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Population dynamics of oxiclinal species in lake Arcas-2 (Spain)

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Abstract

'Oxiclinal' rotifer species show high concentrations just above the oxic-anoxic interface in the hypolimnion of some lakes. The stratification of their populations is best shown by sampling at close depth intervals and quantifying their densities by the Utermöhl technique. With this technique we were able to count males which otherwise pass through filters and more accurately count egg production. We evaluated female, male and egg numbers of the two main oxiclinal species of lake Arcas-2: *Filinia hofmanni* and *Anuraeopsis fissa*, during two annual cycles (1990–91). *F. hofmanni* was an exclusive oxiclinal species. It had an exponential growth phase at the onset of stratification giving a distinct spring peak. The population then maintained a high density during summer, but was almost absent the rest of the year. This cycle is repeated annually but population density can vary among years, depending on winter-spring circulation. Sexuality was always observed when the animal was present in the samples, with a maximum of males and resting eggs at the peak of the population. Resting eggs were always inside females. The annual cycle of *A. fissa* is displaced with respect to that of *F. hofmanni*: *A. fissa* attained greatest densities during summer, until the autumn overturn. Mixis in *A. fissa* was restricted to the end of the stratification period. Moreover, *A. fissa* occured throughout the vertical profile and secondarily occupied the oxicline.

Introduction

High rotifer concentrations in the oxic-anoxic interface of meromictic lakes have been previously reported (Miracle, 1976; Miracle & Vicente, 1983; Armengol *et al.*, 1993; Miracle & Alfonso, 1993). This is also true for the holomictic lake under study, during the periods of steep stratification. When stratified lakes are properly sampled at close depth intervals (Miracle *et al.*, 1991, 1992; Armengol *et al.*, 1993) a biological microlayer structure is found in the interfaces, which includes rotifer species that reach high density peaks at definite zones of the physical and chemical gradients. When these depths are sampled by traditional methods, e.g. sampling bottles, the zonation is destroyed and the peaks are not so apparent.

The aim of the present work is to study the population dynamics of the two dominant rotifer species of lake Arcas-2: *Filinia hofmanni* (Koste, 1980) and *Anuraeopsis fissa* (Gosse, 1851), based on a sampling scheme involving a fine vertical scale and a non-disturbing enumeration technique, as the Utermöhl method used for phytoplankton. These rotifers may be termed oxiclinal or stratifying species because of their massive developments in thin layers of the oxic-anoxic interface. In lake Arcas-2, the scale of such stratification is on the order of decimetres and densities are on the order of 10^5 ind l^{-1}. Therefore, these rotifers could be counted by sedimentation of small samples, also enabling enumeration of males, which are seldom quantified because they pass through filters traditionally used for concentrating zooplankton. In addition, a proportion of eggs may easily unfasten and be lost during filtering. More precision is also gained with the sedimentation method for quantifying the different types of eggs.

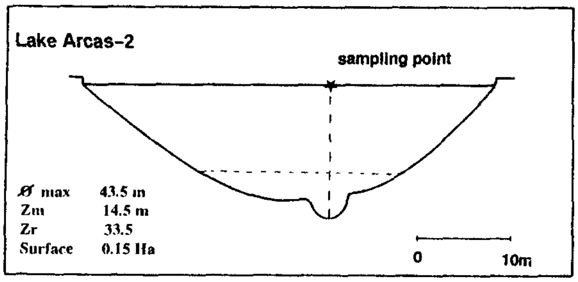

Fig. 1. Vertical cross-section of lake Arcas-2 largest basin, showing the position of the sampling site and the oxygen extinction depth in summer (dashed line). The scale is the same for vertical and horizontal dimensions. Some morphometric parameters to show the high depth/diameter ratio are also indicated (diameter, maximum and relative depth and surface).

Site description

Lake Arcas-2 is formed by two small flooded dolines developed in the gypsum rich paleocene marls, that constitute a wetland area near the town of Arcas (8 km from Cuenca, Spain). The largest doline (43.5 m mean diameter) has near its centre a secondary circular sink hole (3 m diameter) which increases the maximum depth from 12 to 14.5 m (Fig. 1). This doline is quite isolated from the smaller, adjacent one, to which it is connected by a shallow (1 m deep) strip of water.

Lake Arcas-2 is a warm monomictic lake with mineralised sulphato-carbonated waters (conductivity approx. 2.5 mS; mean ratios in meq l^{-1} of SO_4: Alkalinity:Cl^- approx. 100:10:1). Stratification promotes the formation of an oxicline with oxygen extinction at about 9 m depth in summer of the studied years. Some of the main characteristics regarding stratification of environmental factors as well as microorganisms have been described in Vicente *et al.* (1991) and Finlay *et al.* (1991).

