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## **Niche segregation factors in an assemblage of pelagic rotifers of a deep high-mountain lake (Redon, Pyrenees)**

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## **Abstract**

The niche space of a species has been defined as the region in N-dimensional environmental hyperspace in which the fitness of the individuals is positive. In zooplankton assemblages, there has been little consideration of how different density-dependent (i.e. resources) and density-independent (i.e. conditions) environmental factors relate to fitness components in the field, namely survival and reproduction. We studied the abundance and reproduction (egg ratio) variability of seven species of pelagic rotifers living in a high-mountain lake and their relation to a number of environmental factors by means of partial canonical correspondence analyses. The generally higher explanatory capacity of conditions over resources suggests that habitat partitioning among species largely relies on historical processes, which are internalised in life history traits of spatial and temporal habitat use. However, the increase in the relevance of resources when considering reproduction, as compared to abundance, indicates that there is still an on-going interactive niche segregation process among rotifer species, which affects present and future rotifer assemblages in the lake. Our study shows the value of considering measurements close to fitness components (e.g. egg ratio) for detecting on-going niche segregation processes in zooplankton, which may help to resolve paradoxes in relation to species coexistence in natural assemblages.

## Introduction

Hutchinson (1957, 1959) defined the niche space as the region in N-dimensional hyperspace in which the fitness of the individuals is positive. At the population level, fitness can be understood as the balance between growth rates and loss rates. Such a balance depends on the environmental requirements for an individual to complete its life cycle (survival) and to replace itself (reproduction). Approaches that explicitly considered the process of resource depletion (Schoener, 1974; Tilman, 1982) distinguished density-dependent (i.e., resources related) and density-independent (i.e., conditions related) components of fitness, recognizing that each of these components impact on both reproduction and survival probabilities (Liebold, 1995). In aquatic systems and for zooplankton in particular, field studies on species distribution quite often highlight abiotic factors (density-independent descriptors) as relevant in explaining species segregation (Laxhuber, 1987; Dunson and Travis, 1991; Armengol et al., 1998). Only exceptionally has the role of resources been demonstrated when using multivariate analyses (Green, 1971). On the other hand, theoretical ecology and laboratory studies normally consider density-dependent descriptors (i.e. resources and other biological interactions) as key elements of species niche segregation (Zaret, 1980; Tilman, 1982; Grundstörn, 1987; Rothhaupt, 1990), and have paid less attention to density-independent factors, with exceptions studying resource and temperature interactions in large mesocosms (Achenbach and Lampert, 1997; Stelzer, 2006).

The relative significance of conditions and resources in population dynamics (i.e., individuals' life cycles and reproduction) is a traditional, though puzzling question in ecology (Begon et al. 2006). Remarkably, field studies have paid little attention to how different resources and conditions relate to survival and reproduction. Filling in this gap, we studied the abundance and reproduction variability of seven species of pelagic rotifers living in a high-mountain lake and its relation to a number of potentially influential environmental factors. We performed a canonical correspondence analysis with variance partition (partial CCA) to reveal the hierarchical relationships of conditions and resources in describing the two components of the species population dynamics. Reproduction was considered in terms of egg ratios (the ratio of the number of eggs to the number of females) and when possible we distinguished between current-reproduction and delayed-reproduction (i.e. resting eggs). By explicitly looking at the explanatory capacity of various environmental factors on abundance and reproduction we expected to assess better the role of conditions and resources in the process of habitat partition in species assemblages and, as a consequence, in niche segregation.

## Method

### *The Lake*

This study was based on data from Lake Redon (formerly Lake Redó) (42° 38'N, 0° 46'E), a glacial cirque lake located in the Central Pyrenees, Spain, at 2,240 m above sea level. It is a conical lake with a surface area of about 24 ha and a maximum depth of 73 m. It has a volume of  $7.75 \times 10^6 \text{ m}^3$  and a mean residence time of water of ca. 4 years. It occupies a relatively large part of its catchment (16%). The lake mixing regime is dimictic with spring and autumn overturn periods and it is covered by ice and snow for 6-7 months a year. A more complete description of the physical and chemical features of Lake Redon can be found in Catalan (1988) and Ventura et al. (2000).

### *The plankton community*

The plankton community is characteristic of deep and oligotrophic high-mountain lakes (Felip et al., 1999; Felip and Catalan, 2000). In the period studied, phytoplankton dominated the microbial biomass, the ratio between autotrophic (phytoplankton) and heterotrophic (bacteria, heterotrophic flagellates and ciliates) microbial biomass ranged from 1.5 to 6.5, being 4.4 on average (Felip et al., 1999). Throughout the study period phytoplankton biomass was rich in species (ca. 100) and largely dominated (>70%) by flagellates (chrysophytes, small dinoflagellates and cryptophytes), with chrysophytes being the most abundant for most of the time. As a consequence of this flagellate dominance and the established relationship between phytoplankton biovolume and chlorophyll in the lake (Felip and Catalan, 2000), we considered chlorophyll-*a* to be a good proxy for an overall estimation of phytoplankton as a food source for rotifers, although we may lose some specific interactions as a result. Bacteria dominated the heterotrophic biomass (1000 to 4000 g C m<sup>-2</sup>) and ciliates were one order of magnitude less abundant, with biomass ranging from 1 to 100 mg C m<sup>-2</sup>. Heterotrophic nanoflagellates were not quantitatively significant for most of the year; only in April below the ice did they assume some significance, thus they were not considered in our study. Three species of crustacean zooplankton were present: *Diaptomus cyaneus*, *Cyclops abyssorum* and *Daphnia pulicaria*. For the period studied, crustacean zooplankton biomass ranged from 1 to 1500 mg C m<sup>-2</sup>, *D. pulicaria* being the species that contributed the most to zooplankton biomass during the study period.

### *Sampling and analytical procedures*

Organisms were sampled monthly at 3 m intervals from July 1996 to May 1997 at the deepest point of the lake (73 m). Water samples at 23 different depths were obtained each month.

In the ice-covered period we reached surface water by drilling a hole in the ice and snow cover. Rotifer samples were collected in Ruttner bottles (5 L capacity), filtered *in situ* on a 45  $\mu\text{m}$  mesh, and preserved with 4% formaldehyde. Prior to preservation, the animals were narcotised with bicarbonate to facilitate the determination of soft rotifer species. Samples were also obtained in Ruttner bottles for the subsequent determination of microbial abundance. Ciliates were preserved in 200 mL bottles with Lugol's solution (Sournia, 1978), and bacteria in 100 mL bottles with 4% formaldehyde. The rest of the water was filtered on Whatman GF/F filters to estimate chlorophyll-*a* abundances through pigment analysis.

