Hydrobiologia (2005) 546:457–472
A. Herzig, R.D. Gulati, C.D. Jersabek & L. May (eds.) Rotifera X: Rotifer Research: Trends, New Tools and Recent Advances
DOI 10.1007/s10750-005-4289-9

Abiotic vs. biotic factors: lessons drawn from rotifers in the Middle Loire, a meandering river monitored from 1995 to 2002, during low flow periods

Nicole Lair
Laboratoire de Géographie Physique, UMR 6042, Université Blaise Pascal, Maison de la recherche, 63560, Clermont-Ferrand Cedex, France
E-mail: Nicole.LAIR@univ-bpclermont.fr

Key words: large rivers, water discharge, river morphology, rotifer distribution

Abstract

The numbers of rotifers in large rivers never achieve the abundances observed in eutrophic lakes. The adverse conditions of the current have conduct biologists to establish links between particular geomorphologies and biological processes in the plankton of rivers. Recent attempts to examine specific adaptations of rotifers have shown that among several planktonic forms, the loricate species appeared to be better adapted to the current than soft-bodied or littoral-epibenthic species. The eutrophic Middle Loire provides rotifers with more edible biomass than that necessary for their production so, the aim of this study was to determine which other factors were responsible for the origins, growth and survival of rotifer populations in the river. Samples were taken bi-monthly in the current, from end-June to early-October during 8 years, in two sections of the River Loire situated at 550 and 640 km from the source. Flow rate, temperature, dissolved oxygen, suspended matter, biological oxygen demand and algal densities were examined in parallel, and among the 61 rotifer species collected at each site, the 30 dominant species were retained for the analysis. Planktonic loricate species were dominant in the Middle Loire, followed by epibenthic species, soft-bodied species being least abundant. The densities of rotifers and algae changed in parallel and in relation to temperature; flow was clearly unfavourable to algae, represented by the Chlorophytes and to rotifers, whatever the sites. Co-inertia analysis revealed that the assemblage of species was closely grouped at Dam where the immediate environment was dominated by numerous scattered islands. This analysis also illustrated that the consequence of eutrophication in the water quality was more marked downstream. Lessons drawn from this experience of the Middle Loire, which ranks among the richest rivers in terms of species, allowed to highlight that dominance of the Brachionidae is a rule in numerous rivers and may be explained by the capacity of several species to continue growing in a current of 0.2 m s^{-1}. Trichocercids may be relevant indicators of sandy rivers. The flexibility of rotifers in the face of hydraulic conditions, the question of the rotifers' origin, the respective roles of downstream transfer and processes, as well as the role of the rotifers in the river food-web are discussed.

Introduction

As in lacustrine environments, the metazoan potamoplankton that grows in lowland rivers, consists of rotifers and crustaceans, the former usually being dominant (Shiel et al., 1982; Walz, 1995). In streams (Ejsmont-Karabin & Kruk, 1999), but principally in large rivers, the abundance of rotifers can be greater than a few thousand individuals per litre, as has been illustrated for several European rivers, including the Danube (Reckendorfer et al., 1999), Elbe (Holst et al., 2002), Loire (Lair & Reyes-Marchant, 1997), Meuse (Gosselain et al., 1994), Rhine (De Ruyter et al., 1990), Oder

(Schröder, 2001), Po (Ferrari et al., 1989), Pripyat (Galkovskaya & Molotkov, 2001) and Thames (May & Bass, 1998). However, river densities never achieve those observed in eutrophic lakes and such a disparity raises questions about the origin, growth and survival of river zooplankton (i.e. metazooplankon sensu stricto).

In transient habitats, aquatic animals are challenged by a cyclic deterioration in environmental conditions and climate, as a regulator of water flow, exerts an important control over fluvial communities (cf. Admiraal et al., 1994). The 'Age of Water' (Kofoïd, 1903; Baranyi et al., 2002) is important in plankton production, while discharge often initiates changes in river geomorphology and thus plankton samples taken in the river are the result of these complex and unpredictable processes. The floodplains, dead zones and lentic areas were widely suspected to play an essential role, as places exporting planktonic crustaceans and rotifers into the river (Tan & Shiel, 1993; Lair & Reyes-Marchant, 1997; Ejsmont-Karabin & Kruk, 1999; Frisch, 2001) and the success of the latter within the river certainly rests on their shorter development times. Lately several attempts have been made by biologists to establish real links between particular local geomorphology and biological processes in plankton (Reckendorfer et al., 1999; Schiemer et al., 2001; Holst et al., 2002).

Certainly, apart from the typically planktonic rotifers, several species that are caught in the current, mainly inhabit the littoral zone and superficial sediments, where their foot may act as an anchor, preventing displacement, a useful adaptation in flowing water (Ricci & Balsamo, 2000; Schröder 2001). In addition, among several planktonic species the loricate forms appear to be well adapted to the current, in contrast to the soft-bodied forms which are not. Indeed, an analysis of the rotifer distributions in five habitat types on a cross-section of the Middle Loire, shows their affinities for distinctive areas: Brachionids are dominant in the 'current', a region that remains the least populated, while in places with characteristics of open water (in 'pools', above 'sands', behind 'islands', in 'submerged macrophytes'), soft-bodied aloricate species are dominant and Trichocercidae are concentrated above the sandy areas (Picard, 2003). Established species can adapt, and Schröder (2001) investigated how monogonont rotifers cope with alternating aquatic and terrestrial phases and showed that different patterns occurred in different species. However, specific adaptations of rotifers to some adverse conditions remained poorly documented. They have also to overcome the difficulties of feeding and mating, or of activating their responses to predators, in flowing water.

The small particles that dominate in such unstable environments usually provide a surplus of edible food. Indeed, rivers carry high densities of algae and bacteria, associated with numerous heterotrophic flagellates and ciliates which, taken together, also remain poorly studied (e.g., Lair et al., 1998, 1999; Servais et al., 2000; Picard, 2003). However, eating to be fruitful and multiply, remains a challenge for potamoplankton. In fact, although the feeding mechanisms of the rotifers are already well known, one of the questions that remains to be discussed is their ability to feed in lotic conditions, within the limits imposed by their respective feeding mechanisms. Activity measurements are usually carried out in confined conditions (Gosselain et al, 1996; Kobayashi et al., 1996; Viroux, 2000) and the results reflect the potential of entire communities, or of species, that can be far from the reality. The effects of turbulence have been tested solely by measuring grazing rates on *Brachionus calyciflorus* (Pallas) (Miquelis et al., 1998). These authors have shown that in an agitated medium at 0.18–0.22 m s^{-1}, the grazing activity of starved amictic females harvested from the River Seine was not reduced by agitation of the water. Modelling data are generally derived from measurements made in lentic conditions (Schöl et al., 2002), but certainly energy transfers cannot be so efficient in turbulent waters. Indeed, in the Middle Loire, modelling calculations with the bioenergetic model ECOPATH (Chistensen & Pauly, 1992), based on data including algae, bacteria and protozoans caught in the same water stream, have indicated that the high quantities of edible food could theoretically support up to 70 000 rotifers per litre (Picard, 2003), a value ten times as that found in reality.

Furthermore, several workers have concluded that some species reproduce in the main channel at low water (Rzoska, 1978; Saunders & Lewis, 1988; Vasquez & Rey, 1989; Holst et al., 2002), but this has rarely been adequately demonstrated, because estimation of plankton activity remains technically problematic in running water. Experiments have therefore been carried out with rotifers caught in the Middle Loire, using an experimental procedure that mimicked the water flow. The demographic results for the dominant rotifers species reared both in a current of 0.2 m s^{-1} velocity and in lentic conditions, showed large differences between them (Picard & Lair, 2003). Three distinctive groups of species emerged from these results: loricate species such as *Brachionus angularis* (Gosse) and *Keratella cochlearis v. tecta* (Gosse) whose growth rates were never negative, showed that they were capable of growing in the current; the soft-bodied *Asplanchna priodonta* (Gosse) and *Polyarthra dolichoptera* (Idelson) appeared to be unable to grow in the current, while epibenthic species such as *Epiphanes macrourus* (Barrois & Daday), with growth rates sometimes positive, sometimes negative, gave contrasting answers. This again underlines the importance of the physical characteristics of the river in the development of rotifer populations.