Methods

Samples were taken from a boat at the site of the maximum depth of the lake. The sampling site was fixed at the intersection of two perpendicular ropes attached to the lake shores. This site corresponds to the secondary small sink hole sited near the centre of its largest basin (Fig. 1). Detailed *in situ* temperature, conductivity and oxygen (silver-gold electrode) profiles were previously obtained with WTW meters, to determine the depths to be sampled. Water samples were collected using a bi-conical inlet device, with a 1 cm circumferential aperture between the cones, as described in Miracle *et al.* (1992), connected to a surface peristaltic pump by a hose. They were taken at 10 cm depth intervals at the oxicline during stratification. Sampling depths above it were selected according to the position of the thermocline. These vertical profiles were taken from 4 November 1989 to 15 December 1991, more or less monthly (sometimes biweekly) during stratification and less frequently during mixing (Fig. 3).

Water samples (250 ml) were collected at every depth and time and preserved with Lugol's solution. Zooplankton were counted after sedimentation in 100 ml chambers. In the case of very high densities 50 ml sedimentation chambers were used. The whole bottom of the chamber was counted at 100 or 200 × magnifications with an inverted microscope. Replicates were often counted to test the reliability of these small volume samples. The differences between replicates were always less than 10% of their mean. On several occasions, additional samples were taken with the same fine layer sampler, in the same point, pumping two litres of water which were filtered through a 30 μm mesh. These filtered samples were fixed with 4% formalin and counted, as the other ones, with an inverted microscope.

Results

The method described above is only adequate for dominant high density rotifer species because of the small sample size. Therefore this paper is centred on the study of the two most abundant oxiclinal rotifer species of Arcas-2: *Filinia hofmanni* and *Anuareopsis fissa.* However, we estimated higher rotifer densities with the 50 or 100 ml sedimented samples than with the 2 l samples concentrated by filtering, rare exceptions were found only when densities were low. This may be caused by both: losses by filtering and lower collecting efficiency plus stratum disturbance at longer pumping times. With respect to crustaceans, the pumping method is only adequate for small copepods and larval stages of large copepods, due to the escape behaviour of cladocerans and large copepods

The pelagic zooplankton community of Arcas is dominated by the above mentioned rotifer species and several species of ciliates (Finlay *et al.*, 1991). The copepod *Tropocyclops prasinus* (mainly nauplii, Table 1) is also abundant, and only two more crustacean species occur regularly in the plankton: *Cyclops abyssorum* and *Ceriodaphnia reticulata.*