Rotifer individuals were sedimented following the Utermöhl protocol in 50 ml columns (Sournia, 1978) and then counted with an inverted microscope at 150x magnification. All rotifers from each sample were counted. Ciliate biomass ( $\text{fg C } \mu\text{m}^{-3}$ ) was calculated in two steps. First, we estimated ciliate biovolumes by relating ciliate cell shapes to geometric figures of known volume (Sheat et al., 1975). Second, we used a conversion factor from biovolume to biomass of  $190 \text{ fg C } \mu\text{m}^{-3}$  (Putt and Stoecker, 1989). Bacterial numbers were determined by epifluorescence microscopy, using DAPI staining on black Nuclepore filters (pore size, 0.2  $\mu\text{m}$ ) by the method of Porter and Feig (1980). Chlorophyll-*a* was determined by spectrophotometry following the equations of Jeffrey and Humphrey (1975).

Oxygen ( $\text{mg L}^{-1}$ ) and temperature ( $^{\circ}\text{C}$ ) measurements were taken *in situ* at 3 m intervals. The photoperiod (the number of hours of light in a day) was calculated for each sampling day from latitude and longitude, and was considered as zero during the ice-covered period. Water column light extinction was computed as a percentage of superficial light by Secchi disk depth and following Poole & Atkins (1929).

Because of its migratory capacity and heterogeneous distribution crustacean zooplankton was sampled by vertically integrated net hauls from near bottom to the surface with a 200  $\mu\text{m}$  net, therefore preventing potential sample by sample comparison with rotifers.

### *Multivariate analysis*

Ecological niches can be mathematically described as N-dimensional hypervolumes defined by orthogonal environmental axes. Species abundance responds to each of these environmental gradients following a Gaussian function or a unimodal (optimum-like) function. In canonical correspondence analysis (CCA) this statement is rooted in the idea that response variables (species) have unimodal or Gaussian distributions along explanatory variables (environment) (ter Braak, 1985; Legendre and Legendre, 1998). CCA is a technique that has the advantage of directly relating community data to explanatory sets of variables (environmental

descriptors). This distinguishes canonical analyses from other multivariate methods, e.g. principal component analysis or correspondence analysis (ter Braak, 1994). One of the many possibilities of canonical ordination is the partitioning of variance (Borcard et al., 1992), which combines the concepts of ordination (correspondence analyses) and regression (partial linear regression) to measure the amount of variation in response variables (community data) that can be attributed exclusively to one or specific sets of explanatory variables (environmental data), once the influence of other environmental data is subtracted (covariable data). Partitioning methods and, in particular, partial CCA analysis are thus adequate multivariate methods for looking for environmental descriptors of habitat partition between species (Borcard et al., 1992; Legendre, 1993; Borcard and Legendre, 1994).

The environmental factors considered in the analysis were: (i) as environmental factors: photoperiod (h), light in the water column (%), oxygen ( $\text{mg L}^{-1}$ ) and temperature ( $^{\circ}\text{C}$ ), (ii) as resources: chlorophyll-*a* ( $\mu\text{g L}^{-1}$ ), bacterial abundance ( $\text{cell } \mu\text{L}^{-1}$ ) and ciliate biomass ( $\text{mgC ml}^{-1}$ ). Note that here mixotrophic phytoplankton and ciliates can be food items for some rotifers and competitors for food for others. Instead of considering an explicit temporal variable (e.g., day of the year) we used the photoperiod, as a variable which may have a more valid (non spurious) explanatory value. Depth was also considered but was used to correct for variable autocorrelation (see below). Because of the different spatial sampling resolution, crustacean zooplankton was not considered in the analysis. To what extent we were missing an important factor is difficult to assess. Crustacean zooplankton certainly interacts with rotifers. However, indirect effects via common resource consumption were already considered through bacteria, chlorophyll and ciliates. Therefore, only direct effects were not evaluated. A CCA using column-integrated rotifer data showed no significant explanation in relation to crustacean zooplankton of the rotifer species composition and abundance, thus we assumed that direct effects were probably not very large.

For multivariate ordination procedures, environmental descriptors should be expressed in compatible units (i.e. dimensionally homogeneous environmental matrix). Therefore, they were brought to a common scale by a range transformation that eliminates both the scales and part of the variability between descriptors. The method applied reduced the values of our variables to the interval [0,1] by first extracting the minimum observed for each variable and then dividing by the range (Legendre and Legendre, 1998). Although species abundance and egg ratio variance only covered two and three orders of magnitude respectively, both species matrices were also range-transformed. Range transformation of species matrices avoids linearization of variables, which is not relevant to partial CCA analyses (Legendre and Legendre, 1998). Therefore, the multivariate

analyses consisted of the confrontation of two semiquantitative matrices (rotifer abundance *or* rotifer egg ratios *vs.* environmental factors) that could be compared with each other.

The analysis procedure was as follows. We performed two partial CCA analyses (abundance *vs.* environmental, and egg ratio *vs.* environmental matrices) with a stepwise regression procedure, known as ‘forward selection’ in CANOCO software (ter Braak and Smilauer, 1998). This procedure allowed us to add explanatory variables one by one to the regression model, following a hierarchical order of statistically significant environmental descriptors. Forward selection was always done once the influence of depth correlations had been previously extracted, *i.e.* depth entered in the analysis as a covariable. By entering depth as covariable, we extracted spatial autocorrelation effects in the explanatory variables, which may be a main source of spurious relationships. This procedure showed us a hierarchical ordering of explained variance by the different environmental factors. The explanatory value of depth indicated the relative influence of the extreme environmental topological asymmetry imposed by lake morphology that cannot be disentangled among factors. In all cases, explanatory variables were added until our regression models were not improved significantly. Monte Carlo permutation tests of significance (999 trials) were performed before and after inclusion of each variable in the model. After this, we performed partial CCAs (following the hierarchical order obtained in the previous analysis) to obtain the variance explained by each environmental descriptor alone without the effect of the others. For each environmental variable, the previous environmental descriptors were introduced as covariables. Finally, cross-correlations between explanatory environmental variables and rotifer abundances or egg ratios were computed to find the sign of their interactions.

