Aquatic Sciences 58/3, 1996
1015–1621/030253-16 $ 1.50 + 0.20/0

Horizontal distribution of the rotifer plankton of Lake Aydat (France)

Nicole Lair, Hassan Taleb and Patricia Reyes-Marchant

Université Blaise Pascal de Clermont-Ferrand, UPRES A 1562, Hydrosystèmes, 63177 Aubière Cedex, France

Key words: Rotifers, horizontal distribution, resources partitioning, predation.

ABSTRACT

We investigated the causes of the shift which occurs in the horizontal distribution of planktonic rotifers of Lake Aydat. A normalised PCA was used to analyse the spatio-temporal distribution of 18 rotifer species. They are more numerous in the littoral zone, but seasonal changes remain higher than spatial changes. Results illustrate the capability of rotifers to take efficiently advantage of available space and food. The digestive tracts of fry and juvenile roach was also analysed and the index of Ivlev was used to determine prey selection. Fish predation occurs in the nearshore zone and the interactions between invertebrate predators and their prey are illustrated by the quantitative changes in community dynamics. Among the complex cascade of events varying in the course of the year, and despite of resource partitioning, predator-prey interactions as well as the exploitative competition between rotifers and crustaceans produce gradients exhibited in the horizontal distribution of rotifers in Lake Aydat.

1. Introduction

Rotifers generally are an important link in the well documented pelagic food webs of eutrophic lakes, but in contrast the littoral zone remains little studied. Investigations from April 1984 to November 1985, based on demographic analysis, examination of gut contents and laboratory feeding experiments, have illustrated the importance of intrazooplankton predation for the seasonal succession of eulimnoplankton in the eutrophic Lake Aydat (Lair, 1990; Lair and Hilal, 1992), where invertebrate predators effectively control the growth of small-sized zooplankton.

Rotifers are preyed up on by most fish, especially the young, and account for the majority of food items identified in their guts (e.g. Hammer, 1985; Telesh, 1993). Studies of the effects of fish on the zooplankton of both the littoral zone and open water of lake Aydat were, therefore, initiated. These involved analysis of gut contents and feeding activities and calculation of stocks of adult and young fish (Jamet, 1991; Reyes-Marchant, 1993: Taleb et al., 1994).

Many authors have noticed that planktonic rotifers are either limnetic or littoral (Wetzel, 1975; Lemley and Dimmick, 1982), but in contrast to their vertical distribution their horizontal distribution is not well documented (Preissler, 1977; Sauders-Davies, 1989). The present study was undertaken with the aim of studying the spatio-temporal distribution of the rotifer fauna, from the littoral to the limnetic zone and to investigate the possible impact of predation on their horizontal distribution.

2. Site, materials and methods

2.1 The lake

The eutrophic Lake Aydat (France) with a 60 ha surface area and 15.50 m maximum depth, at 825 m a.s.l., usually remains ice-covered for about 1–2 months. Its physical and chemical characteristics were summarised by Hartmann et al. (1993). The littoral zone extended from the margin to 2.50 m depth and is partly covered with a dense vegetation, principally *Elodea* sp. and *Myriophyllum* sp. associated with some less common species (Taleb, 1991).

2.2 The crustaceans

In Lake Aydat, we observed that cladoceran density decreased from the open water to the shore, where *Bosmina longirostris* (O.F. Muller, 1785), small *Daphnia longispina* (O.F. Muller, 1785) and *Chydorus sphaericus* (O.F. Muller, 1785) were fed on by larval and juvenile roach. The low number of cladocerans and the frequent absence of large species in the littoral zone results from predation by fish and/or an avoidance behaviour (Taleb et al., 1994). Being also users of algae, copepods remain sparce during summer; the young stages of *Cyclops vicinus vicinus* (Ulianine, 1875) abundant in spring, and those of *Acanthodiaptomus denticornis* (Wierzejski, 1887) who grow from July onwards remain in lower proportions in the littoral than in the pelagic zone (Taleb, 1991).

2.3 Invertebrate and vertebrate predators

Five invertebrate predators were present: the rotifers *Asplanchna priodonta* (Gosse, 1850) and *Cephalodella gibba* (Ehrenberg, 1832), older instars of the cyclopoid *C. vicinus vicinus*, adults of the calanoid *A. denticornis* and the fourth larvae of *Chaoborus flavicans* (Meigen) (Lair, 1990; Lair and Hilal, 1992; Taleb et al., 1992). There were also three dominant fish species: *Rutilus rutilus* (Linne, 1758), *Perca fluviatilis* (Linne, 1758) and *Gymnocephalus cernua* (Linne, 1758). Adult fish fed only on crustaceans (Jamet, 1991), while their fry fed on the whole zooplankton community (Reyes-Marchant et al., 1992; Taleb et al., 1994). The stock of young fish sampled weekly during the period of their presence in the littoral zone (from April to September 1988) has been calculated by modelling analysis (Reyes-Marchant, 1993).

2.4 Sample collection and data analysis

To completement the precedent studies in Lake Aydat, we chose to perform more spatial samples. Zooplankton samples were collected monthly from January 1988 to January 1989 (except in December when the lake was ice-covered) along a profile of 10 stations from the shore to the centre of the lake. The characteristics of the stations are given in Table 1, the littoral zone being conventionally limited to the extent of macrophyte growth (Wetzel, 1983). Zooplankton was collected in triplicate with a vertical van Dorn bottle (8 litres capacity), at each meter from the water surface to the bottom of each station, except near the shore where an horizontal van Dorn bottle was gently handled between the weeds. Samples were pooled in one jar to obtain a single sample per station. After homogenisation, an aliquot of 5 litres was filtered through a 33 µm mesh filter. Zooplankton were immediately preserved in 10% sucrose-formalin and frozen. For quantitative examination, organisms were placed in a Dollfus counting chamber (a rectangular tank of 5 cm × 10 cm, divided in 200 square tanks) and stained with Rose Bengal. When one species was scarce, all the individuals were counted, otherwise subsamples were enumerated.

Fry and juvenile roach were collected before noon with a beach seine (mesh size of the wings = 4 mm, mesh size of the central part = 3 mm). Immediately after catching them, the young fish were preserved in 4% formalin and kept in group ice to prevent digestion of food items (Reyes-Marchant, 1993). During the period of the rotifer studies, 425 digestive tracts were analysed. The Ivlev (1961) index was used to determine the possible selection of prey.