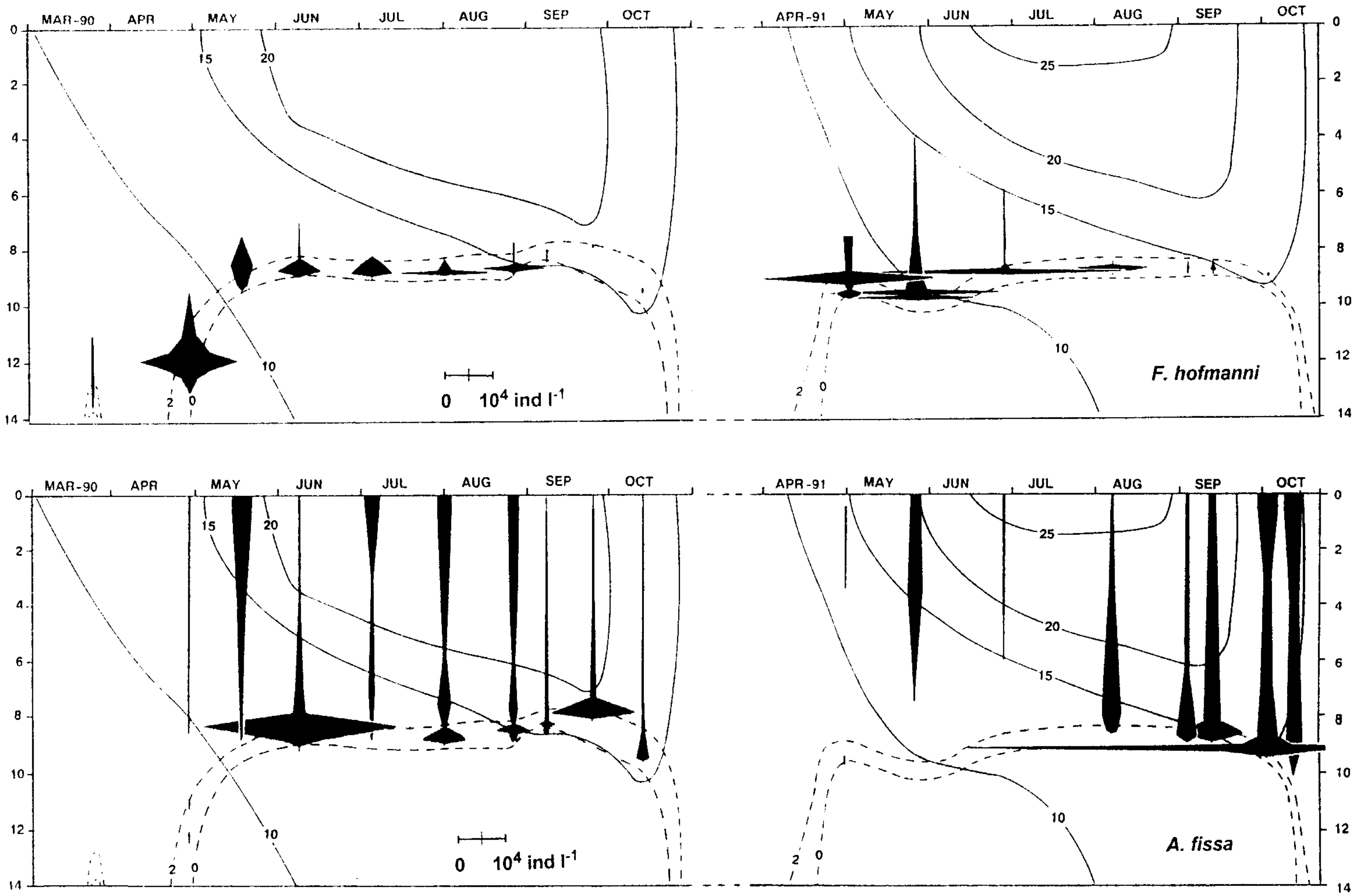

Fig. 2. Vertical profiles of *F. hofmanni* (top) and *A. fissa* (bottom) during the stratification period in 1990 and 1991. Abundance of these species is very low during the mixing period (November-March). Isotherms every 5°C are indicated with solid lines and the oxygen isopleths of 0 and 2 mg l^{-1} with broken lines.