The seasonal succession of the potamoplankton in the Middle Loire, studied in 1995 during a period of low water flow, illustrated the importance of localised lentic areas in plankton abundance in the stream (Lair & Reyes-Marchant, 1997). Considering a series of monitoring data collected from 1995 to 2002, the present study therefore aims to show to what extent river rotifer communities are made up by the development of benthic species, limnoplankton inocula or by potamoplankton, distinguishable as discrete functional groups of river born rotifers and what are the factors that control their development. Then, on the basis of our actual knowledge of animal potamoplankton ecology, questions for the future, related to the geomorphological characteristics of the rivers, will be reviewed.

Description of the site, sampling procedure and methods

Principal characteristics of the Middle Loire and its living communities

The River Loire, rises in the Massif Central of France crosses the 'Val de Loire' and flows to the Atlantic coast (Fig. 1). With a length of 1012 km, this rain-fed river makes it the longest large river in the country. It is known as a rare, wild European river. Indeed, a few reservoirs have been built in the upper basin, but even the more downstream reservoir of Villerest is situated only at 250 km from the source. Extensive studies, including physical and chemical characteristics of the water quality, phytoplankton and zooplankton communities, have been conducted since 1977 within the framework of the surveillance programmes initiated by Electricity of France (EDF), in the region of their four nuclear power plants. Since 1995, at two sites: Dampierre-en-Burly (Dam) situated 550 km from the source and Saint-Laurent-des-Eaux (Slb), situated 90 km downstream of Dam, the records have been supplemented by animal plankton studies. This part of this nutrient-rich river (stream order 8) flows in meandering stretches, with continuous shifting sand banks that creates shallows in the channel and produces areas of low or standing waters among the numerous gravel islands. It is characterised by sharply contrasting flows, with severe low waters and can be very shallow during summer. At low discharge, the current was estimated at 0.2 m s^{-1} in

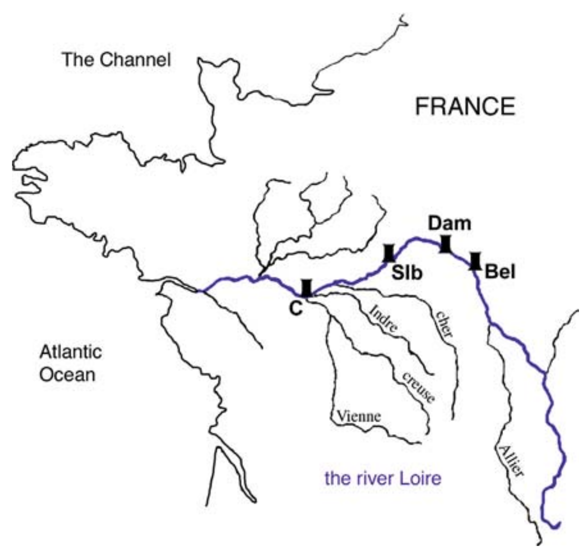

Figure 1. Situation of the power plants on the Middle Loire. The sampling sites are (a) Dampierre-en-Burly (Dam), 123 m elevation, 550 km from the source, the width of the river at this location oscillates around 300 m. (b) Saint-Laurent-des-Eaux (Slb), 85 m elevation, 640 km from the source, it extends approximately between 200 and 325 m width. (Belleville-sur-Loire (Bel) and Chinon (Ch) were studied extensively only in 1999).

the middle of the river. The immediate environment of Dam offers larger areas of lentic water and scattered islands than at Slb (Lair & Reyes-Marchant, 1997, Fig. 1).

The Middle Loire, in which chlorophyll *a* can reach values higher than 200 μg l^{-1} is among the richest European rivers. The algal and rotifer communities have been extensively described by Lair & Reyes-Marchant (1997). The light attenuation varies with the concentration of suspended material and, during low flow, this usually corresponds to the amount of phytoplankton. Briefly, during summer, the algae are classically dominated by small Chlorophytes, known to be an important food source for Brachionids (Pourriot, 1977), associated with numerous centric diatoms. Cyanobacteria, more numerous at Slb, are few and sporadic in occurrence. The microbial food web has also been studied and its importance as additional food for rotifers was determined (Lair et al., 1998; 1999; Picard, 2003). The average densities of the algae (including 77–81% of cells <20 μm) obtained in 1999 from the end of June to early-October, ranged from 20.8 $\pm$ 10.2 10^6 cells l^{-1} (Dam) to 20.9 $\pm$ 12.7 10^6 cells l^{-1} (Slb). Heterotrophic bacteria (including 75–80% of cells <1.3 μm) ranged from 8.6 $\pm$ 1.8 10^9 cells l^{-1} (Dam) to 10.0 $\pm$ 2.5 10^9 cells l^{-1} (Slb), those attached were rare. Heterotrophic flagellates (including 79–93% of cells <5 μm) ranged from 4.1 $\pm$ 2.0 10^6 cells l^{-1} (Dam) to 4.5 $\pm$ .6$10^6$ cells l^{-1} (Slb). Ciliates (including 81–84% of cells <50 μm) ranged from 45.4 $\pm$ 26.4 10^3 cells l^{-1} (Dam) to 50.6 $\pm$ 24.8 10^3 cells l^{-1} (Slb). With regard to the rotifer densities, the biomass of unicells of edible size, was always higher than the incipient limiting level (Walz, 1995) and, since the grazing activity of rotifers was usually saturated at 0.5–1.5 mg C l^{-1} (Rothhaupt, 1990), the edible biomass available was always greater than that necessary for production (Picard, 2003). As confirmed by the ECOPATH calculations noted in the introduction, food can be considered as a non-limiting factor.

Processes of sampling and analysis

Rotifers were sampled from the end of June to early-October, during the period of low discharge that usually lasts for about three to four months. At each site in the Middle Loire (Dam & Slb), three sampling stations were chosen in relation to the reactors. The first station is situated upstream of the plant, the other two are downstream of the cooling water discharge (from a few hundred metres to a few km). Samples were taken with a Van Dorn sampler, from floating platforms situated above the water flow, at approximately 0.50 m below the surface. Each sample consisted of three subsamples (10 l $\times$ 3) mixed together in a large tank and used for chemical and biological analysis. In the approach taken in 1995, sampling stations were considered separately, but on account of displacements of sand banks that occur locally from year to year during flood periods, inducing inevitable morphological changes, the results obtained at each sampling station were grouped in order to have an overview of the situation at every site. Briefly, in the present study, each data set corresponds to the mean of a series of samples (3 samples at each site), taken bimonthly (8 dates), during 8 years (1995–2002) giving, at each site, 64 data extracted from the 192 samples analysed. The procedures for the examination and determination of algae and rotifers are classical and have been described in detail in Lair & Reyes-Marchant (1997).

Of the 29 physical and chemical variables recorded every year in situ with a WTW 196 apparatus or analysed at the Municipal Laboratory, registered by the Ministry of Health, we retained the following: flow (continuously monitored by Electricity de France), temperature (t °C), dissolved Oxygen (O_2), Suspended Matter (SM) and Biological Oxygen Demand (BOD_5), expected to be the more discriminating variables at this time of the year, in the rotifers' distribution. Pearson correlation coefficients were calculated to evaluate the relationships between algae and rotifer densities. In addition, at each site, a co-inertia analysis derived from a classical Principal Component Analysis, made with centred and normed tables of the species densities and environmental variables, was carried out, and the co-structure tested to determine which factors control the species distributions, using the ADE procedures (Chessel & Dolédec, 1992; Dolédec & Chessel, 1994).

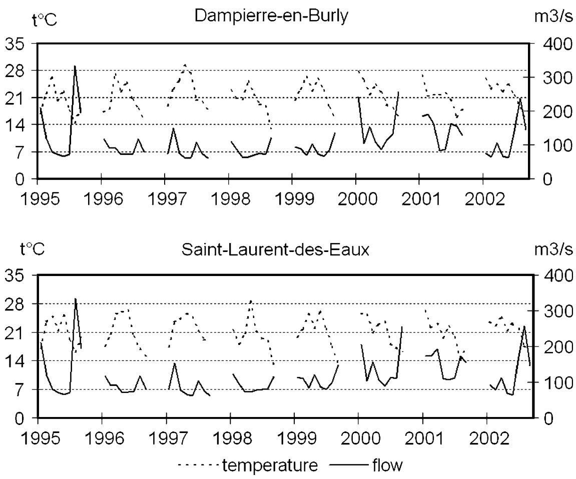

Figure 2. Time series of the variations in flow and temperature in the sampling areas.