Spatio-temporal distribution of the different species of rotifers along the transect was studied by use of a normalised Principal Components Analysis (Depiereux, 1988). Projection of lines and columns of the matrix on the factorial axis (stations and months analysis, followed with an inter-stations analysis) of the centred PCA processed on the 18 species × 120 samples (10 stations, 12 months) to illustrate their organisation. In the inter-stations PCA, each line is the average of 12 months for each species (log standardized); in the inter-months PCA each line is the average of 10 stations for each species (log standardized). The structure of the

Table 1. The different characteristics of each sampling station. Macrophytes: – absent; + few; ++ dense and +++ very dense

Stations (L: littoral; P: pelagic)	Depth (m)	Distance from the shore (m)	Macrophytes (abundance)
1L	0.20	1	++
2L	0.50	4	+++
3L	0.75	5	+++
4L	1.00	14	+++
5L	1.50	25	++
6L	2.50	50	+
7P	4.00	107	–
8P	8.00	164	–
9P	10.00	200	–
10P	14.00	500	–

rotifers community at each station was visualised in histograms, in each axis (F1–Fi) the average of the 18 species was classified (from January 1988 to January 1989) in the order determined in the plane of the principal components.

3. Results and discussion

3.1 Abiotic and biotic data

Transparency was approximately the same at each station. The minimum Secchi depth (0.90 m) occurred in May and June. Temperature and dissolved oxygen differences between the littoral and the upper layer of the pelagic zone did not exceeded 2 °C and 1 mg · l^{-1} respectively. Food was not limiting in this eutrophic lake and small particles (algae, flagellates, ciliates and bacteria) were abundant (Marvalin et al., 1989; Sime-Ngando and Hartmann, 1991; Aleya, 1992). We therefore consider these variables to be insignificant to the distribution of rotifers.

3.2 Species composition and community density

Twenty two species were recorded in Lake Aydat in 1988 (4 were occasional and 18 were present at different stations and periods). Among the Ploima, we found the Asplanchnidae *Asplanchna priodonta*, the Brachionidae *Brachionus calyciflorus* (Pallas, 1766), *Euchlanis dilatata* (Ehrenberg, 1832), *Kellicottia longispina* (Kellicott, 1879), *Keratella cochlearis* (Gosse, 1851), *Keratella quadrata* (Müller, 1786), *Notholca acuminata* (Ehrenberg, 1832) and *Rhinoglena frontalis* (Ehrenberg, 1853), the Lecanidae *Lecane luna* (Müller, 1776), the Notommatidae *Cephalodella gibba*, the Synchaetidae *Polyarthra dolichoptera* (Idelson, 1925), *Polyarthra remata* (Skorinkow, 1896) and *Synchaeta pectinata* (Ehrenberg, 1832), the Trichocercidae *Trichocerca cylindrica* (Imhof, 1891) and *Trichocerca elongata* (Gosse, 1886) and among the Flosculariacea the Testudinellidae *Filinia hofmanni* (Koste, 1980) and the Conochilidae *Conochilus natans* (Seligo, 1900) and *Conochilus* sp. (Ehrenberg, 1834) of the *unicornis-hippocrepis* group (designated *C. u* on the graphs). A study performed in the nearshore zone of the lake during summer 1993 with an apparatus designed to sample macrophytes, cut them and collect the enclosed plankton did not revealed new species (Lunot, unpublished data).

In eutrophic lakes where both algal and detrital food are abundant, rotifers may reach densities varying from 400–1800 ind · l^{-1} in open lakes (e.g. Herzig, 1979) to 17700 ind · l^{-1} (Orcutt and Pace, 1984). In Lake Aydat rotifers generally grow between May and September (Oulad Ali et al., 1990; Taleb, 1991). In 1988 they increased in density in May–June and their maximum occurred in July before they decreased dramatically in August. The maximum (and average) density was 10000 (1060) ind · l^{-1} in the littoral zone and 4200 (668) ind · l^{-1} in the pelagic zone (Fig. 1). This density of rotifers confirms the eutrophic state of this lake.

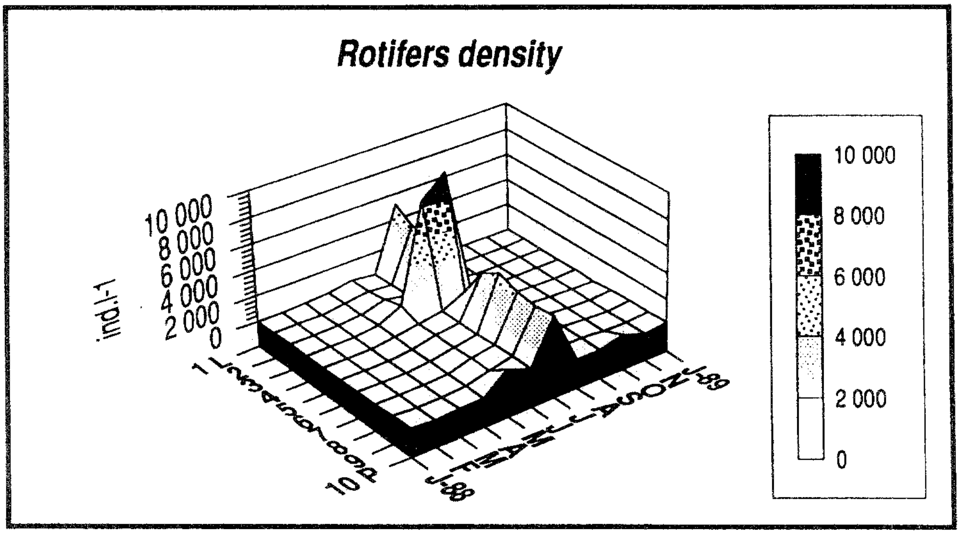


Figure 1. Temporal distribution of the rotifer community at the 10 stations from the littoral (1 L) to the pelagic (10 P) zone

3.3 Seasonal succession

The principal components analysis in reduced space, extracted from the correlation matrix explains 64.3% of the information on the four first dispersion and significant axes. In the inter-months analysis, the projection of species on the planes F1 × F2 and F3 × F4 gives a picture of the temporal community evolution (Fig. 2). The right negative part of the plane F1 × F2, corresponds to the end of winter – early spring species *R. frontalis, B. calyciflorus, T. elongata* and *C. natans*, correlated with axis 1. These species are close to *N. acuminata* which grows in spring and summer (correlated with axis 2). *E. dilatata* situated on axis 2 grows both in winter and summer. The left negative part of the plane groups the summer species *F. hofmanni, K. cochlearis* and *A. priodonta* (correlated with axis 2), *T. cylindrica* and *P. remata* (correlated with axis 1).

