat (Saunders & Lewis, 1988) and so, the density would remain relatively low. Anyway, the influence of the geomorphology upon the zooplankton dynamics was predominant in the Middle Loire, as already invoked by Lair & Reyes-Marchant (1997) and observed in other rivers (Saunders & Lewis, 1988; Junk et al., 1989; de Ruyter van Stevenick et al., 1992; Reynolds & Glaister,1993; Basu & Pick, 1996; Reynolds & Descy,1996; Viroux, 1997; Gosselain et al., 1998; Reckendorfer et al., 1999) and this seemed to be mainly responsible for the inter-site fluctuations observed during this study.

Conclusions

Little research on rivers has focused on the various components discussed in this paper (de Ruyter Van Steveninck et al., 1990; Baross et al., 1994; Arvola & Nurmesniemi, 2000; Servais et al., 2000), and most work has concerned only some groups of organisms and/or their respective activities. Throughout the 255-km stretch, the biotic component appeared responsible for the oxygen depletion on end-summer. At the downstream site of 4Ch, the development of the abundant algal and bacterial communities was supported by the nutrients inputs of the two tributaries.

The Chlorophyta dominant all along the 255-km stretch, are not disadvantaged by any particular habitat, in contrast, the Cyanophyta were favoured by the lentic conditions and the Bacillariophyta by the turbulent ones, as in lake systems. In terms of composition, the heterotrophic

unicellulars, comprising bacterioplankton and protozooplankton, were not influenced by the river morphology. Conversely, the zooplankton diversity was clearly influenced by the physical habitats of the river. Thus, the copepods and the large rotifer predators, which can grow only in standing water, were indicators of a lentic origin. The river heterogeneity interfered strongly with the zooplankton dynamics. On the one hand, the lentic zones enhanced their growth, but also on the other hand, their predation was favoured by the standing habitat. Hence, the riverine morphology indirectly impacted their preys distribution and in this case, the ciliates density. In fact, the sampling sites characterised by large standing zones sheltered more abundant zooplankton and we hypothesise that these predators consumed the ciliates protozoan, which in return favoured the flagellates ones. Conversely, in a narrower channel where the water velocity was higher, the zooplankton development was limited by the physical constraints as observed during our experimental study (Picard & Lair, 2003) and the abundant ciliates could prey on the flagellates. Hence, the two successive sites of 2Dam and 3Slb seemed very similar in terms of community composition and dynamics, conversely to the extremes sites 255-km apart, of which similar geomorphology induced relatively close organisms distribution.

With regards to studies carried out to examine locally the spatial distribution of the five planktonic communities and the effects of water turbulence on the rotifer demography (Picard, 2003; Picard & Lair, 2003), it appears that in such a large meandering river, in addition to classical bottom-up and top-down controls, the micro-organisms composition and dynamics depended largely on local processes. At our scale of observations, such an assertion disagrees with the river continuum concept (Vannote et al., 1980), since recruitment comes not only from upstream and enrichment along the river is not progressive. Hence, our results rejoin the work of Junk et al. (1989) on the importance of the lateral dimension of the river, also called 'moving littoral', 'dead zones' (Reynolds & Glaister, 1993) or 'storage zones' (Reynolds & Descy, 1996).

This study shows the strong influence played by the hydrological and morphological characteristics of the Middle Loire in potamoplankton structure and dynamics. However, the following questions remain: are protozoans able to feed and reproduce in a strong current? How are these five communities distributed across a transect of the Middle Loire? Work in progress, based on experimental analysis and on the sampling of the major facies of the river, should supply further information.

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