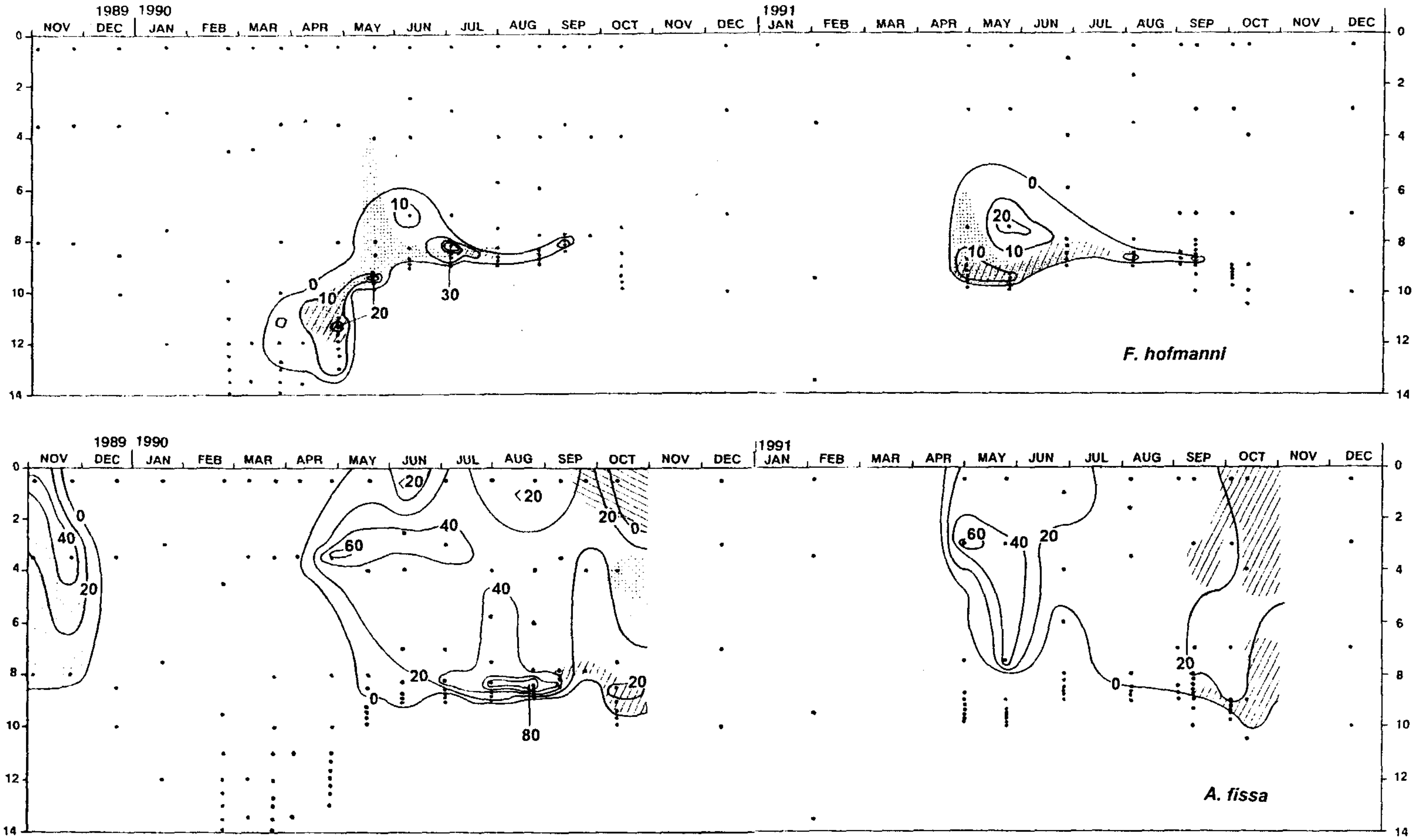

Fig. 3. Isopleths for *F. hofmanni* (top) and *A. fissa* (bottom) showing depth-time distribution of the amictic egg per female percentages, considered only when female densities were higher than 100 ind l^{-1}. The dots indicate the sampling points during the whole studied period and the shaded areas show the presence of resting eggs (dotted) and the presence of males (lines). The *A. fissa* graph has been left incomplete for November 1990 and 1991, because of the lack of samples during these months (December samples always had practically no individuals).

Table 1. Maximal density (max) in ind l^{-1}, and the depth where it was reached, for the main rotifer species and copepod nauplii at different dates selected to have corresponding estimates during the stratification period in 1990 and 1991. For *F. hofmanni* temperature (°C) and oxygen (mg l^{-1}) at the depth of the maximum is also indicated. (–) indicates none present in the corresponding date.

	nauplii		*K. quadrata*		*A. girodi*		*H. mira*		*P. dolichoptera*		*A. fissa*		*F. hofmanni*			
	max	depth	max	depth	max	depth	max	depth	max	depth	max	depth	max	depth	temp	oxyg
28/4/90	1740	11.9	20	11.6	–	–	–	–	–	–	200	3.5	14160	11.9	9.4	0.2
1/5/91	400	9.0	–	–	–	–	–	–	–	–	150	0.5	23560	9.0	8.3	0.4
8/6/90	540	8.7	40	7.0	220	4.0	–	–	–	–	28700	8.3	6340	8.7	10.8	0.2
25/5/91	600	9.5	40	3.5	–	–	–	–	20	0.5	1942	3.5	23860	9.5	9.9	0.6
4/7/90	4050	8.7	20	7.0	60	0.5	340	3.0	360	0.5	1900	0.5	5927	8.8	11.5	0.2
27/6/91	7540	8.7	–	–	600	8.7	20	1.0	840	1.0	445	4.0	36220	8.8	11.1	0.7
30/7/90	5280	8.8	20	7.5	40	6.0	100	4.0	540	7.5	6360	8.7	12960	8.8	12.7	0.2
6/8/91	14933	8.7	–	–	20	8.0	600	3.5	280	8.0	2960	8.0	10339	8.7	12.5	0.5
25/8/90	5044	8.6	10	7.8	100	8.2	43	6.0	360	7.8	4800	8.4	9117	8.6	14.0	0.4
3/9/91	1500	8.7	–	–	–	–	240	7.0	180	8.5	2800	8.7	480	8.7	13.8	0.5
24/9/90	900	7.8	–	–	–	–	40	4.0	20	0.5	12580	7.8	120	7.8	18.0	0.8
2/10/91	800	9.2	–	–	40	7.0	60	3.0	60	3.0	86900	9.1	40	9.0	17.3	5.6

The other important rotifer species in the lake are *Hexarthra mira*, *Keratella quadrata* and *Polyarthra dolichoptera*, their distribution being mainly epi-metalimnetic (Table 1). *Asplanchna girodi* is also abundant when it occurs, but its presence is restricted to June and July. It often has a maximum near the oxicline (Table 1). Examination of gut contents of *A. girodi* confirmed that *F. hofmanni* is an important part of its diet, as well as *A. fissa*.

Filinia hofmanni

The morphological features of *Filinia hofmanni* in Arcas-2 correspond to those given in the original species description (Koste, 1980) and in later studies of it (Shaber & Schrimpf, 1984; Sanoamuang, 1993) according to the number of unci teeth, which is 15/15 in the Arcas population (counted using both light microscopy and SEM) and also to the ventral insertion of the caudal seta and lengths of the body and setae and their relationships (Table 2). The morphometry of *F. hofmanni* of Arcas is very similar to that of the species in other Spanish karstic lakes; for instance, in Banyoles Lake the mean lengths of contracted body, lateral and caudal seta were respectively 138, 330 and 238, being the ratio between the two setae 1.39 (Miracle, 1976, the species was then named *F. longiseta longiseta*).

F. hofmanni in Arcas has a distribution completely bound to the oxicline (Fig. 2). It disappears during the mixing periods and initiates its development as soon as the lake begins to form an oxicline. In the small sink hole near the centre of the lake (Fig. 1) an oxicline can be readily established. In years with a mild winter, as in 1990, an incipient stratification may be implanted at the end of winter and an oxicline develops in the hole, immediately followed by the presence of *F. hofmanni*. This stratification can be eroded and so also the *F. hofmanni* population. In the fortnightly sampling during 1990, we found alternatively an oxicline with *F. hofmanni* (February 23, March 23) or the lake mixed to the bottom with almost no *F. hofmanni* (February 14, March 10, April 10). It was not until the establishment of a permanent stratification (April 28) when *F. hofmanni* formed an important population, but confined inside the small sink hole. The population then migrated with the oxicline (Fig. 2) and extended to a wider area of the lake, corresponding to the extent of the oxicline.