On the right negative part of the plane F3 × F4 are the winter-spring species *K. quadrata, K., longispina* and *P. dolichoptera.* On the left negative part are associated *C. gibba* and *L. luna* which grow in August–September (correlated with axis 4). The spring species *S. pectinata* and the abundant autumnal species *Conochilus* sp., were not discriminated on these four first axis.

Few species in Lake Aydat are cold (*C. natans, R. frontalis*) or warm stenothermal (*T. cylindrica, P. remata*), but most are eurythermal. This pattern is in agreement with the general ecological data of species given by Pourriot (1965) and Ruttner-Kolisko (1974), which will also be used for the examination of resource partitioning (see below, part 3.5).

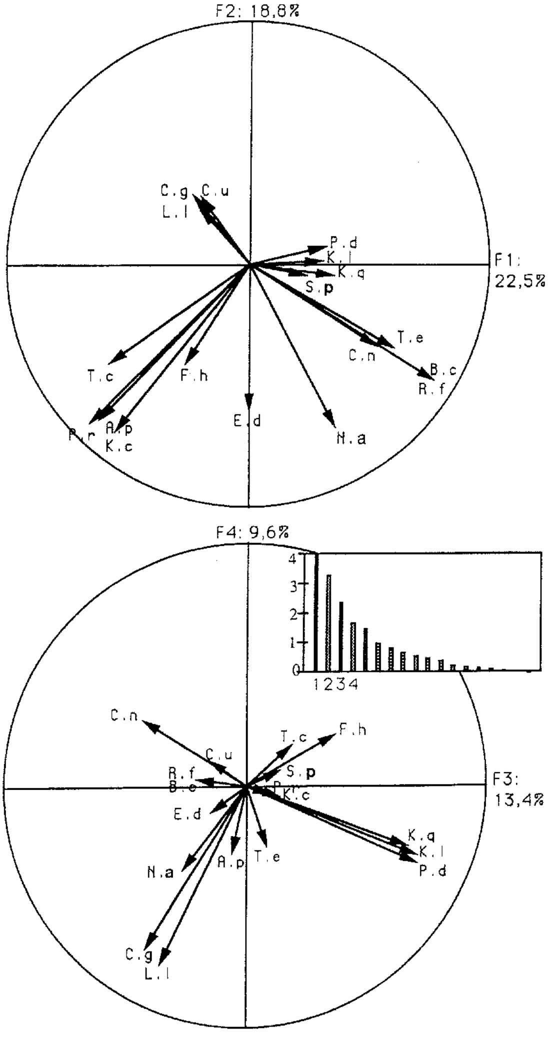


Figure 2. Situation of the species (designated by their initials) in the planes of F1×F2 and F3×F4, resulting from inter-month analysis. Eigen values (y axis) of factor (x axis) discriminated by the global PCA analysis

3.4 Horizontal distribution

In the stations-months analysis, the projection of sampling stations on axis 1, gives the horizontal distribution of corresponding species. *R. frontalis* (with a small winter population in the pelagic zone), *B. calyciflorus, T. elongata* and *C. natans*, grow in the littoral zone from February to May (positive part of the axis), while *K. cochlearis, A. priodonta, P. remata* grow in July at each station, *T. cylindrica* and *F. hofmanni* being more in the pelagic zone (negative part of the axis) (Fig. 3).

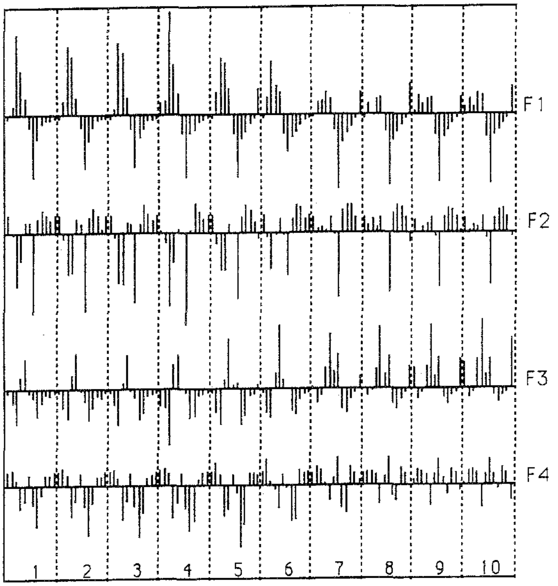


Figure 3. Normalised sampled data defined by the four first axis of the PCA. Numbers correspond to the stations 1 to 10 and, for each station bars are in the chronological order (January 1988 to January 1989)

The projection of the sampling stations on axis 2 does not indicate any preference for sampling stations in the positive part of the axis. The negative part illustrates the March–April growth of *N. acuminata* in the littoral zone, added to the summer growth of *N. acuminata* and *E. dilatata*. Positive coordinates of axis 3 illustrate the growth of *L. luna* and *C. gibba* in both zones. The lower part of this axis corresponds to *K. quadrata, K. longispina* and *P. dolichoptera* (with its winter growth) which are more abundant in the pelagic zone, in comparison with the littoral. The negative coordinates of axis 4, gives species located more in the littoral zone (*C. gibba* and *L. luna*).

We proceeded to the graphic representation of the PCA, in order to reconstruct the situation of the different sampling stations, in relation with the distribution of species (Fig. 4). This analysis discriminates between the littoral zone (stations 1 to 5) and the pelagic zone (stations 7 to 10), station 6 being intermediate (data rebuilt by axes 1 and 2 give the position of species), showing that no sudden shift occurs between the two zones. The variance between stations is 0.6, while in the between-months analysis it was 4.1 (see eigen values of the y axis resulting from PCA graph of Fig. 2), which means that the seasonal changes are higher than the spatial changes.