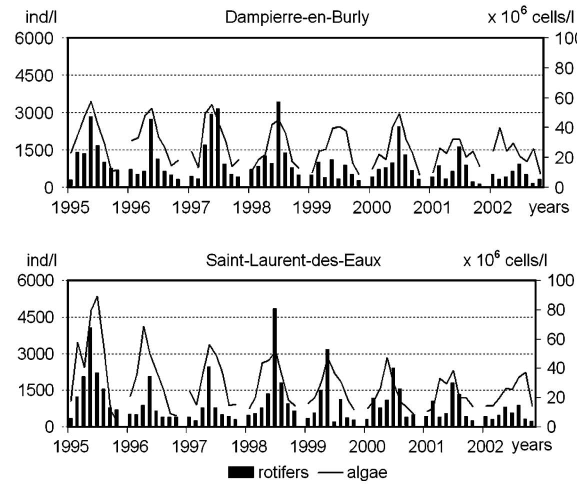

Figure 3. Time series of the variations in density of the algae and rotifers.

Results

During the eight sampling periods, the water temperature varied between 14.5 and 29.0 °C. The flow rates ranged between 60 and 334 $m^3\ s^{-1}$ at Dam and between 63 and 340 $m^3\ s^{-1}$ at Slb and were characteristic of the low discharges of the Val de Loire during summer. The highest flows in the period, generally occur from September onward and, except in 2000–2001, they stayed below 100 $m^3\ s^{-1}$ in the middle of summer, the time of high temperatures (Fig. 2). Cross-correlation between the variables measured at these two sites revealed that they functioned in parallel, with regard to flow rates ($R^2 = 0.94$) and temperature ($R^2 = 0.85$). Every year the most common riverine plankton groups, rotifers and algae, peaked at low river discharges and high water temperatures. The changes in rotifer density were parallel to those of the algae and the distribution patterns revealed summer maxima, with large peaks in some years and several successive maxima in others (Fig. 3). The algal densities ranged on average from 26×10^6 cells l^{-1} (Dam) to 28×10^6 cells l^{-1} (Slb) and the rotifer densities ranged on average from 897 to 945 ind l^{-1}, confirming the up-downstream increase observed in 1995. The densities of algae ($R^2 = 0.61$), and among them Chlorophytes ($R^2 = 0.56$), total rotifers ($R^2 = 0.61$), and filter feeding rotifers ($R^2 = 0.70$) were also very closely related from Dam to Slb, but not those of the predaceous species ($R^2 = 0.35$) which peaked in some years, depending on the sites.

Rotifer species composition of the Middle Loire

In the course of the eight years of investigation, a total of 13 families, 25 genera and 61 rotifer species were collected at these sites. The variations in percentage representation of the families illustrate the marked dominance of the Brachionidae and Trichocercidae (Table 1). The principal species (30 retained in total) were *Anuraeopsis fissa* (Gosse), *Ascomorpha ovalis* (Bergendal), *Asplanchna priodonta*, *Brachionus angularis*, *B. bennini* (Lessling), *B. bidentata* (Anderson), *B. calyciflorus*, *B. leydigii* (Cohn), *B. quadridentatus* (Hermann), *B. urceolaris* (O.F. Muller), *Cephalodella gibba* (Ehrenberg), *Colurella adriatica* (Ehrenberg), *Epiphanes macroura*, *Euchlanis dilatata* (Ehrenberg), *Gastropus stylifer* (Imhof), *Keratella cochlearis* (Gosse) and its form *tecta*, *Lecane bulla* (Gosse), *L. closterocerca* (Schmarda), *L. luna* (O.F. Muller), *L. lunaris* (Ehrenberg), *Polyarthra dolichoptera*, *P. major* (Burckhardt), *P. vulgaris* (Carlin), *Rhinoglena frontalis* (Ehrenberg), *Sinantherina socialis* (Ehrenberg), *Trichocerca brachyura* (Gosse), *T. elongata* (Gosse), *T. pusilla* (Lauterborn) and *T. similis* (Wierzejski).

These species have been classified with reference to their affinities to the current, giving a view

Table 1. Percentages of the different rotifer families in samples from the Middle Loire for the period 1995–2002

	1995	1996	1997	1998	1999	2000	2001	2002
Dampierre-en-Burly								
Asplanchnidae	3	6	3	4	6	16	4	14
Brachionidae	49	40	35	60	51	25	41	45
Colurellidae	4	2	5	3	1	3	2	2
Epiphanidae	4	3	1	1	5	13	6	10
Euchlanidae	1	1	2	1	2	1	1	1
Flosculariidae	2	4	3	0	1	18	13	5
Gastropodidae	1	2	1	7	5	3	3	3
Hexarthridae	0	1	0	0	0	1	0	0
Lecanidae	7	7	5	5	5	3	9	2
Notommatidae	7	8	9	4	4	2	7	3
Synchaetidae	7	5	7	6	6	6	6	5
Testudinellidae	2	4	3	1	1	1	1	1
Trichocercidae	11	16	26	7	14	6	8	10
Saint-Laurent-des-Eaux								
Asplanchnidae	5	9	7	11	26	22	2	13
Brachionidae	50	33	32	49	25	23	26	39
Colurellidae	4	2	3	5	2	3	1	2
Epiphanidae	7	4	5	1	4	11	3	10
Euchlanidae	2	1	1	1	2	2	1	1
Flosculariidae	2	2	2	1	0	3	17	4
Gastropodidae	1	1	1	9	4	3	5	5
Hexarthridae	0	1	0	0	0	0	0	0
Lecanidae	6	5	4	6	4	4	8	3
Notommatidae	6	13	12	4	3	4	8	6
Synchaetidae	7	6	7	6	8	12	18	5
Testudinellidae	2	2	2	1	1	1	1	1
Trichocercidae	7	22	22	6	21	13	10	13

of the importance of their preferred habitats (Fig. 4). The first group (39% at Dam & 40% at Slb) corresponded to the loricate species, typically planktonic and better adapted than the rest to growing in the current. Depending on the years, they were less abundant at Dam than at Slb. The second group (37% at Dam & 35% at Slb) consisted of the littoral-epibenthic taxa and, depending on the years, they appeared more numerous at Dam. The third group (24% at Dam & 25% at Slb), composed of soft-bodied planktonic taxa, also occurred in significant quantities. Globally, 63% of the species at the downstream site Slb, were planktonic while at the upstream site Dam, there were fewer planktonic species (60%) and littoral-epibenthic taxa were more frequent.

Interactions between environmental variables, algae and rotifers

Among these living communities, the algae were most strongly correlated with flow at both sites (Table 2). Soft-bodied and loricate species of rotifers were more strongly correlated with flow at Dam than at Slb, in contrast to the epibenthic species. Temperature remained a discriminating factor for rotifers and algae at both sites, epibenthic species appearing reactive and the soft-bodied species not {correlations between algae, rotifers and the other variables (SM, O_2 and BOD_5) were not significant}. Correlations between rotifers and the three dominant groups of algae, were particularly significant with the green algae

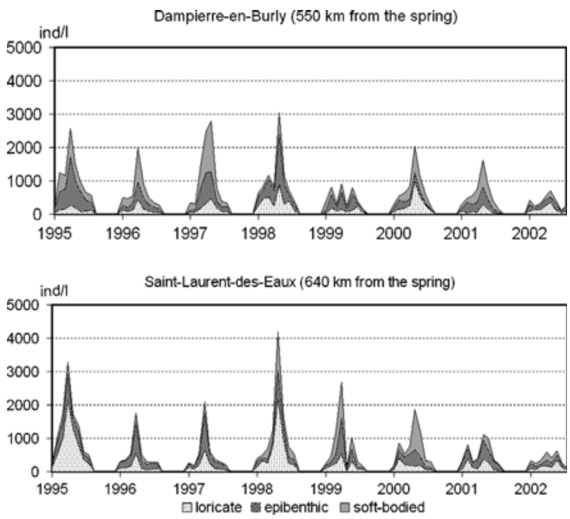

Figure 4. Time series of the variations in density of the epibenthic and planktonic ('loricate' and 'soft-bodied') rotifers at two sites in the Middle Loire.