Winter of 1991 was much colder, without earlier pre-stratifications. Although the two years of study

Table 2. Measurements, in μm, of *F. hofmanni* in two different dates (end and beginning of its development period) showing the mean ± standard deviation and the range of variation. The total number of individuals measured was 100, 50 for each date. Sl = lateral seta, Sc = caudal seta, Bl = body length, Bw = body width and D = distance between Sc and the end of the body. Sl/Sc is the mean of ratios of individual measurements of seta lengths (± standard deviation).

	Sl	Sc	Bl	Bw	D	Sl/Sc
25/8/90						
mean	318 ± 26	213 ± 15	122 ± 9	74 ± 5	26 ± 3	1,5 ± 0,1
range	275 - 410	175 - 235	100 - 135	65 - 85	20 - 30	1,4 - 1,8
1/5/91						
mean	332 ± 17	238 ± 16	138 ± 11	83 ± 6	26 ± 3	1,4 ± 0,1
range	300 - 360	205 - 260	110 - 155	70 - 90	20 - 33	1,2 - 1,7
Total						
mean	325 ± 23	225 ± 20	130 ± 13	79 ± 7	26 ± 3	1,4 ± 0,1
range	275 - 410	175 - 260	100 - 155	65 - 90	20 - 33	1,2 - 1,8

were quite different, a general cycle of population dynamics of *F. hofmanni* is repeated (Fig. 2). That is, a high density peak in spring is followed by a decline in mid-summer to very low numbers by the end of summer. The population is always concentrated at the level of the oxicline, with a marked maximum always within 0.2–0.6 mg O_2 l^{-1} (Table 1).

The percentage of eggs per female (Fig. 3) also indicates the restricted temporal distribution of *F. hofmanni* and its circumscribed growth in the oxic-anoxic interface. This egg ratios are rather small but similar to those found for *F. hofmanni* in Pluß-see (Hofmann, 1987). The population grows exponentially from resting eggs or from very low numbers in spring to peak abundance, coinciding with the highest production of all types of eggs. The periods with high egg/female percentages in spring and early summer indicate intense reproduction. (However, for an estimate of growth rate, we should also consider the time of egg development which depends on temperature). The summer population maintains high densities until August, but is much more concentrated in a thinner layer of water at the oxicline. Its egg production is lower and it is even more narrowly confined at the oxic-anoxic interface.

Sexual reproduction has been continuously observed during the whole period of population development, with maxima of male and resting egg production taking place at the time of the highest densities (Fig. 4). Males, and the small eggs from which males develop, were limited to the oxicline (Fig. 3). Resting eggs, inside females, were found in a wider range of sampling depths, especially during periods of maximum production, when they spread to more superficial waters (Fig. 3) implying they must have some buoyancy adaptations. The number of males plus male eggs was higher than that of resting eggs and a time displacement between their maxima can be observed (Fig. 4). Male/female ratios were most frequently 2 to 4% and in general were greatest early in the season. Percentages of resting eggs per female were more variable, but also higher early in the season (Table 3).

Anuraeopsis fissa

The distribution and sexual cycles of *A. fissa* was very different from *F. hofmanni* in Arcas-2 (Fig. 2). Its population began its main occurrence one month later than *F. hofmanni* and in the epilimnion. It stayed throughout summer and autumn until overturn, occupying the entire vertical profile with maxima at different depths. It was usually abundant in the epilimnion and had a peak at the oxicline at the end of summer, just when *F. hofmanni* population declined. Only in 1990, *A. fissa* had also a peak near the oxicline at the end of spring, probably due to this year warm winter conditions.

The percentage of *A. fissa* amictic eggs per female was always much higher (over double) than *F. hofmanni* (Fig. 3). *A. fissa* had two centres of high egg production: one at the incipient thermocline in spring, and the other at the oxicline in late summer-early autumn. Near or at the initiation of the autumn overturn a new, smaller increment in egg production can occur, mainly in the superficial waters, and right after the population practicaly disappears until next spring. In *A. fissa* sexual