3.5 Resource partitioning

Except for the sparse *N. acuminata* which was found only at stations 1 to 6, all others were sampled at all stations (Fig. 5). In each time and site there are species with

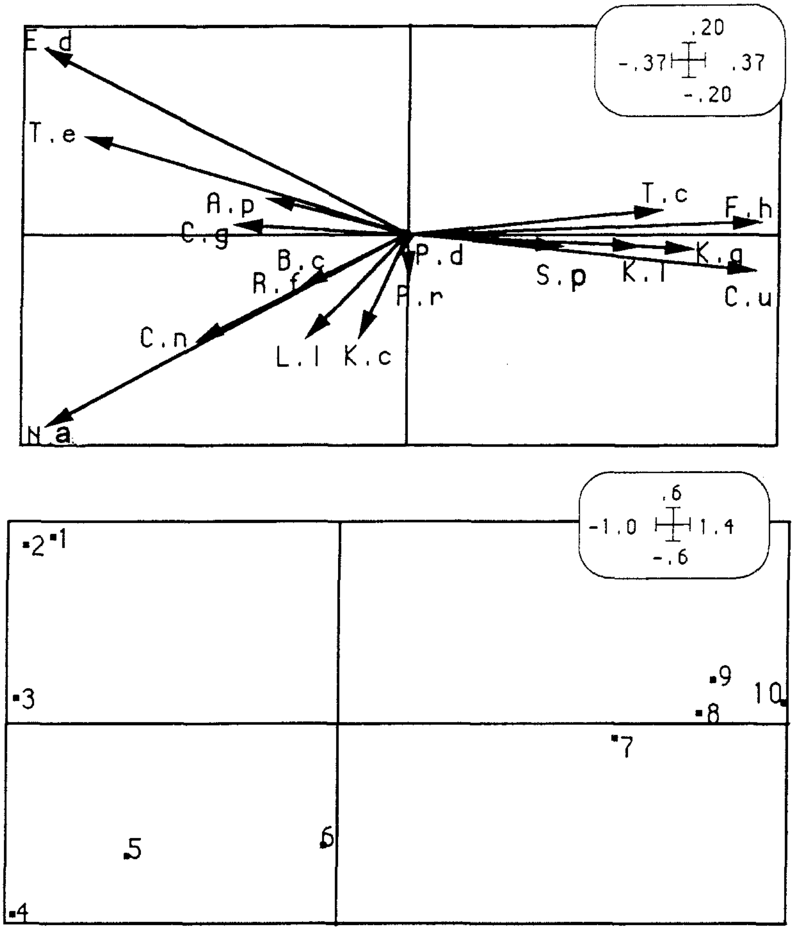
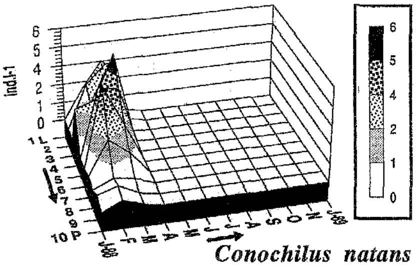
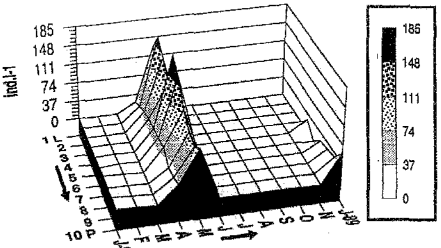


Figure 4. Situation of the measurable variables in the plane of axis I and II, resulting from inter-stations analysis (species are designated by their initials and numbers 1 to 10 correspond to the stations)

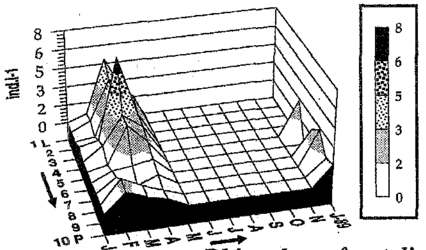
different food habits; in winter and early spring, associated with the algivorous *C. natans*, we observed species with a broad food spectrum like *R. frontalis*, *N. acuminata* (density < 4 ind · l^{-1}), *E. dilatata* and *B. calyciflorus* followed later by the algivorous *P. dolichoptera* in both zones and the herbivo-detritivorous *K. quadrata*, *T. elongata* (density < 4 ind · l^{-1}) and *K. longispina* in the littoral. In June the algivorous *T. cylindrica* peaked in the pelagic zone, in July, it was the detritivorous *F. hofmanni*, while the large food spectrum species *K. cochlearis* peaked in the littoral. At that time, they were associated with the algivorous *P. remata* in both zones, while the predator *A. priodonta* attained its maximum density in the littoral. In August there was a shift and only two species remain until autumn, the colonial and detritivorous *Conochilus* sp. was dominant in pelagic, while the carnivorous *C. gibba*, associated with its small prey *L. luna*, occurred in both zones.