## Results

### *Lake dynamics*

In the present study, summer (ice-free) and winter (ice-covered) stable periods lasted from June to September and from December to May, respectively. Continuity between these two periods was broken briefly by the autumn mixing period that lasted for two months. The melting of ice cover and the spring mixing period occurred in June. Temperatures ranged from 12.8 °C (August in the epilimnion) to 0 °C (surface water in the ice-covered period). The strongest thermocline was present in September after three months of progressive development. In October it started to become weaker and deeper, and finally it broke down. In November, the whole water column was mixed and temperature was homogeneously distributed. The ice-covered period started in December with a gentle inverted gradient of temperature in depth that lasted until May (Fig. 1). Oxygen ranged from 10 mg L<sup>-1</sup> to 2 mg L<sup>-1</sup>. During most of the study period lake water was well

oxygenated, we only observed increasingly hypoxic conditions at deep layers as the ice-cover period progressed; complete anoxia was never observed (Fig. 1).

Chlorophyll-*a* ( $\mu\text{g mL}^{-1}$ ) and bacteria ( $\text{cell } \mu\text{L}^{-1}$ ) followed different spatiotemporal patterns (Fig. 1). As was expected in a deep high-mountain lake, we observed two maximum peaks of chlorophyll-*a* during the year (Catalan et al., 2002). The first abundance peak developed in the upper hypolimnion during summer. The second one was larger and developed in winter under the ice cover (December). Bacterial abundance ranged over one order of magnitude: from 1,592 cell  $\mu\text{L}^{-1}$  (October, 33 m) to 152 cell  $\mu\text{L}^{-1}$  (July, 15 m), however, for most of the samples it was fairly similar. Ciliate biomass was low throughout the study period.

### *Rotifer life cycles*

Seven pelagic rotifer species were found in Lake Redon during the study period: *Kellicottia longispina*, *Polyarthra dolichoptera*, *Asplanchna priodonta*, *Synchaeta lakowitziana*, *Collotheca pelagica*, *Keratella hiemalis* and *Ascomorpha ecaudis*. For *Polyarthra*, we found a continuum of phenotypes between *P. vulgaris* and *P. dolichoptera*, with *P. dolichoptera* being the most abundant one.

*K. longispina* and *P. dolichoptera* were the two dominant species. Their abundances were frequently above 50 ind  $\text{L}^{-1}$ , with maxima around 125 ind  $\text{L}^{-1}$ . *K. hiemalis*, *S. lakowitziana*, and *C. pelagica* were considered as subdominant species. They are characterised by their continuous incidence throughout most of the season with abundances around or below 1 ind  $\text{L}^{-1}$ . Finally, *A. priodonta* and *A. ecaudis* were seen as rare species. Their incidence was not as regular as in the previous species, though clear spatiotemporal patterns could be observed. Maximum abundance for these species reached 1 ind  $\text{L}^{-1}$ .

In general, the abundance of the different rotifer species showed high spatiotemporal segregation (Fig. 2 and 3). Spatiotemporal patterns of egg abundances also showed seasonality (Fig. 2 and 3).

***Kellicottia longispina*:** This was the most abundant and the most ubiquitous rotifer in the lake (Fig. 2). Its population underwent two growth maxima: one in advanced summer (when the thermocline became weaker), and one in early winter (just after the formation of the ice cover). Although the rotifer was found throughout the lake, maximum population abundance was observed above 30 m: upper hypolimnion in summer and below the ice cover in winter. Two abundance maxima for the eggs were observed at 20-25 m depth in September and December. The maximum egg ratio was observed in September in the epilimnion. Thus, for *K. longispina*, maximum



reproductive rates, i.e. the highest production rates of amictic eggs by females during the year, was in the epilimnion in September.

***Polyarthra dolichoptera*:** This is a summer epilimnetic species. Its population decreased during the mixing period to finally disappear at the beginning of ice cover. *P. dolichoptera* has the complex life cycle of Plöimate rotifers. Amictic females reproduce by parthenogenesis and produce (amictic) eggs with a diploid number of chromosomes. Mictic females produce eggs that undergo a meiotic division and, therefore, are haploid. The mictic females can be fertilized by males. If fertilisation does occur, the fertilised eggs are thick-walled and highly resistant to adverse environmental conditions, and these are called resting eggs. If mictic females are not fertilized then they produce eggs that promptly hatch into males (Ruttner-Kolisko 1974). In our observations, we distinguish between amictic, and mictic eggs and within the latter between mictic eggs still carried by females at different stages of development and fully developed resting eggs free in the samples. For brevity, hereafter we will refer to these two groups of mictic eggs as mictic and, resting eggs, respectively. In the summer period (from July to September), we found amictic and mictic eggs in the epilimnion (Fig. 2). Probably amictic reproduction allowed *P. dolichoptera* to quickly invade summer epilimnetic waters, whereas mictic reproduction was more relevant from July to November. As the thermocline gradually deepened, resting eggs were found in deeper waters. In November, just before the formation of ice cover, resting eggs were more abundant; their density peaked at 50 m depth, and progressively settled to deeper layers during the following month (Fig. 2). The presence of resting eggs indicated that sexual reproduction occurred, however, no males were observed. Probably, because the dwarf, short-life males of *Polyarthra* were not retained on the 45 µm mesh net used in this study. Males have length a length of 42 – 44 µm and a smaller width (Koste, 1978). Amictic and mictic eggs represented current and delayed reproduction, respectively. Depending on the type of egg (amictic, or mictic), maximum egg ratios differed in their location in time and space. Therefore, in our multivariate analysis they were considered separately; however, we did not include the free-floating resting eggs in the analysis, because we considered that they were a delayed indication of mictic eggs carried by females.

***Asplanchna priodonta*:** This was a summer epilimnetic species. The life cycle of *A. priodonta* is similar to that of *P. dolichoptera* (Fig. 2). It also reproduced sexually at the end of the seasonal population cycle, and had the maximum egg ratio during October and November following the destabilization of the thermocline. As *A. priodonta* is an ovoviviparous rotifer, all the eggs that were freely floating in the water column were considered to be resting eggs (delayed reproduction effort). These free eggs or resting eggs were mainly observed in December when the ice cover was formed. Resting eggs were probably buried rapidly in sediment at the beginning of

winter and reappeared in spring (March). Although this species can have asexual reproduction, we did not observe any females with embryos in the study period.