(determination coefficients (50%). Total rotifers and their sub-categories were positively correlated with density and biomass of the green algae. Planktonic loricate rotifers were the most strongly correlated (determination coefficients (50%), epibenthic species to a lower extent, and soft-bodied forms least. To a lesser extent, significant correlations were observed with the other groups of algae, especially the Cyanobacteria.

In the river, the dominant predaceous species were *C. gibba* (a small epibenthic species) and *A. priodonta* (a large planktonic soft-bodied species). *Asplanchna* can occasionally reach densities >1000 ind l^{-1} (a maximum of 1490 ind l^{-1} was counted at a station at Slb in 1999). Correlations giving a view of the potential preys encountered showed that *Cephalodella gibba* appeared linked to algae ($r = 0.59$, $p = 0.0001$ at Dam and Slb) and particularly Chlorophytes ($r = 0.54$, $p = 0.0001$ at Dam and $r = 0.58$, $p = 0.0001$ at Slb) but not *Asplanchna*. In relation to potentially encountered species, the presence of *Asplanchna* was correlated with epibenthic or soft-bodied species, which are more diversified at Slb (Table 3).

In the multivariate analysis carried out with the 30 species and the abiotic variables previously listed, the density of Chlorophytes was added as an indicator of food. In the co-inertia analysis, the co-repartition between environmental and biotic variables was significant at both sites. The results illustrate that, in contrast to *t* °C, flow was clearly unfavourable to algae (represented by the Chlorophytes) and to rotifers, that were totally rejected in opposition, whatever the sites. SM were few significant giving the view that in this shallow river, light is not the essential limiting factor of algal growth and rotifers feeding. However, differences did appear between the sites.

At the upstream site of Dam, Chlorophytes (and SM) were more strongly linked to the F1 axis (that explained 86% of the inertia) than flow and also *t* °C, and the F2 axis (that explained 10% of the inertia) clearly discriminated BOD_5, (Fig. 5). Such a scheme illustrated the classical links between low water discharge, high temperature, high oxygen production and high density of algae. Most of the species were grouped together close to the origin, the 7 species more distant were those more numerous in the samples: the trio *B. angularis, B. calyciflorus* and *K. tecta* (three loricate species), situated in the upper part of the F1 axis, was linked to Chlorophytes, while the trio *T. brachyura, T. pusilla* and *C. gibba* (three epibenthic species) appeared more linked to temperature. *R. frontalis* (a soft-bodied species) isolated close to the F2 axis, may be more reactive to the water quality, as expressed by the BOD_5 and to a lesser extent by O_2.

At the downstream site of Slb, flow and temperature linked to the F1 axis (that explained 76% of the inertia) were the discriminant variables for living material. SM linked to the F2 axis (that explained only 12% of the inertia), was opposed to Chlorophytes that were linked to BOD_5 (Fig. 6). Such a pattern illustrated the answer to the river eutrophication and its consequences for the water quality. The species distribution was more spread out from the origin of the axis than at the upstream site, except *S. socialis* which peaked only in 2001 (cf. Table 1). *A. priodonta* that strongly peaked in this area in 1999 and 2000 remained close to *E. macrourus* and *P. major* (2 soft-bodied species that peaked in the same years) and to *L. luna* (an epibenthic species). Among species far away from the origin of the axis, the genus *Brachionus*, *Anuraeopsis* and *Keratella* were more distant from the F1 axis (strictly linked to *t* °C) than *T. pusilla*, *P. vulgaris*, *C. gibba, E. dilatata* and *P. dolichoptera*. These epibenthic species may have greater affinity to the temperature. On the F2 axis, SM data were opposed to O_2 and *L. closterocerca* was the least abundant species at the site.

Discussion

Lessons drawn from experience of the Middle Loire

Among European rivers, the Middle Loire remains a place of extremes. Summer is the time in which the slightest change in water flow induces increase or decrease of the lentic areas which are strongly swept by thermal winds. These areas offer a high diversity of habitats and are good for the growth of opportunistic species. During low water discharge, the river looks like a shallow lake, productive from surface to bottom, shallow depths resulting also in high ambient light levels and, as a consequence, high primary production. Indeed from 1995 to 2002, the absence of flood events has maintained numerous lentic areas and the main bed has remained isolated from lateral backwaters (the nearest reservoir is situated 290 km upstream from Dam). The results showed that the two sites function similarly with regard to flow rates (there is no tributary in between) and water temperature, and the densities of the classical components of the potamoplankton were very similar, increasing from up to downstream.

The cladocerans found in the digestive tracts of young fish caught in the open water of the margins

Table 2. Set of Pearson correlations fitted to evaluate the relationships between abiotic variables, available food and rotifer densities in the Middle Loire

Variables	Flow rate				Temperature			
	Dam	R^2	Slb	R^2	Dam	R^2	Slb	R^2
Total algae	−0.47***	0.29	−0.39***	0.23	0.43***	0.19	0.44***	0.22
Total rotifers	−0.38**	0.16	−0.29*	0.13	0.34**	0.16	0.27*	0.12
Soft−bodied species	−0.33**	0.15	−0.24*	0.14	0.14	0.08	0.18	0.07
Loricate species	−0.34**	0.16	−0.26*	0.08	0.29*	0.11	0.23	0.08
Epibenthic species	−0.26*	0.11	−0.29*	0.13	0.38**	0.14	0.31*	0.14
Asplanchna priodonta	−0.14	0.02	−0.14	0.02	0.12	0.02	0.18	0.03
	Total algae				Chlorophytes			
	Density		Biomass		Density		Biomass	
	Dam	Slb	Dam	Slb	Dam	Slb	Dam	Slb
Total rotifers	0.73***	0.66***	0.45***	0.40***	0.77***	0.78***	0.71***	0.63***
Soft−bodied species	0.38**	0.29*	0.39**	0.25*	0.38**	0.26*	0.39***	0.25*
Loricate species	0.71***	0.69***	0.39**	0.33**	0.72***	0.74***	0.68***	0.67***
Epibenthic species	0.66***	0.60***	0.40***	0.41***	0.65***	0.56***	0.66***	0.55***
	Diatoms				Cyanobacteria			
	Density		Biomass		Density		Biomass	
	Dam	Slb	Dam	Slb	Dam	Slb	Dam	Slb
Total rotifers	0.22	0.01	0.24*	0.14	0.35**	0.31**	0.05	0.00
Soft−bodied species	0.09	0.03	0.24*	0.18	0.24*	0.33**	0.23	0.05
Loricate species	0.21	0.05	0.17	0.08	0.31**	0.14	0.05	−0.09
Epibenthic species	0.24*	0.1	0.24*	0.15	0.36**	0.44***	0.01	0.04

Significance of statistical tests is indicated by either one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

Table 3. Set of Pearson correlations fitted to evaluate the relationships between *Asplanchna priodonta* and other rotifer species in the Middle Loire

Potential prey items	*Asplanchna priodonta*	
	Dam	Slb
Colurella adriatica	0.45***	–
Epiphanes macrourus	0.59***	0.56***
Euchlanis dilatata	–	0.55***
Polyarthra dolichoptera	0.25*	0.57***
Polyarthra major	–	0.60***
Polyarthra vulgaris	–	0.54***
Trichocerca brachyura	–	0.72***
Trichocerca elongata	–	0.62***
Trichocerca similis	–	0.54***
Trichocerca pusilla	–	0.45***

and littoral vegetation, are solely littoral species (e.g., Steiner C. and Ducher C, university degree projects, unpublished), extremely rarely caught in the current. In addition, in the 64 data series obtained during the low water periods of 1995–2002, typically planktonic crustaceans were absent from the samples collected in the current. Obviously, the role of the 'Age of Water', underlined at the dawn of the XX^e century by Kofoïd, and demonstrated one century later by Baranyi et al. (2002) for Danube zooplankton, cannot be doubt in the control of rotifer production.