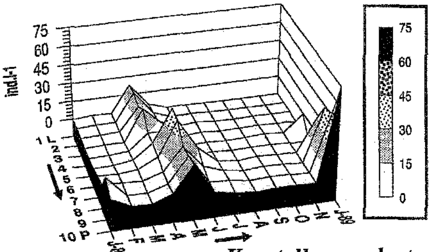
Conochilus natans



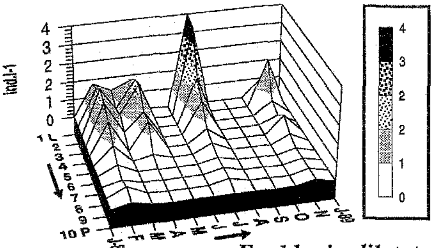
Polyarthra dolichoptera



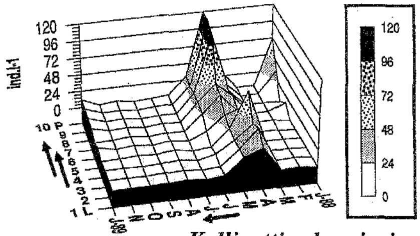
Rhinoglena frontalis



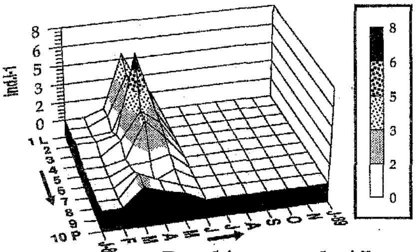
Keratella quadrata



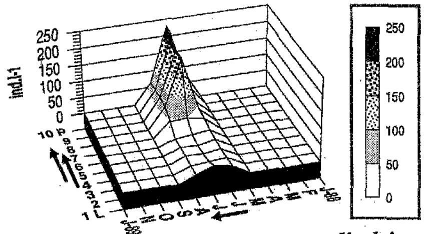
Euchlanis dilatata



Kellicottia longispina

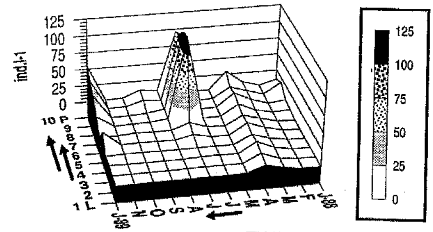


Brachionus calyciflorus

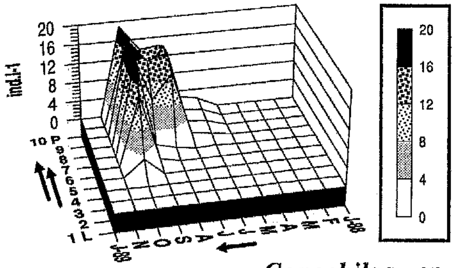


Trichocerca cylindrica

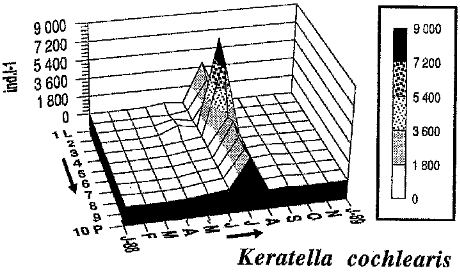
Figure 5. Spatio-temporal distribution of the principal species of rotifers plotted in seasonal succession order



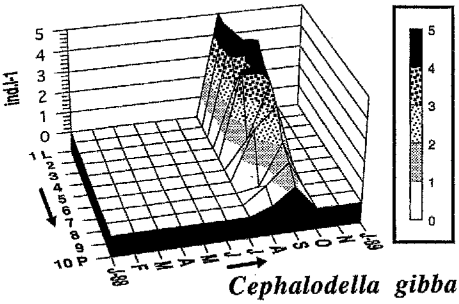
Filinia hofmanni



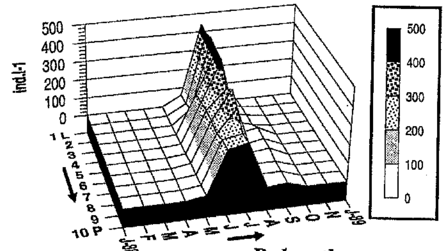
Conochilus sp.



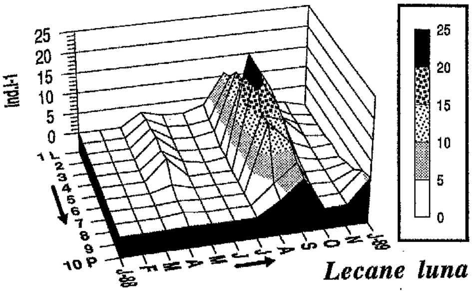
Keratella cochlearis



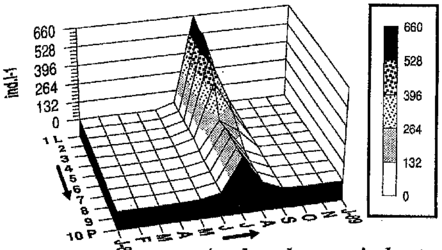
Cephalodella gibba



Polyarthra remata



Lecane luna



Asplanchna priodonta

Figure 5 (continued)

In previous studies, conducted biweekly in June–July 1975 and weekly from April to November 1984, with samples taken at 7 depths in the lake, we observed a remarkable spatio-temporal autogenic succession. Species lived alternately in surface and/or deep layers, depending on their ability to live (or not) in anoxic water, to stay in cold (or warm) water, and on their food preferences (Lair, 1978; Oulad Ali et al., 1990). As in the vertical scale, we observed that broad food spectrum species and algivorous species lived alternately in the littoral and pelagic zones during the year. These broad spectrum species developed during summer associated with the detritivorous species which occurred from June to October in the pelagic zone, probably due to the abundance of bacteria near the thermocline, following decomposition and sedimentation of cyanobacteria and algae (Marvalin et al., 1989). During this study, our observations confirmed that rotifers have the capability of efficiently taking advantage of the available space and food.

3.6 Invertebrate predation

The impact of vertebrate and invertebrate predation on planktonic communities is well documented in the pelagic, in contrast to the littoral zone, which is more complex, but also the most productive area of many lakes (Wetzel, 1983). Predators can influence the local Shannon's diversity of their prey and in 1988 in Lake Aydat we observed that rotifer diversity decreased from May to August in the littoral zone, and to a lesser extent in the pelagic zone. This suggests an impact of predation (Lair et al., 1993).

A. priodonta is a voracious predator of rotifers (Ejsmont-Karabin, 1974; Williamson and Gilbert, 1980; Zaret, 1980; Hofmann, 1983). In previous studies on the invertebrate predators of Lake Aydat, direct observations of stomach contents showed that *A. priodonta* consumes *F. hofmanni, K. cochlearis, P. remata* and *P. dolichoptera* (Oulad Ali et al., 1990). In the littoral and pelagic zones, the density of *A. priodonta* starts to increase from May (simultaneously with *P. dolichoptera* which fell in June), reaches its highest value in July, in parallel with its potential prey *F. hofmanni* and *K. cochlearis*, and decreases in August. We hypothesise that *A. priodonta* plays a part in this decline. A similar pattern was observed with *C. gibba* and the small *L. luna* which both peaked in September before crashing in October.