***Synchaeta lakowitziana*:** This species appeared at low densities in summer hypolimnetic waters and increased steadily during the mixing period (Fig. 3). The maximum population abundance was observed in winter just under the ice cover. For this species, we only observed resting eggs, the maximum being located below the thermocline in September. There were two possible origins of September resting eggs (they could come from summer hypolimnetic populations or directly from the sediment). The abundance of resting eggs steadily declined and deepened, following thermocline deepening. At the beginning of the mixing period, there was probably a mixed adult population (resting eggs coming from the sediment and produced by summer population). The maximum egg ratio was observed in December at 60 m. For this species, we could not be certain whether the egg ratio was attributed strictly to current reproduction (i.e. amictic produced by females of the year) or to delayed reproduction (i.e. mictic and resting eggs produced by females of the year or coming from the sediment egg bank). Finally, though winter populations under the ice cover are thought to reproduce asexually, we did not observe any amictic eggs.

***Collotheca pelagica*:** This species was mostly present in the summer hypolimnion, but seemed to expand its population throughout the water column in November (just before the mixing period) from amictic or resting eggs (origin unknown) located near the sediment (Fig. 3). After the mixing period, some individuals persisted under the ice cover, but most of the population disappeared. The population was found at low densities, but was present at a wide range of temperatures and oxygen concentrations. Maximum abundance was observed within a very low range of the two factors (Fig. 3). *C. pelagica* started reproduction after the mixing period near the sediment surface and went on reproducing intermittently throughout the winter. Maximum egg ratio was developed in February at different depths. We assumed that all the eggs observed from December to March (and therefore the egg ratios) represented current reproduction (from the sediment surface to the water just under the winter ice cover).

***Keratella hiemalis*:** This species appeared sporadically from September to April in the deepest parts of the water column (50 m or deeper) (Fig. 3). Its maximum population densities and maximum egg ratios overlapped in time and space. *K. hiemalis* produced pseudosexual eggs at the bottom of the lake (Fig. 3). Pseudosexual eggs are resting-like eggs produced parthenogenetically and not sexually (Bosselman, 1981; Nogrady et al., 1993). We could not distinguish current-reproduction from eggs produced earlier (delayed reproduction).

*Ascomorpha ecaudis*: This species was mainly found at great depth throughout the ice-free period, reaching its population maximum in October, but was also present in surface waters in early summer (July, September) (Fig. 3). We did not observe eggs of *A. ecaudis*, so were unable to gain information on its life-cycle dynamics.

### *Variance partition*

Environmental factors were of different hierarchical importance in explaining spatiotemporal variance in abundance (Fig. 4) and egg ratios (Fig. 5). Depth was forced to be the first explanatory variable in the hierarchy because it entered the analysis as a covariable to reduce spatial correlation (see Methods). When depth relevance was low, it meant there was no problem of spatial autocorrelation, whereas when it was high this indicated that the relevance of other factors do not show up because the high spatial autocorrelation. The remaining variance associated with either abundance or egg ratios was explained by different hierarchies of environmental factors. The spatiotemporal patterns (variance) observed for rotifer abundances in Lake Redon were mostly explained by temperature, oxygen and light, whereas chlorophyll-*a* and ciliates had much less explanatory value. At the bottom of the hierarchy, we found photoperiod and bacteria (Fig. 4a). Although temperature, oxygen and light were inter-correlated, the stepwise regression procedure showed that there was still some significant variance to be explained by each factor when the others were included in the model. A radically different hierarchy of environmental descriptors was obtained in relation to the spatiotemporal distribution of rotifer egg ratios (Fig. 5). In this analysis, once spatial correlations were extracted (depth as covariable), photoperiod and oxygen were the environmental descriptors explaining most of the variance, followed by some environmental factors indicative of resource availability: ciliates and chlorophyll-*a*. At the bottom of the hierarchy we found temperature, light and bacteria.

Apart from the distinct hierarchical relationships, the environmental factors studied explained differing amounts of variance (Fig. 4a, 5a) and involved different representativity in each species analysed and/or egg ratio computed (Figs. 4b, 5b). Indeed, the consideration of an environmental variable as a potential habitat partitioning descriptor should be based not only on its relative position in the general hierarchy, but also on its representativity when the species are considered one by one (Figs. 4b, 5b). For example, photoperiod, though it only involved temporal information, is represented in several species in both analyses. The same is true for temperature, ciliate biomass and chlorophyll-*a*. However, the relative positions of oxygen were basically due to its strong correlation with a single species (*K. hiemalis*). This is particularly so in the egg ratio

analysis (Fig. 5, Table I). In such cases, the environmental variable should not be considered as an ecologically meaningful descriptor of the community.

## Discussion

### *Abundance factors*

The analysis of the seasonal pattern of rotifer species abundance in Lake Redon suggested a hierarchy of environmental descriptors in which abiotic conditions (temperature, oxygen and light) explained much more variability than resources (chlorophyll-*a*, ciliates and bacteria). Because of this, conditions (and not resources) should be seen as the main environmental descriptors of habitat partitioning (Fig. 4a). Based on the correlations observed for the most important environmental factors (Table I), we could clearly distinguish between temperature-dependent (*P. dolichoptera*, *A. priodonta* and *S. lakowitziana*), oxygen-dependent (*K. hiemalis*), and light-dependent species (*A. ecaudis*, *C. pelagica*). The spatiotemporal distribution of *K. longispina* was explained by the three factors (temperature, oxygen and light) in equivalent proportions. Previous studies of rotifers showed similar results (Laxhuber, 1987; Mikschi, 1989; Esparcia et al., 1989). The capacity of conditions (temperature and oxygen, above all) to summarise the seasonal patterns of abundance of planktonic species was documented early on (Hutchinson, 1967; Miracle, 1974; Makarewicz and Likens, 1975; Dunson and Travis, 1991). Effects of temperature on rotifers are multiple (on life-cycle parameters, ingestion rates, etc.) at both individual and population levels (Ruttner-Kolisko, 1978; Galkovskaja, 1987). Clearly, oxygen concentration is a relevant environmental factor in deep and stratified lakes, but also in high temperate and saline waters (Esparcia et al., 1989). In fact, some rotifer species are literally trapped between the warm epilimnion and deoxygenated hypolimnion of lakes (Herzig, 1987). Most rotifers need concentrations above 1 mg O<sub>2</sub> L<sup>-1</sup> to survive (Nogrady et al., 1993). However, some studies have found adaptations of rotifers to low oxygen concentrations: from 1 to 0.1 mg O<sub>2</sub> L<sup>-1</sup> (Esparcia et al., 1989; Nogrady et al., 1993). Light is related to certain other factors such as turbidity, changes in phytoplankton abundance and species composition. Most of the invertebrate responses to light are related to daily migratory movements, taxis and/or kinesis (Hutchinson, 1967). Relationships between rotifers and light are not well documented, though one could expect the same kind of significance as for other invertebrates.