In comparison with the species richness of rotifer populations among rivers of the world, listed by Kobayashi et al. (1998), the Middle Loire ranks among the highest. The changes in dominance from site to site, as well as from year to year, illustrated once again the opportunism of these organisms. The changes in rotifer density were parallel to those of the algae, a general scheme usually associated with increases in temperature and decreases in water discharge (Pace et al., 1992; Thorpe et al., 1994; Kobayashi et al. 1998; Schröder, 2001), since small Chlorophytes constitute a large part of their edible food. The progressive decrease in density of the algae observed during the course of these 8 years resulted from the reduction in phosphates discharges from wastewater treatment plants in the catchment area, while nitrates have also decreased every summer (Lair, 2002, synthesis paper published in Hydroécologie Appliquée, the national revue of EDF). In contrast to the algae, the changes in rotifer densities, linked in some years to several excavation works (documented in Lair et al., 1999), were not significant.

As for the algae (e.g., Bauer et al., 2002), the proportion of rotifer species that grow in storage zones illustrates the importance of habitats to the distribution of rotifers (Picard, 2003). Soft-bodied species remained the least numerous in the Middle Loire, and the main group continued to be loricate species, with the short-spined *B. angularis* (on average in the eight years survey, this species was 1st in density at Dam and 3rd at Slb) and *K. cochlearis* v. *tecta* (2nd at Dam, 4th at Slb), as well as *B. calyciflorus* (5th at both sites). The dominance of Brachionids is a general rule in numerous rivers, insofar as several species of this genus can continue to grow in a current experienced at 0.2 m s^{-1}, while the soft-bodied forms cannot. In addition, current may act as a refuge from predation by other plankton. Indeed, because of the passive transportation of plankton in such an unsettled and viscous environment, it appears evident that predators have difficulty in encountering, detecting, capturing, piercing, sucking out, and/or ingesting prey. Filtering, also remains problematic. Are the feeding mechanisms of rotifers, with a well-developed buccal rotatory organ at the apex of a protective lorica, more efficient in these circumstances?

The epibenthic species that can attach to substrates came second in abundance in the Middle Loire, with the dominance of *C. gibba* (4th in density at Dam, 2nd at Slb). Trichocercids (*T. brachyura* and *T. pusilla*) were among the more numerous and their abundance seemed to be particularly relevant as indicators of the river habitats. Indeed, as underlined in the introduction, in the Middle Loire, they were found concentrated above the sandy areas (Picard & Lair, 2004). This complements the results of Holst et al. (2002) who considered exceptional the striking dominance of *Trichocerca pusilla* in the potamal region of the Elbe, another 'sandy sediments, near-natural river'. In their small scale approach with a transverse section of the river, these authors did not find significant differences in the abundance of rotifers between the main stream and groyne fields. However, this section of the river was straightened, current velocity was not documented and the

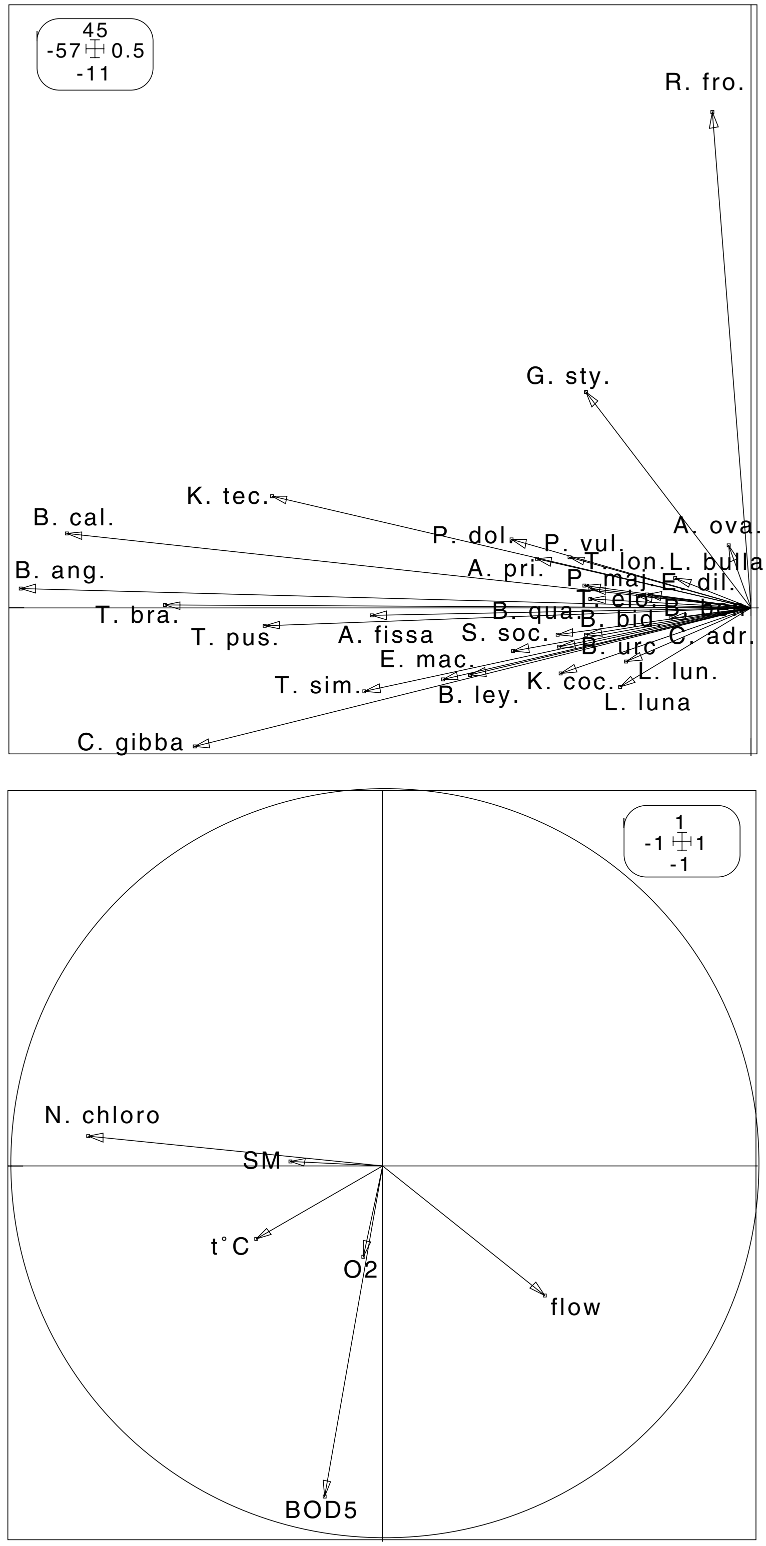

Figure 5. Co-inertia analysis between environment and species variables for the site at Dampierre-en-Burly.