Each year, *A. denticornis* took over from July, as the other rotifers decreased, before it reached a maximum in winter (Taleb, 1991). In previous studies we hypothesised that predation pressure by *A. denticornis* might be the cause of the rotifer decline from mid-summer onwards (Lair, 1990). Subsequently, feeding experiments demonstrated that adults of this copepod feed on *K. cochlearis* (Lair and Hilal, 1992), *S. pectinata* (Hilal, unpublished data) and large ciliates (Hartmann et al., 1993). In 1988, *A. denticornis* was dominant in the pelagic zone in January and February, increased from June and peaked from September onwards. The shift in rotifer density from August onwards was linked to the development of that species. Both the competition with the young stages of the copepod and predation by adults can influence the rotifers' decline.

Since Fryer (1957) observed that cyclopoids are important predators of rotifers, numerous other authors have made the same observation (Williamson and Gilbert, 1980; Stemberger, 1982; Williamson, 1983). Our gut analysis of late copepodite stages and of adults showed that during spring, the food of *C. vicinus* was essentially composed of *Polyarthra* spp. and *K. cochlearis* (El Ghachtoul, 1987) the most abundant species in the lake. The carnivorous stages of *Cyclops* were abundant in May in the littoral, simultaneously with the maximum density of *P. dolichoptera* and in

June in the pelagic zone, simultaneously with *P. remata*. At the end of spring this copepod may contribute to the decrease in density of these rotifers species.

3.7 *Fish predation*

In the littoral zone, young roach were associated with young perch which occurred in low numbers and fed on copepods (Phillipart, 1993, internal report). The 0+ roach hatched in summer 1987 returned in the littoral in April 1988, followed by a new generation born in June–July. After the hatching period, the young fishes spent their first months in this shallow area, before leaving it in October. The total number of young fish was estimated and the total density of ingested rotifers (and cladocerans) was calculated (Reyes-Marchant, 1993) (Table 2). In April, May and July the guts of young fish contained mostly rotifers, which coincided with the decrease in their species diversity (Lair et al., 1993). In June and August these rotifers were preyed upon in lower proportions, small cladocerans being added to the diets of the young fish (Taleb et al., 1994).

Reference to the study on the diel feeding activities of the roach fry, run in July 1988, the period of the maximum development of rotifers showed that *A. priodonta, K. cochlearis* and *L. luna* were consumed day and night by the young *R. rutilus*. The Ivlev index suggested that the dominant species *K. cochlearis* was avoided at 6:00 pm, 10:00 pm, 2:00 am, 10:00 am and 6:00 am and selected moderately

Table 2. Numerical contribution of the prey species in Lake Aydat and in the gut of 0+ *Rutilus rutilus* and Ivlev index calculations (G = N · ind. in the guts and F = density ind · l^{-1} in the field)

Species	April	May	June	July	August	September
Asplanchna priodonta (G)	0	0	3	0	20	0
Asplanchna priodonta (F)	1720	8060	40160	105655	160720	8000
IVLEV	–1	–1	–0,99	–1	–0,99	–1
Keratella quadrata (G)	2365	1844	0	614	179	217
Keratella quadrata (F)	20300	13833	0	1100	250	600
IVLEV	–0,15	0,34		0,99	0,86	0,51
Keratella cochlearis (G)	13742	25306	26076	7404	4529	6390
Keratella cochlearis (F)	90066	404400	385900	4567700	3200	46566
IVLEV	0,01	0,02	0,04	–0,13	0,95	0,08
Lecane luna (G)	829	553	45	512	229	218
Lecane luina (F)	4333	5766	700	1333	17233	10500
IVLEV	0,08	0,2	0	0,99	–0,4	–0,7
Daphnia longispina (G)	194	133	30	204	111	68
Daphnia longispina (M)	180	260	107	447	120	127
IVLEV	0,83	0,24	0,24	0,09	0,69	–0,22
Bosmania longirostris (G)	511	538	120	1053	661	197
Bosmina longirostris (M)	909	9633	3775	1784	258	258
IVLEV	0,71	–0,69	–0,69	0,22	0,87	–0,05
Chydorus sphaericus (G)	1799	2862	1518	1229	1190	496
Chydorus sphaericus (M)	23330	1067	5433	4367	10767	433
IVLEV	–0,1	0,79	0,22	–0,14	–0,2	0,14

at 2:00 pm and 6:00 pm; *A. priodonta* was avoided at any time, which indicates that roach fry feed on the most abundant species without marked selection. In contrast, the rare species *L. luna* was selected at 6 out of 7 different times of the day (Taleb et al., 1993). Such results are worth thinking about. The same Ivlev calculations conducted only with day-time observations, gave quite different results: when run with morning sampling they showed that both prey were avoided by the fish (Table 2).

In our July data, the horizontal distribution of *K. cochlearis* and *L. luna*, shows lower densities at stations 1, 2 and 3 (nearshore area), a situation only observed for these two species. As a consequence, on the basis of our diel observations we can hypothesise that the lower density of *K. cochlearis* and *L. luna* in the nearshore zone is linked to the predation exerted by the young fish: if *A. priodonta* was not affected, both *K. cochlaris* selected moderately and *L. luna* largely selected are removed faster than they can be produced. The results obtained on other dates would require knowledge of the diel feeding behaviour of the young fish to be validated.

4. Conclusion

Rotifer distribution has been the subject of debate: on one hand species are designated either littoral or exclusively pelagial, on the other hand planktonic rotifers are equally limnetic and littoral (Straskraba, 1965; Pennak, 1966; Makarewicz and Likens, 1979). It has been suggested that planktonic rotifers follow the same pattern as pelagic crustaceans, in relation to the shore (Ruttner, 1974; Preissler, 1977) which was not observed in lake Aydat. At diurnal scale and in experimental conditons, Dumont (1972) observed the competition between *Asplanchna* and crustaceans induced a reverse vertical distribution. Telesh (1993) showed that population densities of some rotifer species increased as a result of the elimination of large crustaceans by fish during summer and autumn. We conclude that the distinction between euplanktonic and strictly littoral species is the result of complex interactions between planktonic rotifer, crustacean species and fish. However, to understand the nature of species interactions and determine the extent to which they can explain observed patterns and dynamic properties we can deduce the resultant trophic interconnections between this species-rich food web.