The statistical significance of chlorophyll-*a* was related to both negative (*K. hiemalis* and *S. lakowitziana*) and positive correlations (*A. ecaudis*, *A. priodonta*) (Table I). In the latter case, it should be considered as a direct resource (*A. ecaudis*) or as an indirect signal of resources (*A. priodonta*). Ciliate biomass in the epilimnion during the ice-free period could be mainly attributed

to *Pelagostrombidium fallax*, with its presence positively correlated with *P. dolichoptera* (a potential competitor) and negatively correlated with *A. priodonta* (a potential predator). Summer hypolimnetic species (*S. lakowitziana* and *C. pelagica*) correlated negatively with *P. fallax*, and *K. hiemalis* correlated positively with other hypolimnetic species of ciliates (oligotrichia). Photoperiod and bacterial abundance were not relevant explanatory variables. As the former only involved temporal information (seasonal indicator), its explanatory power relating to spatial patterns was nil; and the latter had a very constant pattern in space and time. Despite this, bacterial abundance explained part of the variance of some species (*K. longispina*, *A. ecaudis* and *C. pelagica*), although the two latter species are not bacterivorous but feed on mid-size phytoplankton.

### *Egg ratio factors*

The analysis of the seasonal patterns of rotifer egg ratios in Lake Redon showed other factors (photoperiod and oxygen) as the main components of habitat partitioning, followed by environmental descriptors indicative of resource availability: ciliate biomass and chlorophyll-*a*. Photoperiod and temperature are the two most frequently demonstrated cues for diapause termination (egg hatching) in zooplankton (Gyllström and Hansson, 2004). In addition, photoperiod has been shown to be closely linked to the reproductive cycle of rotifers, in particular to the production of mictic or diapausing (resting) eggs (Pourriot and Clement, 1975; Pourriot et al., 1981). Although temperature has a great impact on rotifer life-cycle parameters (Snell and King, 1977; Ruttner-Kolisko, 1978; Walz, 1997), it was a rather weak descriptor of seasonal community productivity patterns. This result may suggest complex interactions of temperature with other biological and non-biological components (Galkovskaja, 1987; Zoufal, 1989; Yúfera, 1987; Miracle and Serra, 1989), resulting in effects and counter-effects related to egg production. Oxygen concentration summarized most of the spatial information contained in egg ratio patterns. However, its explanatory power was mainly related to a negative correlation to *K. hiemalis* egg ratios (Table I). *K. hiemalis* was present exclusively under hypolimnetic conditions, in which there were lower oxygen concentrations.

Ciliate biomass (mostly *P. fallax*) was the third factor in the hierarchy, mainly due to the existence of positive and negative correlations with those rotifer species achieving the highest egg ratios in the summer epilimnion (*P. dolichoptera*) or superficial hypolimnion (*A. priodonta* and *K. longispina*), respectively (Table I). The egg ratio pattern of *K. hiemalis* was also linked to the presence of small deep hypolimnetic ciliates. Overall, in egg ratio analysis, ciliate biomass should

be considered a direct resource for *A. priodonta*, and an indicator of resources for *P. dolichoptera* and *K. hiemalis* (though *P. fallax* could be a competitor).

Chlorophyll-*a* increased its representativity in most of the species considered, compared with the abundance analysis (compare Fig. 3b and 4b). Indeed, chlorophyll-*a* explained much more variance than temperature (Fig 3b). Chlorophyll-*a* positively and directly correlated with *P. dolichoptera* egg ratios, and positively and indirectly correlated with *A. priodonta* egg ratios (this species may predate *P. dolichoptera* or *P. fallax*). The egg ratios of bacterivorous (*K. longispina*, *K. hiemalis*) or mid-size phytoplankton consumers (*C. pelagica*) correlated negatively with chlorophyll-*a*. Felip and Catalan (2000) showed that chlorophyll-*a* peaks in Lake Redon were related to changes in spatial or successional trends in species dominance, with flagellated chrysophytes being the main group related to the chlorophyll maximum. Thus, we can relate quantitative changes in chlorophyll-*a* to changes in the proportion of different phytoplankton species or food types (cell size, dominant groups). Similarly, Devetter and Sed'a (2003) showed that rotifer fecundity was intimately linked to chlorophyll-*a* concentration. However, food quality and quantity are not only related to population growth (Rothhaupt, 1990; Walz, 1997), but also to diapause induction (Gyllström and Hansson, 2004).

Unlike chlorophyll-*a*, bacterial abundance showed little variability through the seasonal cycle and so was not relevant to egg ratio variability. Constancy of bacterial spatiotemporal distributions in the water column has been described and discussed by some authors (Güde, 1989; Giorgio and Gasol, 1995).

### *Conditions vs. resources*

The seasonal succession of species abundance in the lake was adequately explained by conditions such as temperature, oxygen and light. However, the egg ratio analysis revealed a change in the hierarchy of the most relevant conditions (basically temperature was replaced by photoperiod) and, more interestingly, showed an increased role for resources (chlorophyll-*a*, ciliates) as environmental descriptors of habitat partition.

These results indicate (i) that there is a large proportion of niche segregation among species that is already internalised in their life history traits, either because previous competitive interactions (Brown and Wilson, 1956; Connell, 1980) or due to independent species evolutionary histories, and (ii) that at the present time, there is little competitive exclusion based on resource depletion (Hardin, 1960; Ghilarov, 1984; Tilman, 1982; Leibold, 1995). Detailed consideration of more specific food items (e.g cryptophytes for *Synchaeta*) might have increased the explanatory

power of resources, in any case, this will be unlikely to dismiss the high explanatory power of density-independent factors.

Niche segregation among species do not start from zero each year, and to some extent the high explanatory capacity of environmental conditions on abundance and reproduction patterns could be a measure of those past interactions. However, segregation adjustment among life histories would never be perfect, among other aspects because the environment, both physical and biotic, is never the same, thus there is a constant local niche re-shaping to fine-tune niche segregation, which in turn decreases competition over time, as it has recently been shown empirically in co-existing *Daphnia* species (Steiner et al., 2007). Noticeably, when we consider a parameter critical to fitness, such as the egg ratio, the role of resource in explaining variability among species increases, suggesting an on-going interactive dynamics of niche segregation. Seasonal egg ratio maxima in the lake can be interpreted as “hot spots” of reproductive fitness that determine niche segregation mechanisms not only through real-time impacts on the lake ecosystem (current-reproduction), but also through their effect on future rotifer generations and seasonal cycles (delayed-reproduction). In this sense, some of the egg ratios computed in the present study clearly involved adaptive responses of organisms to their changing environments, which are known to have an influential effect on changes in future population sizes and dynamics (Gyllström and Hansson, 2004).