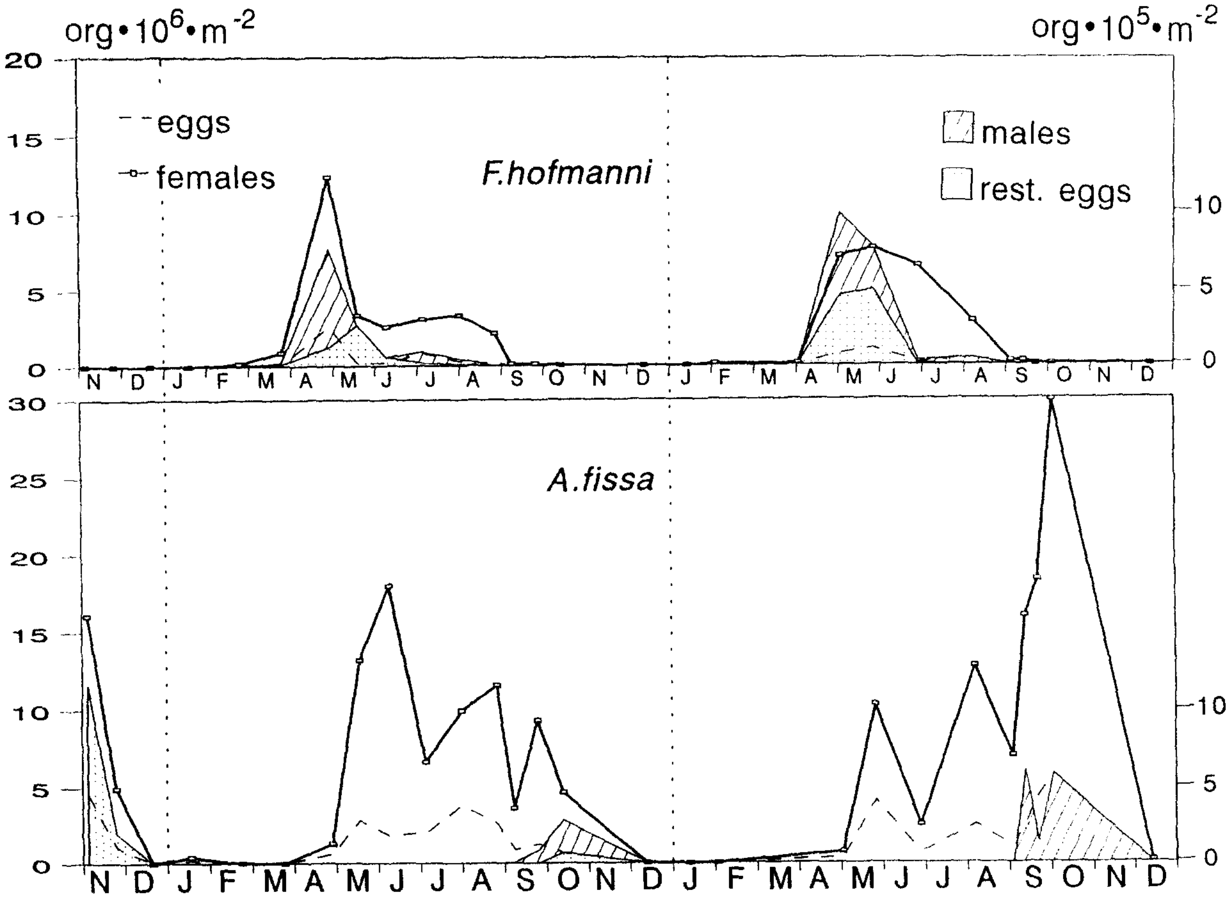

Fig 4. Integrated number per water column of females and of amictic eggs in 10^6 organisms.m^{-2} (left scale) and of the sum of male+male eggs+resting eggs in 10^5 organisms.m^{-2} (right scale) for *F. hofmanni* (top) and *A. fissa* (bottom) from November 1989 to October 1991. The different proportions of males+male eggs and resting eggs are also shown.

reproduction was limited to the end of its main occurrence period. Males and resting eggs were found in all the vertical profile but only during a short time, from September to November (Figs 3 and 4; Table 4). Resting eggs were rare and only found at the very end of *A. fissa* population development. Males were more frequent but heterogeneously vertically distributed, they were only observed near the surface and in the upper oxicline.

Differences between years

The years 1990 and 1991 presented marked differences. The winter of 1991 was much colder than that of 1990. Minimum water temperatures in winter 1990 were around 6°C while in 1991 we measure temperatures around 4°C. That 1991 had a colder winter can be also seen in the position of the 10°C isotherm in Fig. 2. On the other hand, the summer of 1991 was slightly warmer than that of 1990 (Fig. 2). Therefore, the epilimnion was warmer and the hypolimnion colder in 1991. Because of the cold 1991 winter there were no pre-stratifications and mixing was more intense until the end of April. The intense mixing enhanced spring primary production, indicated by the larger metalimnetic oxygen maximum for 1991 shown in Fig. 5. This explain the higher zooplanktonic densities attained at the oxicline during this year. At the onset of stratification of 1991 *F. hofmanni* reached extraordinarily high densities in the oxicline, circumscribed in a very thin water layer. The water was still cold in early summer and growth of *A. fissa* took place mainly in the upper waters (without any oxiclinal maximum like in 1990). When *F. hofmanni* declined in mid-summer 1991, nauplii (up to 15 ind ml^{-1}, Table 1) peaked in the oxicline, where later, at the beginning of autumn, *A. fissa*

Tables 3A and 3B. Dates and depths intervals (m) where resting eggs and/or males+male eggs of *F. hofmanni* (A) and *A. fissa* (B) were found. For each date, their maximum density (n° l^{-1}) in the vertical profile and corresponding percentage per female is indicated together with the depth of this maximum. If the corresponding percentage was not also the maximum, a new line has been added to show the maximum percentage per female, together with its corresponding density and depth. (–) indicates none present