Demographic analysis of the rotifer species living in Lake Aydat has shown high growth rates and high turnover rates, supplemented by high mortality rates (Oulad Ali, 1988), and the remarkable seasonal succession (Lair and Ayadi, 1989), illustrated by studies on their vertical distribution (Oulad Ali et al., 1990) is corrobotated by the analysis of their horizontal distribution. For an apparently uniform habitat, species occupy alternately littoral or pelagic sites, such a resource partitioning gives possible for species to coexist and acts as an important factor.

In that eutrophic lake, where resource partitioning occurs, association between strongly competing species remains certainly limited even if larger cladocerans can suppress rotifers through exploitative competition for shared food resources (Wickham and Gilbert, 1990). Among species ecologically similar in Lake Aydat, we can deduce the reverse horizontal pattern we observed between crustaceans and rotifers certainly tends to reduce the exploitative competition. More, larger daphnids remain in low numbers which is not relevant to their possible interference with rotifers which are also known to be vulnerable to cladoceran interference.

The boundaries between competition and invertebrate predation are not easy to distinguish. However the interactions between invertebrate predators and their prey species were reflected in quantitative changes in community dynamics at weekly and vertical scales (Lair, 1990), as well as at monthly and horizontal scales (that study). They remain all the more important since the invertebrate predators does not occur in the same proportions in the littoral and pelagic areas.

Rotifers are the principal food of fish fry; the similar percentage of rotifers found in their guts as well as in the water samples indicates the passive intake of the young fish on the dominant species during the day (Reyes-Marchant et al., 1994). All 0+ roach, hatched in summer 1987, which returned the littoral zone in April 1988, fed essentially on rotifers which are removed more quickly than they are produced. After the hatching period of June–July the smallest fish continue to feed on rotifers, from June onwards the others ingesting essentially cladocerans. Thus, the boundaries within which vertebrate predation is exerted must be clearly delineated to the shallow littoral area, as far as adult fish do not fed on rotifers (Jamet, 1991). However at some periods in Lake Aydat, the reduction in crustacean competitive pressure on rotifers, as well as the reduction in rotifers vulnerability to the possible interference competition with larger cladocerans, may be caused by adult fish.

Among the complex cascade of events varying in the course of the year, and despite of resourse partitioning, predator-prey interactions as well as the exploitative competition between rotifers and crustaceans produce gradients exhibited in the horizontal distribution of rotifers in Lake Aydat. We hypothesise that the combination of competition and invertebrate predation in the pelagic zone, added to the vertebrate predation in the nearshore zone, are the dominant process of such a distribution.

ACKNOWLEDGEMENTS

We thanks Denis Sargos whon ran the PCA analysis and Henry Dumont as referee for improving the manuscript.

REFERENCES

Aleya, L., 1992. The seasonal succession of phytoplankton in an eutrophic lake through the coupling of biochemical composition of particles, metabolic parameters and environmental conditions. Arch Hydrobiol. 124:69–88.

Depiereux, E., 1988. Multivariate analysis in the description of community structure: principal component and cluster methods. In: M. Hermy an A. Wilmotte (eds.), Multivariate Analysis of Biological Data. Bull. Soc. Roy. Belg. 121:127–158.

Dumont, H.J., 1972. A competition based approach of the reverse vertical migration in zooplankton and its implications, chiefly based on the study of the interactions of the Rotifer *Asplanchna priodonta* (Gosse) with several Crustaceae, Entomostraca. Int. Revue Ges. Hydrobiol. 57:1–38.

El Ghachtoul, Y., 1987. Dynamique des populations des copépodes d'un lac eutrophe du Massif Cetral français: le lac d'Aydat. Vie active et vie latente. Thesis (3^{e} Cycle). Univ. Blaise Pascal de Clermont-Ferrand. Aubière, France. France. 137 p.

Ejsmont-Karabin, J., 1974. Studies on the feeding planktonic polyphage *Asplanchna priodonta* (Gosse) Rotatoria. Ekol. Pol. 22:311–317.

Fryer, G., 1957. The feeding mechanism of some freshwater cyclopoid copepods. Proc. Zool. Soc. Lond. 129:1–25.

Hammer, C., 1985. Feeding behaviour of roach (*Rutilus rutilus*) larvae and the fry of perch (*Perca fluviatilis*) in Lake Lankau. Arch. Hydrobiol. 103(1):61–74.

Hartmann, H.J., H. Taleb, L. Aleya and N. Lair, 1993. Predation on Ciliates by the suspension-feeding Calanoid Copepod *Acanthodiaptomus denticornis*. Can. J. Aquat. Sci. 50:1382–1392.

Herzig, A:, 1979. The zooplankton of the open lake. In: H. Loffler (ed.), Neusiedleresee. Limnology of shallow lake in Central Europe. Dr. W. Junk Publ., The Hague. Mongr. Biol. 37:281–335.

Hofmann, W., 1983. On temporal variation in the rotifer *Keratella cochlearis* (Gosse): the question of "Lauterborn-cycles". Hydrobiologia 101:247–254.

Ivlev, V.S., 1961. Experimental Ecology of the feeding of fish. Yale Univ. Press. New Haven. 302 p.

Jamet, J.L., 1991. Importance de la faune ichthyologique dans le lac d'Aydat, milieu eutrophe de la zone tempérée Nord; ses relations trophiques avec les autres composantes de l'écosystème. Doctorat d'Université, Univ. Blaise Pascal de Clermont-Ferrand, Aubière, France. 263 p.

Lair, N., 1978. Répartition spatio-temporelle, biomasse et production des populations zooplanctoniques du lac d'Aydat en période estivale. Hydrobiologia 61:237–256.

Lair, N., 1990. Effects of invertebrate predation, on the seasonal succession of zooplankton community: a two years study in Lake Aydat France. Hydrobiologia 198:1–12.

Lair, N. and H. Ayadi, 1989. The seasonal succession of planktonic events in Lake Aydat. A comparison with the PEG model. Arch. f. Hydrobiology 115:589–602.

Lair, N. and M. Hilal, 1992. *Acanthodiaptomus denticornis* another omnivorous calanoid copepod: description of its mouth appendages and feeding experiments on animal prey. Hydrobiologia 248:137–142.

Lair, N., H. Taleb and P. Reyes-Marchant, 1993. Zooplankton diversity responses to predation pressure in littoral and limnetic zones of eutrophic lake, in France. Verh. int. Ver. Limnol. 25:603–607.