Overall, in population dynamics terms, conditions should be understood as the physical template in which the potential coexistence equilibriums are established each year, and resources might play the role of dynamic impacts that regulate these coexistence equilibriums by affecting the stability properties of present or future rotifer species assemblages in the lake. These changes in stability continuously reshape niche characteristics and reframe the potential coexistence equilibria. In Lake Redon, for example, resources were strongly correlated to rotifer reproductive efforts which in turn controls the appearance of present (within the same seasonal cycle) and future pelagic species assemblages in the lake. As suggested in the revised niche-theory (Liebold, 1995; Chase and Liebold, 2003), species also play important roles in dynamic aspects of community stability *via* their relative ability to influence the environment (impact niches). In this sense, the effects on niche segregation of *per capita* egg production rates may be closely related to those generated by impact niche variables such as resource depletion rates or predation rates (Liebold, 1995, 2003).

The relative significance of conditions and resources as niche segregation factors in a community will vary, depending on species biology, the ecosystem and/or the spatiotemporal scales under study. However, in our study we have shown that it is worth considering

measurements closer to fitness components of populations (e.g. reproduction) for detecting ongoing niche segregation processes. Such studies on fitness component dynamics, rather than simply on abundance patterns, should help resolve paradoxes in relation to species coexistence (Ghilarov, 1984) and lead to a better understanding of niche segregation mechanisms in natural communities.

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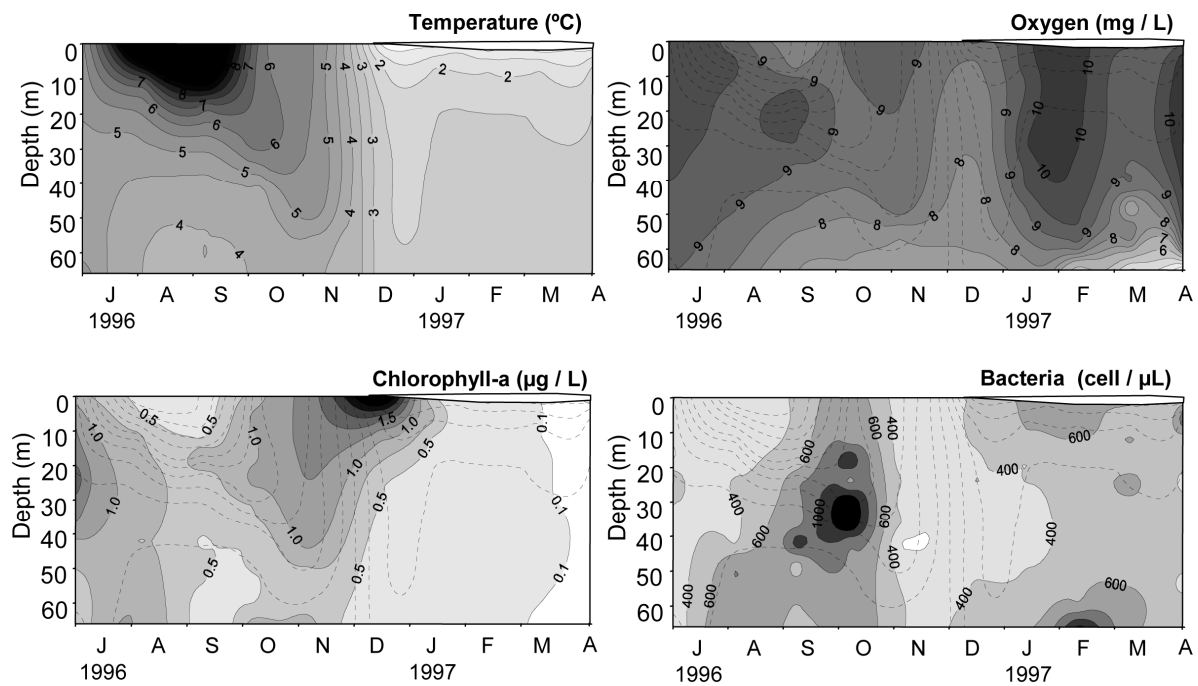
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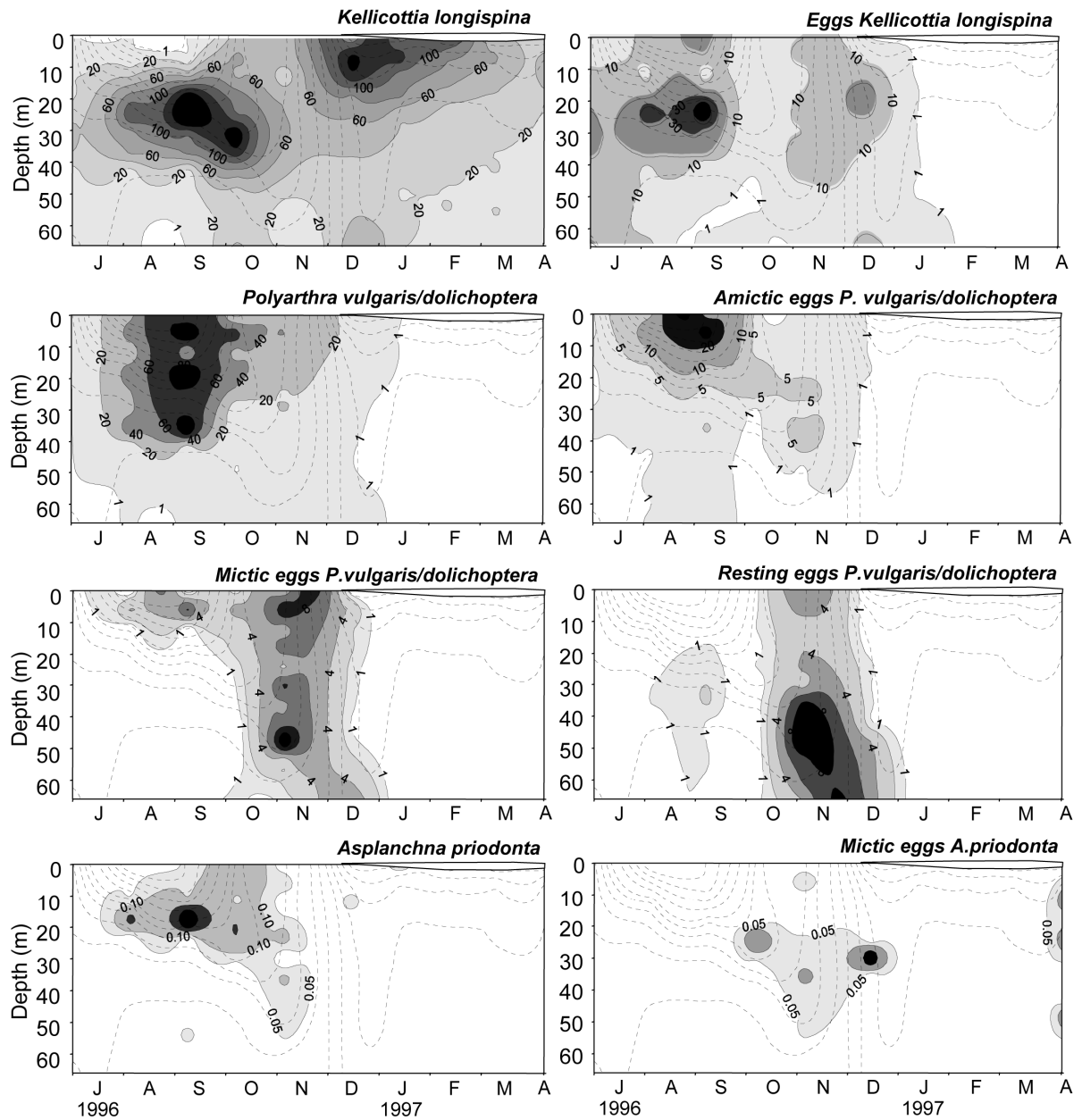
## Table and Figure legends