Table 3A

F. hofmanni		Resting eggs			Males+male eggs		
Date	Depths	n° l^{-1}	%	(depth)	n° l^{-1}	%	(depth)
28/3/90	11	10	4	(11.0)	10	4	(11.0)
28/4/90	10–13	120	1	(11.9)	1140	8	(11.9)
		60	7	(10.0)			
17/5/90	4–10	133	4	(8.5)	–	–	–
		20	20	(9.4)			
8/6/90	8–9	120	26	(8.2)	–	–	–
4/7/90	8–9	33	<1	(8.8)	125	4	(8.5)
30/7/90	8–9	20	9	(8.3)	30	1	(8.7)
1/5/91	7–10	1480	6	(9.0)	3000	12	(9.0)
		500	27	(9.2)			
25/5/91	9–10	2100	9	(9.5)	1440	6	(9.6)
		640	20	(9.4)			
27/6/91	8–9	60	<1	(8.8)	300	1	(8.8)
		20	1	(8.7)	20	6	(8.3)
4/8/91	8–9	–	–	–	200	2	(8.7)
					67	33	(8.9)

reached its highest abundance. Moreover, resting egg production and number of males and male eggs of both species were also higher in 1991 than in 1990 (Fig. 4, Table 3).

Discussion

Lakes such as Arcas-2, with a high relative depth (Fig. 1), are easily stratified, thus developing an oxic-anoxic interface. There is usually the paradoxical contrast between quite clear top waters and densely populated deep waters, at the level of that interface. Microbial (ciliates, algae, prokaryotes) concentrations at the oxicline in Arcas-2 have been previously described (Finlay *et al.*, 1991; Vicente *et al.*, 1991). What it is not so known is the high densities that invertebrate plankton can attain in the oxiclines. These high densities can only be revealed with a proper sampling of microlayers, because zooplankton can have massive maxima constrained within 10 cm of the water column. Densities of planktonic rotifers as high as those recorded here, 87 ind ml^{-1} for *A. fissa* and 36 ind ml^{-1} for *F. hofmanni*, have only been reported in very few studies in which a microlayer sampler was used. For instance, densities of 33 ind ml^{-1} of *A. fissa* were reported from

Table 3. (continued).

Table 3B

A. fissa		Resting eggs			Males+male eggs		
Date	Depths	n° l^{-1}	%	(depth)	n° l^{-1}	%	(depth)
4/11/69	3–8	140	10	(8.0)	–	–	–
24/11/69	3–8	20	7	(3.5)	–	–	–
7/09/90	8–9	–	–	–	20	3	(8.1)
24/09/90	0–8	–	–	–	20	4	(0.5)
12/10/90	0–10	20	4	(4.0)	100	7	(9.0)
					80	36	(0.5)
12/09/91	4–9	–	–	–	233	11	(6.0)
2/10/91	0–10	–	–	–	100	<1	(9.1)
					60	2	(0.5)
11/10/91	0–10	–	–	–	140	6	(0.5)
					13	32	(10.0)

the oxicline of Lake La Cruz (Armengol-Diaz *et al.*, 1993) and of several hundreds of ind ml^{-1} of *A. fissa* from the oxicline of the rich Cisó Lake (Gasol *et al.*, 1991, 1992).

Filinia species often coexist in one lake. This has generated some confusion in distinguishing them (Ruttner-Kolisko, 1989), but there is doubtless a complex of several closely related species within this genus occupying narrow niches (Miracle & Alfonso 1993). One of the species of this genus of recent description is *F. hofmanni* (Koste, 1980). In Arcas, it is the sole *Filinia* species and its distribution corresponds clearly to its restricted ecology. In early spring, it stays restricted to the oxicline although it has almost no competition in the above waters. Moreover its sexual cycle is very important, with sexuality observed in almost all the period of its presence. This is also true in other lakes (Miracle, 1976) where it coexists with *Filinia terminalis*, having also the latter species continuous sexuality. This observation contradicts the argument that asexuality or pseudosexuality is common in *Filinia* populations (Ruttner-Kolisko, 1989), used to question the validity of species differentiation within this genus.