Lemley, A.D. and J.F. Dimmick, 1982. Structure and dynamics of zooplankton communities in the littoral zone of some North Carolina lakes. Hydrobiologia 88:299–307.

Makarewicz, J.C. and G. Lineks, 1979. Structure and function of the zooplankton community of Mirror Lake, New Hampshire. Ecol. Monogr. 49:109–127.

Marvalin, O., L. Aleya, H.J. Hartmann and S. Lazarek, 1989. Coupling of the seasonal patterns of bacterioplankton and phytoplankton in a eutrophic lake. Can. J. Microbiol. 35:706–712.

Orcutt, Jr. J.D. and M.L. Pace, 1984. Seasonal dynamics of Rotifer and Crustacean zooplankton populations in a eutrophic monomictic lake with a note on Rotifer sampling techniques. Hydrobiologia 119:73–80.

Oulad Ali, H., 1988. Rôle et importance des rotifères planctoniques dans un écosystème lacustre eutrophe de la zone tempérée nord: le lac d'Aydat (France). Dynamique des populations, biomasse, production, activités de broutage et efficacité d'assimilation. Doctorat d'Université, Univ. Blaise Pascal de Clermont-Ferrand, Aubière, France. 241 p.

Oulad Ali, H., N. Lair and H. Ayadi, 1990. The seasonal succession of Rotifers in the eutrophic Aydat lake. Spatio-temporal organisation. Ann. Sci Nat. Zool., Paris 13 ème Série, Vol. II:113–121.

Pennak, R.W., 1966. Structure of zooplankton populations in the littoral macrophyte zone of some Colorado lakes. Trans. Amer. Microsc. Soc. 85(3):329–349.

Pourriot, R:, 1965. Recherches sur l'écologie des rotifères. Vie et Milieu Suppl. 21, 224 p.

Preissler, K., 1977. Do Rotifers show "Avoidance of the shore"? Oecologia (Berl.) 27:253–260.

Reyes-Marchant, P., 1993. Impact des alevins de gardon (*Rutilus rutilus*, L.) sur les communautés planctoniques littorales. Modélisation du fonctionnement trophique du lac d'Aydat. Doctorat d'Université. Univ. Blaise Pascal de Clermont-Ferrand, Aubière, France. 181 p + 50 annexes.

Reyes-Marchant, P., A. Cravino and N. Lair, 1992. Food and feeding behaviour of roach (*Rutilus rutilus*, Linné 1758) juveniles in relation to morphological changes. J. Appl. Ichtyol. 8:77–89.

Reyes-Marchant, P., H. Taleb and N. Lair, 1994. Relationships between predation and growth rates of fish fry (*Rutilus rutilus*) in littoral zone of Lake Aydat (France). Verh. int. Ver. Limnol. 25:2153–2157.

Ruttner, F., 1974. Fundamentals of Limnology. Univ. of Toronto Press, 150 pp.

Ruttner-Kolisko, A:, 1974. Plankton Rotifers, Biology and Taxonomy (English translation). In: Die Binnengewässer, 26: 1 suppl. Stuttgart Schweizerbzrt'sche Verlagsbuchhandlung (Nägele u. Obermiller: 99–234

Saunders-Davies, A.P., 1989. Horizontal distribution of the plankton rotifers *Keratella cochlearis* (Bory de St Vincent) and *Polyarthra vulgaris* (Carlin) in small eutrophic lake. Hydrobiologia 186/187:153–156.

Simé-Ngando, T. and H. Hartmann, 1991. Short-term variations of the abundance and biomass of planktonic ciliates in an eutrophic lake. Eur. J. Protistol. 27:249–263.

Stemberger, R.S., 1982. Mechanisms controlling selection and rates of predation on rotifers in *Cyclops bicuspidatus thomasi*. Ph. D thesis, Univ., Mich., 95 p.

Straskraba, M., 1965. Contributions to the Productivity of the Littoral Region of Pools and Ponds. I. Quantitative study of the littoral zooplankton of rich vegetation of the Backwater Labicko. Hydrobiologia 25:421–443.

Taleb, H., 1991. Distribution spatio-temporelle du zooplancton dans un lac eutrophe. Rôle de la prédation dans la structure des communautés littorales et pélagiques. Doctorat d'Université, Univ. Blaise Pascal de Clermont-Ferrand. Aubière. France. 269 p.

Taleb, H., N. Lair and J.L. Jamet, 1992. Estival diel vertical migration of *Acanthodiaptomus denticornis* (Wierzejski, 1887) (Calanoida: Copepoda) in an eutrophic lake of the temperate zone. Ann. Sc. Nat. Zool., Paris, 13^{e} série, 13:149–156.

Taleb, H., N. Lair, P. Reyes-Marchant and J.L. Jamet, 1993. Observations on vertical migrations of zooplankton at four differents stations of a small, eutrophic, temperate zone lake, in relation to their predators. Arch. Hydrobiol. Beih. Ergebn. Limnol. 39:199–216.

Taleb, H., P. Reyes-Marchant and N. Lair, 1994. Effect of vertebrate predation on the spatio-temporal distribution of cladocerans in a temperate eutrophic lake. Hydrobiologia 294: 117–128.

Telesh, I.V., 1993. The effect of fish on planktonic rotifers. Hydrobiologia 255/256:289–296.

Wetzel, R.R., 1975. Limnology. Sauders, W.B. Co. Philadelphia. 743 p.

Wetzel, R.R., 1983. Limnology. CBS College Publishings., 767 p.

Wickham, S.A. and J.J. Gilbert, 1990. Relative vulnerability of natural rotifer and ciliate communities to cladocerans: laboratory and field experiments. Freshwat. Biol. 26:77–86.

Williamson, C.E., 1983. Invertebrate predation on planktonic rotifers. Hydrobiologia 104:385–396.

Williamson, C.E. and J.J. Gilbert, 1980. Variation among zooplankton predators: the potential of *Asplanchna, Mesocyclops* and *Cyclops* to attack, capture and digest various Rotifer prey. In Kerfoot (red.). Evolution and ecology of zooplankton communities. American Society of Limnol. and Oceanogr. Special symposium 3:509–517.

Zaret, T.M., 1980. Predation and freshwater communities. New Haven and London Yale University Press. 187 p.

Received 18 August 1993;
revised manuscript accepted 13 August 1996.