**Table I.** Cross-correlations for the two canonical correspondence analyses performed, based on species abundance and egg ratios, respectively. The correlations above 0.7 are highlighted. Codes: Aspp, *A. priodonta*; Colp, *C. pelagica*; Kell, *K. longispina*; Kerh, *K. hiemalis*; Synl, *S. lackowitziana*; Pold, *P. dolichoptera* (**m**, mictic, **a**, amictic); Asce, *A. ecaudis*.

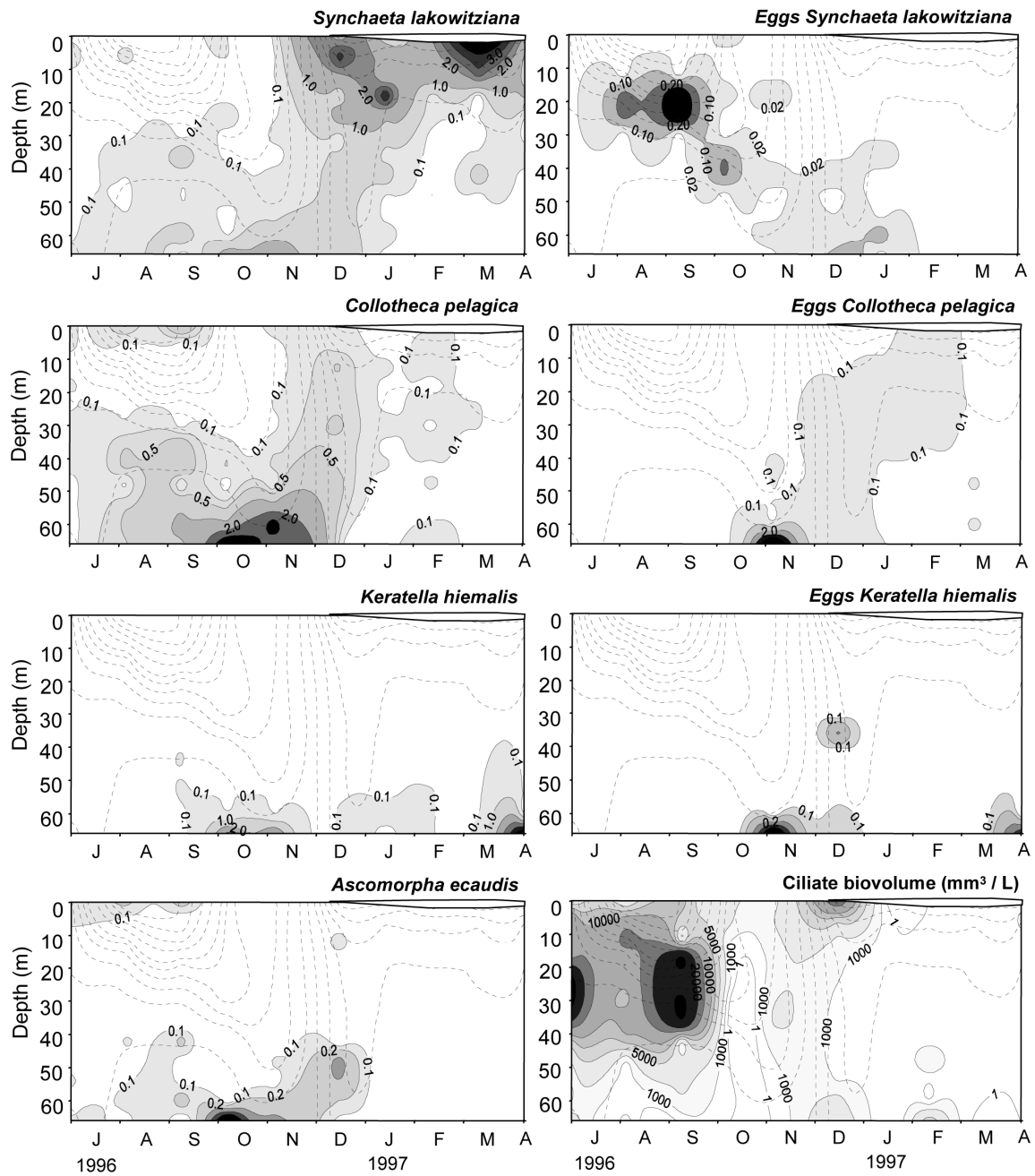
**Fig. 1.** Spatiotemporal patterns of environmental factors (temperature, oxygen, chlorophyll and bacteria) of the rotifer community of Lake Redon during the study period.



**Fig. 2.** Adult females and egg abundance of three of the seven most representative pelagic rotifers of Lake Redon during the study period. Data in  $\text{ind L}^{-1}$  (adult females) and  $\text{egg L}^{-1}$  (eggs).