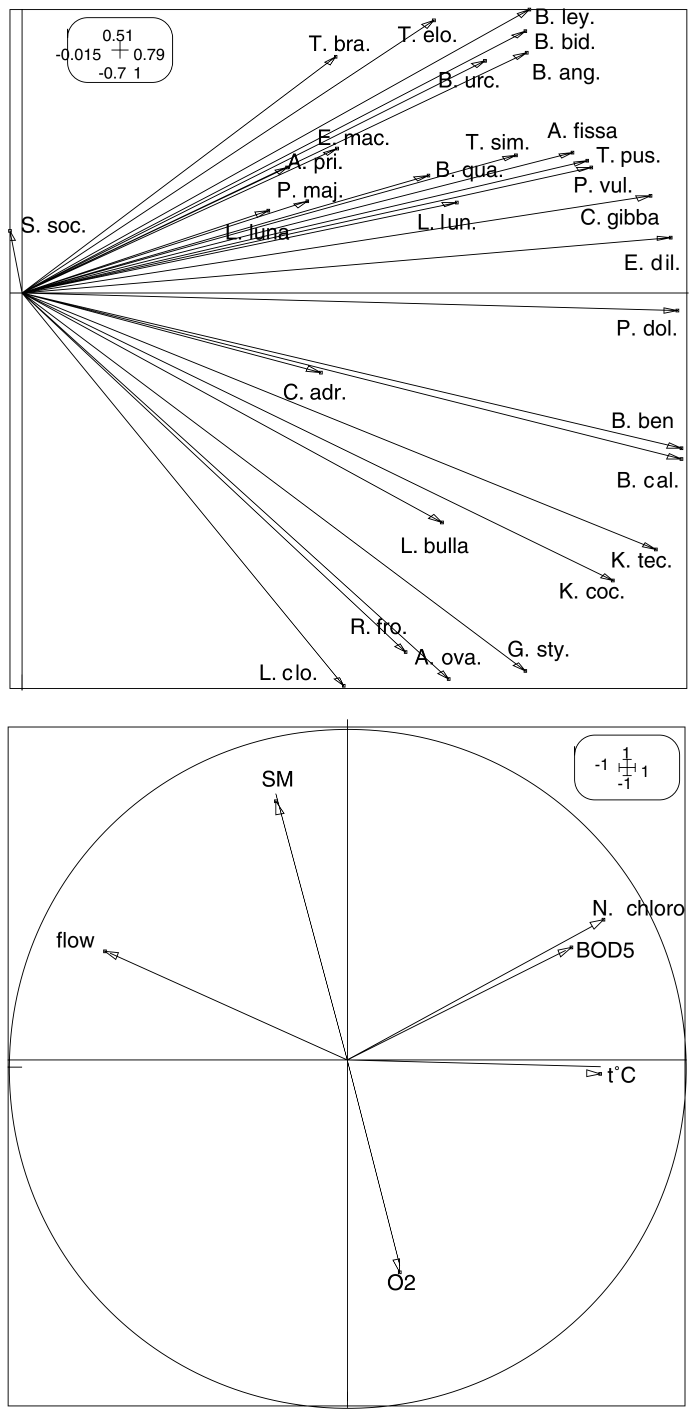

Figure 6. Co-inertia analysis between environment and species variables for the site at Saint-Laurent-des-Eaux.

supposition of a simple dilution effect was not excluded.

Top-down control by predaceous rotifers is also at the heart of the matter. *A. priodonta*, whose density achieved first position at Slb, reached high densities, depending on the years. This predator is known to be capable of adjusting its diet to its environment and to be more of a grazer than a predator (Kappes et al., 2000) and its success in the Middle Loire was certainly because the river provides more food resources than are required. The strong correlation between *Asplanchna* and other species, such as the soft-bodied *E. macrourus*, *P. major*, may be more indicative of their co-existence in the same environment, the comparison with the very low density of small rotifer prey being in contradiction with theoretical predator-prey relationships.

The results derived from the co-inertia analysis illustrate that flow was clearly unfavourable whatever the living material and the sites. This confirms that low water discharge, high temperature and food are essential to allow planktonic rotifers to multiply, and that Monogononts of the Order Ploima are incapable of withstanding high flow velocities (Linhart, 2002). While retention zones tended to expand in the region close to Dam, in this section the water flow weighted slightly less in the rotifer species distribution than at Slb. The aggregation close to the origin of most of the species at Dam contrasted with the more dispersed distribution observed at Slb, giving two distinct patterns between the sites. Dominant species, such as *B. angularis, B. calyciflorus* and *K. cochlearis* v. tecta which largely dominated the rotifer communities at both sites and discriminated at Dam, were diluted with the pool of other species at Slb. Moreover, several epibenthic species appeared more sensitive to the temperature at both sites. The morphological characteristics of the river (and as a consequence the current velocity) may act as the dominant force, lentic areas being more numerous in the section at Dam than at Slb. This pattern may underline more local processes at Dam, with more species swept from stagnant water, while longitudinal transfers would be more important at Slb. Several species that have appeared more linked to the temperature were exported at both sites.

The great flexibility of rotifers in responding to hydraulic conditions

Plankton communities are undoubtedly carried downstream at various speeds (Reynolds, 1988), and refuge habitats from the disturbance of flow remain numerous in rivers. Rivers such as the Middle Loire, in which typically planktonic crustaceans are absent from the current during low flow, emphasize that rotifers would be best adapted to running water conditions and particularly those species of Brachionids that proliferate also in other rivers. Their shorter turnover time than that of crustaceans is beneficial. However, during dispersal, their habitat is not chosen by the rotifers and may be unsuitable for their growth. Admitting that fast growing rotifers can proliferate in a place, the production of protective cover under the influence of sudden and stochastic increases in water flow seems to be problematic. It poses the question of how the installed populations persist locally, particularly in sections in which hydraulic backwaters remain sparse, as in regulated rivers in which the structural properties are degraded (Schiemer et al., 2001). Facilities for several species to feed in the current were underlined above, and the difficulties for males to come across females, is a constraint deleted by heterogony. In addition, the production of resting eggs can take place either when population growth reaches its maximum, or at low densities in some populations (Schröder, 2001). Moreover, this author showed that rotifers can produce resting eggs during inundation periods, but also in the permanent water during the rest of the year, adjacent storage zones being able to preserve potential colonisers producing resting eggs, and rebuild populations with few individuals. Such a situation is particularly relevant in unregulated rivers. William & Smith (1996) showed that individual rotifers may respond to hydraulic conditions in a species-specific way, and the results from the Middle Loire confirm existing differences among species. Moreover, Schröder (2001) emphasized the dominance of the ubiquitous *B. calyciflorus, K. cochlearis, Keratella quadrata* and *Polyarthra* spp. in the permanent waters of the floodplain, and they can stock the rivers. The example of the Middle Loire has confirmed that lentic areas are more densely populated than flowing reaches; but, these aquatic biota are also refuges for fish that reside there, particularly during droughts (Magoulick & Kobza, 2003). However, the constraint remains and the final chance for species to become dominant may be their capability of sustaining a minimum feeding activity and continuing to grow and reproduce at low rates in the current, and of hatching a few resting eggs at just the right time, while the current acts as a refuge from predation by predaceous plankters.

Are rivers unique and the plankton origin too?

Rivers provide dispersal routes for both animals and plants that are important for maintaining the diversity of the riparian zooplankton. It has been postulated that zooplankters may be effectively dispersed by waterfowl. If so, and assuming that dispersal can be provided by wind, rain or waterfowl, the experiments of Jenkins & Underwood (1999) do not support 'the premise of readily dispersed zooplankton'. The origin of plankton remains a complex issue, developed for example in the 'flood pulse concept' of Junk et al. (1989), and in the 'inshore retention concept' of Schiemer et al. (2001), but the importance of the physical environment has often been neglected by planktonologists.

The plankton communities are undoubtedly carried downstream at various speeds (Reynolds, 1988) and numerous authors have explained the downstream increase in zooplankton by the time needed to build significant populations. Downstream transfer certainly plays a key role, thanks to the provision of organic matter and algae provided to rotifer plankton and other communities and, if the food available can be limited in headwaters, it is certainly not in the lowland parts of rivers. However, the longitudinal changes in geomorphological features, responsible for retention time and water discharge, and the complexity of the hydraulics often make it difficult to evaluate accurately the extent of longitudinal transportation of plankton.

Most investigations have focused on large-scale longitudinal changes of abundance and species composition, based on samples taken from the main stream, but few have considered small-scale transverse variations (e.g. Holst et al., 2002). The recent increase in research at smaller scales has indicated an enhanced role of localised areas, and the results from the Middle Loire where flood pulses still occur, have contributed greatly to underlining the importance of local processes in which inoculation points are possibly located within distances as short as a hundred meters (Lair & Reyes-Marchant, 1997). The increases in density observed over short distances cannot be explained by the transit time, because it is not the 'Age of Water', *sensus* turnover time in which most of the organisms built their successive generations. Indeed, their origin, strictly linked to the morphology of the rivers, remains an important aspect and, in rivers characterised by a paucity of hydraulic backwaters in their catchment areas, dispersal of potamoplankton localised to the margins could be a more general rule as was suspected.