The two dominant rotifer species of Lake Arcas-2 are stratifying species, which reach their maximum densities at the oxicline, together with the copepod *Tropocyclops prasinus*. The distribution of these two dominant rotifers is different and exclusive, i.e. they segregate clearly their major occurrences, according to their environmental requirements. *F. hofmanni* is adapted to low temperature and low oxygen, but also to water stability. Temperature could be a key factor for *F. hofmanni* drastic population decrease at the end of summer, when the thermocline deepens and temperature reaches 14°C at the oxicline level. Schaber & Schrimpf (1984) discuss the cold water stenothermy of *F. hofmanni* and give the 12°C isotherm as a limit of its distribution. As the main example, they describe a collapse of the population in a lake subjected to artificial mixing, which they interpret is the result of the subsequent rise of temperature. This may not be so simple, since *F. hofmanni* apparently needs both low temperature and stability in the water column. In the warm monomictic not very deep lakes, as Arcas-2, *F. hofmanni* stars an exponential growth at the onset of stratification in the oxicline and declines in midsummer, when the thermocline comes close to the oxicline and there is an increase of temperature and turbulence

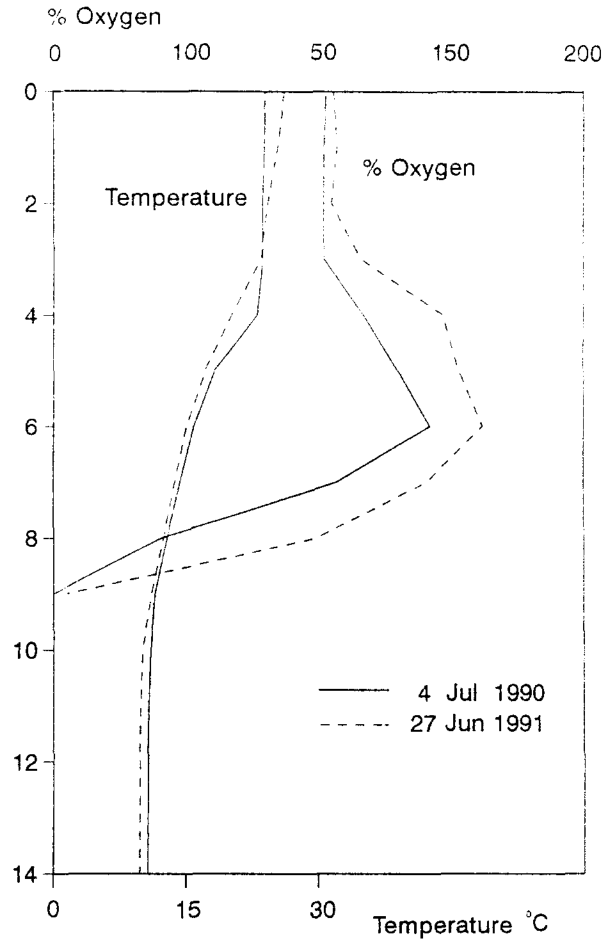

Fig 5. Comparison of temperature and oxygen vertical profiles between the beginning of summer of 1990 and that of 1991.

in it. In dimictic lakes of northern latitudes or high altitudes *F. hofmanni* has an additional development in the low oxygen conditions established during winter stratification under ice (Hofmann 1982, 1987, Schaber & Schrimpf, 1984; Mikschi, 1989) and it is more or less permanent at the oxicline of meromictic lakes, depending on the stability of this interface (Ruttner-Kolisko, 1989; Bogaert & Dumont, 1989; Miracle & Alfonso, 1993; Armengol-Diaz *et al.*, 1993). In all cases, *F. hofmanni* is extremely bound to the oxicline and has its development centres located there.

On the other hand, *A. fissa* is considered a warm water species (Ruttner-Kolisko, 1974). Temperature could be also a factor, together with water stability, contributing to its main abundance distribution: at the incipient thermocline in spring, at the upper oxicline in late summer, when the temperature gets higher there due to the deepening of the thermocline, and finally its break down in November and almost disappearance during the colder more turbulent months. *A. fissa* has a dispersion centre at the epi-metalimnion and only secondarily extends its niche to the oxicline, where it can have great maxima when there is not competition.

The sexual reproductive strategies of the two dominant species also differ: the winter-spring species (*F. hofmanni*), has sexuality induced at the very first of its exponential growth phase, with maxima on its density peak, and its sexuality persists during the whole period of occurrence. (Other winter-spring species such as *F. terminalis* have the same strategy, Miracle, 1976). The summer species (*A. fissa*) has sexuality only at the end of its main occurrence, in its last peak of abundance, close to the autumn overturn.

The annual cycles for both species seem rather regular in Arcas-2; the same cycles were observed in previous years showing only slight differences (Esparcia *et al.*, 1991; unpublished data). Differences between years are due to climatic variations which influence mixing and stratification. The mild winter of 1990 promoted an earlier onset of stratification followed by the quick segregation of primary production and decomposition. This has the effect of an earlier exponential growth of *F. hofmanni* and also an early shift of *A. fissa* to the enriched oxicline after the spring algal bloom. *A. fissa* could exploit in June this year, but not the next year, the layers above those occupied by *F. hofmanni*. The more severe winter of 1991 enhanced winter mixing, thus heightening spring primary production. Then during stratification, temperature and oxygen gradients were sharper. Rotifer densities at the interface depend on the balance between dispersion and net growth rate. The latter is higher when primary production is higher because population growth in the oxicline depends on the remaining end products of photosynthesis. Dispersion is lower if gradients are more acute. Therefore, 1991 rotifer populations reached higher densities more narrowly concentrated in the interface and the seasonal segregation between the main oxiclinal species increased.

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