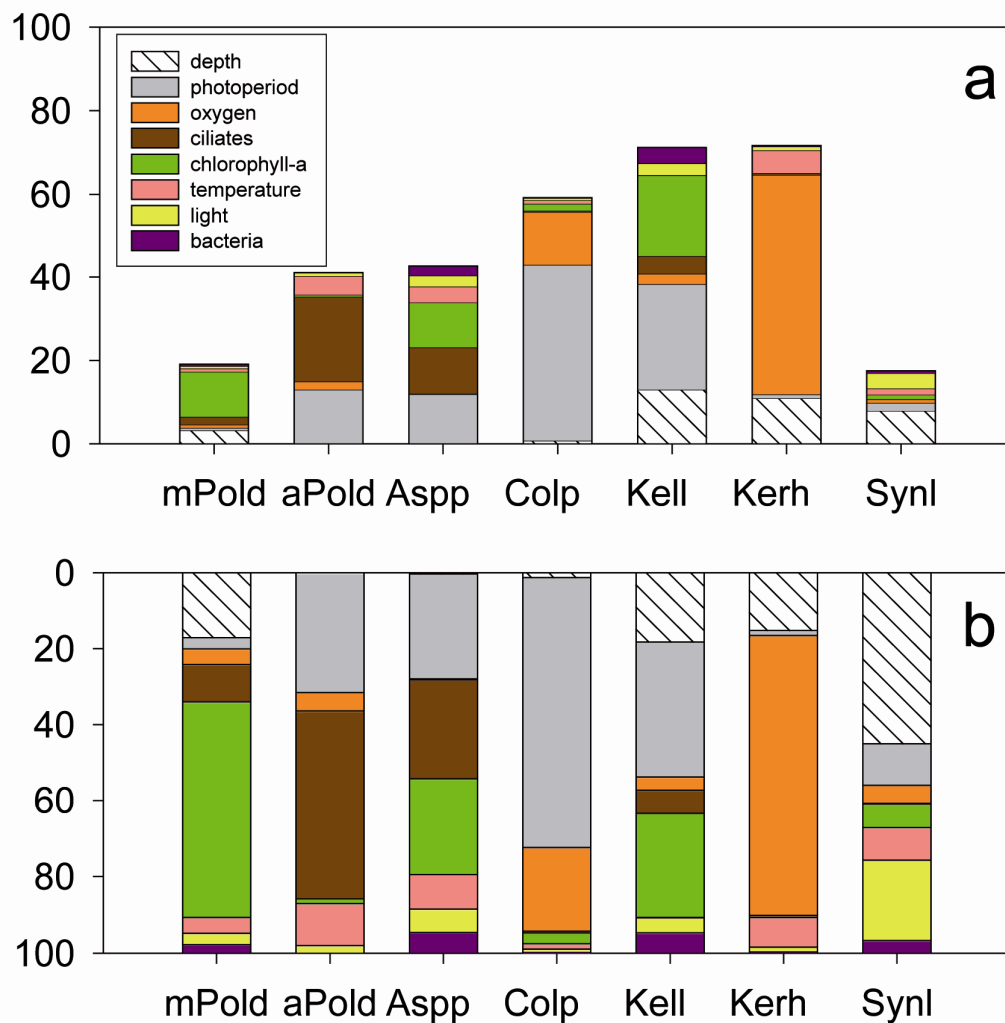


**Fig. 3.** Adult females and egg abundance of four of the seven most representative pelagic rotifers of Lake Redon during the study period. Data shown are given in ind L<sup>-1</sup> (adult females) and egg L<sup>-1</sup> (eggs).





**Fig. 5.** Variance partitioning based on species egg ratio patterns. The percentage of variance explained by each of the environmental factors on each species' specific egg ratios is shown: (a) non-standardised, (b) standardised. Within the legend the factors are listed by the order they entered the forward selection. Depth was included as a co-variable to correct for autocorrelation patterns related to the lake vertical gradient, thus it is listed in first place. In each bar, the explicative value allocated to each factor does not include the variance shared with the preceding factors in the hierarchy. Codes: AspP, *A. priodonta*; Colp, *C. pelagica*; Kerh, *K. hiemalis*; Kell, *K. longispina*; Synl, *S. lackowitziana*; aPold, *P. dolichoptera* (amictic); mPold, *P. dolichoptera* (mictic).





**Table I.** Cross-correlations for the canonical correspondence analyses.

<i>Species</i>							
	<b>Aspp</b>	<b>Colp</b>	<b>Kell</b>	<b>Kerh</b>	<b>Synl</b>	<b>Pold</b>	<b>Asce</b>
<b>depth</b>	-0.384	<b>0.898</b>	-0.135	<b>1.550</b>	-0.436	-0.316	<b>0.903</b>
<b>temperature</b>	<b>0.918</b>	-0.050	-0.179	-0.379	<b>-0.885</b>	<b>0.937</b>	0.197
<b>oxygen</b>	-0.006	-0.074	0.170	<b>-1.897</b>	-0.016	-0.011	-0.097
<b>light</b>	-0.052	0.177	-0.079	0.044	-0.030	-0.050	0.498
<b>chlorophyll a</b>	0.208	0.079	0.038	<b>-0.540</b>	-0.291	0.070	0.134
<b>ciliate</b>	-.161	-0.155	-0.031	0.436	-0.040	0.269	-0.120
<b>photoperiod</b>	-0.003	0.105	-0.058	0.043	-0.004	0.014	0.173
<b>bacteria</b>	-0.068	-0.171	0.128	0.129	-0.130	0.008	-0.264
<i>Egg ratios</i>							
	<b>Aspp</b>	<b>Colp</b>	<b>Kell</b>	<b>Kerh</b>	<b>Synl</b>	<b>m Pold</b>	<b>a Pold</b>
<b>depth</b>	-0.082	-0.102	<b>-0.780</b>	<b>1.538</b>	<b>1.112</b>	0.250	-0.022
<b>photoperiod</b>	<b>0.747</b>	<b>-0.768</b>	<b>1.082</b>	-0.451	<b>-0.547</b>	-0.104	<b>1.264</b>
<b>oxygen</b>	0.057	0.359	-0.287	<b>-2.846</b>	0.303	-0.103	0.417
<b>ciliate</b>	<b>-0.630</b>	-0.054	0.395	0.257	0.056	-0.164	<b>1.374</b>
<b>chlorophyll a</b>	<b>0.535</b>	-0.114	<b>-0.709</b>	-0.032	-0.312	0.339	0.187
<b>temperature</b>	0.188	-0.047	0.021	-0.479	0.213	0.054	-0.329
<b>light</b>	-0.172	-0.041	0.176	-0.216	0.368	0.050	-0.151
<b>bacteria</b>	0.288	-0.033	-0.365	-0.191	0.262	0.078	0.045