Examining the lateral distribution of the river plankton in the Meuse, Marneffe et al. (1996) observed the maxima in algae and zooplankton close to the banks. An attempt to illustrate this was also made by Reckendorfer et al. (1999) in the Austrian part of the river Danube, to which end they developed an index of lentic habitat availability, based on length of the shoreline and water velocity. In a similar way, the example of the Middle Loire emphasizes the importance of fine-scale patchiness and illustrates the role of lentic areas in the supply of rotifers to the main channel. For example, the observations made at the scale of the sites in the Middle Loire, showed that during summer, the rotifer density increased over short distances up and downstream of the plants, despite the fact that they need a minimum of 34 km to double their biomass (Lair & Reyes-Marchant, 1997). Sampling only in the channel might result in an underestimate of global rotifer densities, which occur in higher densities in the lentic areas of this river (Picard, 2003).

Abiotic vs. biotic factors

In the light of these considerations, the presence of plankton in rivers, classically linked to potamal environments, needs to be reassessed. Indeed, in headwater reaches characterised by gravel bedloads with riffle and pool morphology, diel and seasonal drift have been observed for several species such as *E. dilatata, K. cochlearis* etc. (Schram et al., 1998), and rivers with slow-flowing upper reaches can show much higher plankton densities upstream than downstream (Reckendorfer et al., 1999). These results underline once again the importance of the river morphology.

In the middle reaches, the example of rotifer distribution in the Middle Loire showed that downstream transport was linked to the availability of lentic areas situated in the immediate environment and the downstream increase in density observed from Dam to Slb was not the general rule in this river. Indeed, the site at Belleville-sur-Loire, situated 40 km upstream of Dam (Fig. 1), whose communities were studied again in 1999, was more densely populated than the site at Dam (Picard, 2003). In the section at Bel, the river frequently extends up to 500 m in width and more local sources of plankton may supply the main stream. In contrast, in regulated rivers in which the channel is deeply incised into its floodplain and few permanent waters occur, plankton increase downstream may be a more general rule. Drifting from adjacent water bodies connected to the river is inevitable, and this would happen particularly at those periods when large flood events occur. Rotifers originating from reservoirs, from which zooplankton species are flushed passively and then observed in downstream outlets after a long time (Chandler, 1937), are not questioned and there is a widespread literature on this matter. Zooplankton drift in rivers, such as the Rhine (Admiraal et al., 1994), also reproduced the seasonal succession of plankton classically observed in lakes, indicating its origin. Further, downstream the rotifer density may be limited by the presence of suspended matter (Miquelis et al., 1998), that also limits light penetration and primary production. Continuing down the course of the river, large changes in flow rates at the river-estuary interface induce not only large changes in animal plankton densities, but also in species composition.

Conclusion

Among the many interesting aspects of studying rotifers in rivers, the question that remains is their role in the food web. Several investigations have indirectly shown the modest to considerable influence of grazing by zooplankton (e.g., Schöl et al., 2002) and the role of rotifers in the regulation of the algae, which is open to debate, is linked to the problem of their feeding efficiency in rivers. The grazing effect of the numerous filter-feeders was suspected to cause the summer decline in the algae of the Middle Loire (Lair & Reyes-Marchant, 1997). However, experiments carried out in agitated waters have demonstrated the low efficiency of the species concerned. Furthermore, to our knowledge, studies including all the actors involved in the trophic network are lacking and, in addition, to quantify the top down control by fish remains a problem. Obviously, the observations during eight years, of the dynamics of algae and rotifers that have evolved in parallel in the Middle Loire cannot support the assertion 'the more phytoplankton, the more rotifers in' as much as the food available (including other protists and bacteria) is excessively greater in abundance than are the rotifers. In addition, their population development, enhanced during low discharge/high temperature periods, remains limited to a few weeks. We can reasonably admit that top-down control of the algae by river rotifers, preferentially exerted at low or null flow, may remain very limited over all, whereas predation by predaceous plankton may certainly be exerted in lentic areas. Vertebrate predation, whose intensity depends on the synchronisation of the respective timing of births that vary from year to year, may be limited to fish larvae during a short period, the young of the year being observed to go quickly from cladocerans to insect larvae (Reyes-Marchant et al., 1992, and unpublished data of Steiner and Duchet, noted above). The shift in the rotifers density observed every year at the end of the summer, is certainly due essentially to the increase in water discharge, decrease in temperature (and as a result, decrease in food), that largely act as forcing variables.

As a general rule, from headwater to middle reaches and estuaries, the origin of rotifers seems to be strictly linked to the morphological characteristics of the rivers (including man-made structures), the rotifer species caught in the course of the rivers acting as indicators of their various origins. Finally, the increase in density of rotifers may undoubtedly be limited by 'the Age of Water' and, if the role of the floodplain is fundamental during high flow, the importance of local processes illustrated by several authors may become the key factor in the functioning of river plankton.

For the future, programmes are needed that work towards a better knowledge of rotifers' strategies and feeding ecology at a species level, which remains poorly documented in rivers. Further, to obtain a holistic approach to the rotifers' ecology in rivers, multidisciplinary research is needed. A good example was that conducted from Vienna on the Danube (Reckendorfer et al., 1999) including river habitats and river inhabitants. In fact, we now have at our disposal a formidable arsenal of techniques including computer processing of aerial photographs and digitisation for field mapping of storage zones, including backwaters, which can be finalised with Geographical Information Systems. Calibration of storage zones, including submerged macrophytes, using a Global Positioning System can be associated with series sampling of living material, based on random sampling strategies (as was done in a section of the Middle Loire in 1999) in successive stretches, in order to obtain a better knowledge of the life in rivers.

Acknowledgements

Data used in this work comes from monitoring programmes supported by Electricité de France. We thank Patricia Reyes-Marchant, Jean-Luc Peiry and Aude Beauger for their help with data and work processing and anonymous reviewers for their valuable suggestions that improved the manuscript. Mary Burgis was the English reviewer.

References

Admiraal, W., L. Breebaart, G. M. J. Tubbing, B. Zanten Van, E. D. De Ruyter Van Steveninck & R. Bijkerk, 1994. Seasonal variation in composition and production of planktonic communities in the lower River Rhine. Freshwater Biology 32: 519–531.

Baranyi, C., T. Hein, C. Holarek, S. Keckeis & F. Schiemer, 2002. Zooplankton biomass and community structure in a Danube River floodplain system: effects of hydrology. Freshwater Biology 47: 473–482.

Bauer, D. E., M. E. Conde & N. Gomez, 2002. Phytoplankton of a small lowland stream related to water quality and hydraulic discontinuities. Archiv für Hydrobiologie 153: 421–442.

Chandler, D. C., 1937. Fate of typical lake plankton in streams. Ecological Monographs 7: 445–479.

Chessel, D. & S. Dolédec, 1992. ADE Software. Multivariate Analysis and Graphical Display for Environmental Data. Université Lyon 1.

Christensen, V. & D. Pauly, 1992. ECOPATH II – a software for balancing steady – state ecosystem models and calculating network characteristics. Ecological Modelling 61: 169–185.

De Ruyter, E., D. Van Steveninck, W. Admiraal & B. Van Zanten, 1990. Changes in plankton communities in regulated reaches of the lower Rhine river. Regulated Rivers 5: 67–75.

Dolédec, S. & D. Chessel, 1994. Co-inertia analysis: an alternative method for studying species-environment relationships. Freshwater Biology 31: 277–294.

Ejsmont-Karabin, J. & M. Kruk, 1999. Effects of contrasting land use on free-swimming rotifer communities of streams in Masurian Lake District, Poland. Hydrobiologia 387/388: 241–249.

Ferrari, I., A. Farabegoli & R. Mazzoni, 1989. Abundance and diversity of planktonic rotifers in the Po River. Hydrobiologia 186/187: 201–208.

Frisch, D., 2001. Life cycles of the two freshwater copepods *Cyclops strenuus* Fischer and *Cyclops insignis* Claus (Cyclopoida, Copepoda) in an amphibious floodplain habitat. Hydrobiologia 453/454: 285–293.

Galkovskaya, G. A. & D. V. Molotkov, 2001. Species diversity and dominance in the planktonic rotifer community of the Pripyat River in the Chernobyl region (1988–1996). Hydrobiologia 446/447: 179–185.

Gosselain, V., J. -P. Descy & E. Everbecq, 1994. The phytoplankton community of the river Meuse, Belgium: seasonal dynamics (year 1992) and the possible incidence of zooplankton grazing. Hydrobiologia 289: 179–191.

Gosselain, V., C. Joaquim-Justo, L. Viroux, M. Mena, A. J. -P. Metens Descy & J. -P. Thomé, 1996. Laboratory and in situ grazing rates of large river rotifers and their contribution to community grazing rates. Archiv für Hydrobiologie, Supplement 113: 353–361.

Holst, H., H. Zimmermann-Timm & H. Kausch, 2002. Longitudinal and transverse distribution of plankton rotifers in the potamal of the River Elbe (Germany) during late summer. International Review of Hydrobiology 87: 267–280.

Jenkins, D. G. & M. O. Underwood, 1999. Zooplankton may not disperse readily in wind, rain, or waterfowl. Hydrobiologia 387/388: 15–21.

Junk, W. J., P. B. Bayley & R. E. Sparks, 1989. The flood pulse concept in River-Floodplain Systems. Canadian Special Publication of Fisheries and Aquatic Sciences 106: 110–127.

Kappes, H., C. Mechenich & U. Sinsch, 2000. Long-term dynamics of *Asplanchna priodonta* in Lake Windsborn with comments on the diet. Hydrobiologia 432: 91–100.

Kobayashi, T., P. Gibbs, P. Dixon & R. J. Shiel, 1996. Grazing by a river zooplankton community: importance of microzooplankton. Marine and Freshwater Research 47: 1025–1036.

Kobayashi, T., R. J. Shiel, P. Gibbs & P. I. Dixon, 1998. Freshwater zooplankton in the Hawkesbury-Nepean River: Comparison of community structure with other rivers. Hydrobiologia 377: 133–145.

Kofoïd, C. A., 1903. The plankton of the Illinois River, 1894–1896, with introductory notes upon the hydrography of the

Illinois River and its basin. Part I. Quantitative investigations and general results Ill. State Laboratory of Natural History Bulletin 6: 95–629.
Lair, N. & P. Reyes-Marchant, 1997. The potamoplankton of the Middle Loire and the role of the moving littoral' in downstream transfer of algae and rotifers. Hydrobiologia 356: 33–52.
Lair, N, P. Reyes-Marchant & V. Jacquet, 1998. Développement du phytoplancton, des ciliés et des rotifères sur deux sites de la Loire moyenne (France), en période d'étiage. Annales de Limnologie 34: 35–48.
Lair, N., V. Jacquet & P. Reyes-Marchant, 1999. Factors related to autotrophic potamoplankton, heterotrophic protists and micrometazoans abundance at two sites in a lowland temperate river, during low water flow. Hydrobiologia 394: 13–28.
Linhart, J., 2002. Bdelloidea/Monogononta abundance ratio: a possible measure of the relation of stream rotifers to flow velocity ?. Biologica 39/40: 101–110.
Magoulick, D. & R. M. Kobza, 2003. The role of refugia for fish during drought: a review and synthesis. Freshwater Biology 40: 1186–1198.
Marneffe, Y., J. -P. Descy & J. -P. Thomé, 1996. The Zooplankton of the lower river Meuse, Belgium: seasonal changes and impact of industrial and municipal discharges. Hydrobiologia 319: 1–13.
May, L. & J. A. B. Bass, 1998. A study of rotifers in the River Thames, England, April-October, 1996. Hydrobiologia 387/388: 251–257.
Miquelis, A., C. Rougier & R. Pourriot, 1998. Impact of turbulence and turbidity on the grazing rate of the rotifer *Brachionus calyciflorus*: Pallas. Hydrobiologia 386: 203–211.
Pace, M., S. Findlay, E. G. Stuart & D. Links, 1992. Zooplankton in advective environments: the Hudson River community and a comparative analysis. Canadian Journal of Fisheries and Aquatic Sciences 49: 1060–1069.
Picard, V. 2003. Structure et dynamique du potamoplancton de la Loire moyenne (France) en période de basses eaux. Analyse spatio-temporelle de la distribution des algues, des bactéries hétérotrophes, des protozoaires flagellés et ciliés et des rotifères. Influence des variables hydrogéomorphologiques et modélisation écotrophique. Thèse de Doctorat, Université de Clermont-Ferrand (France), 145 pp.
Picard V. & N Lair, 2003. Laboratory approach of the growth of rotifers sampled in Middle Loire (France) under turbulence. Journal de Recherche Oceanographique 28: 196–199.
Pourriot, R., 1977. Food and feeding habits of Rotifera. Archiv für Hydrobiologie 8: 243–260.
Reyes-Marchant, P., A. Cravino & N. Lair, 1992. Food and feeding behaviour of roach (*Rutilus rutilus*, Linné 1758) juveniles in relation to morphological changes. Journal of Applied Ichthyology 8: 77–89.
Reckendorfer, W., H. Keckeis, G. Winkler & F. Schiemer, 1999. Zooplankton abundance in the River Danube, Austria: The significance of inshore retention. Freshwater Biology 41: 583–591.
Reynolds C. S, 1988. Potamoplankton: paradigms, paradoxes and prognoses. In Round FE (Ed), Algae and the aquatic environment. Biopress Ltd, Bristol, 285–311.
Ricci, C. & M. Balsamo, 2000. The biology and ecology of lotic rotifers and gastrotrichs. Freshwater Biology 44: 15–28.
Rothhaupt, K. O., 1990. Changes of the functional responses of the rotifers *Brachionus rubens* and *Brachionus calyciflorus* with particle size. Limnology and Oceanography 35: 24–32.
Rzoska, J., 1978. On the Nature of Rivers. Dr W. Junks. The Hague, 67 pp.
Saunders, J. F. & W. M. Lewis Jr., 1988. Zooplankton abundance in the Caura River, Venezuela. Biotropica 20: 206–214.
Schiemer, F., H. Keckeis, W. Reckendorfer & G. Winkler, 2001. The 'inshore retention concept' and its significance for large rivers. Large Rivers 12. Archiv für Hydrobiologie Supplement 135: 509–516.
Schöl, A., V. Kirchesch, T. Bergfeld, F. Schöll, J. Borcheding & D. Müller, 2002. Modelling the Chlorophyll a content of the River Rhine – Interrelation between riverine algal production and population biomass of grazers, rotifers and the Zebra Mussel, *Dreissena polymorpha*. International Review of Hydrobiology 87: 295–317.
Schram, M. D., M. Gunter & D. B. Engle, 1998. Diurnal vertical distribution and drift of zooplankton in an Ozark headwater stream pool. Journal of Freshwater Ecology 13: 47–54.
Schröder, T., 2001. Colonising stategies and diapause of planktonic rotifers (Monogononta, Rotifera) during aquatic and terrestrial phases in a floodplain (Lower Oder Valley, Germany). International Review of Hydrobiology 86: 635–660.
Servais, P., V. Gosselain, C. Joaquim-Justo, S. Becquevort J.-P. Thomé & J.-P. Descy, 2000. Trophic relationships between planktonic micro-organisms in the River Meuse (Belgium): a carbon budget. Archiv für Hydrobiologie, 149: 625–653.
Shiel, R. J., K. F. Walker & W. D. Williams, 1982. Plankton of the Lower River Murray, South Australia. Australian Journal of Marine and Freshwater Research 33: 301–327.
Tan, L.-W. & R. J. Shiel, 1993. Responses of billabong rotifer communities to inundation. Hydrobiologia 255/256: 361–369.
Thorpe, J. H, A. R. Black, K. H. Haag & J. D. Wehr, 1994. Zooplankton assemblages in the Ohio River: seasonal, tributary, and navigation dam effects. Canadian Journal of Fisheries and Aquatic Sciences 51: 1634–1643.
Vasquez, E. & J. Rey, 1989. A longitudinal study of zooplankton along the Lower Orinoco River and its delta (Venezuela). Annales de Limnologie 25: 107–120.
Viroux, L., 2000. An attempt to evaluate zooplankton longitudinal dynmics in a lowland river using a small still-standing 'potamocorral' enclosure. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen 27: 2979–2982.
Walz, N., 1995. Rotifer populations in plankton communities: energetics and life history strategies. Experientia 51: 437–453.
Williams, D. D. & M. R. Smith, 1996. Colonization dynamics of river benthos in response to local changes in bed characteristics. Freshwater Biology 36: 237–248.