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Differential distributions of *Brachionus* species in three coastal lagoons

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With 3 figures and 1 table in the text

Introduction

Brachionus is the most important genus of rotifers in the coastal wetlands of Mediterranean Spain. In a previous paper (MIRACLE et al. 1987) *Brachionus* species were used to show how a congeneric guild occupies a large variety of environments in a geographical area subject to seasonal change. Statistically treated data from 57 locations in the Spanish Mediterranean coast showed that the cosmopolitan species of *Brachionus* had clear differential distributions in this area. These could be associated with patterns of some physico-chemical parameters, mainly temperature, sulphate and chloride or their ratio and the ratio alkalinity to alkaline earths. Many of these localities provided a habitat suitable for several coexisting species of *Brachionus*, but in these cases large differences in relative species numbers were observed. The present paper investigates the differential distributions of *Brachionus* species within one locality in three selected coastal lagoons. Seasonal change is the main factor segregating *Brachionus* species, but also spatial heterogeneity, based on salinity, water flow and bioenergetic (food, oxygen concentrations) gradients, is also significant.

Methods and study lakes

Three coastal lagoons were selected: (1) "La Ricarda" is a eutrophic elongated lagoon (1.3 × 0.1 km) perpendicular to the sea in the Llobregat delta, 10 km south of Barcelona (Fig. 1), with a maximum depth of 3 m at the centre. It is a brackish water lagoon without vertical stratification, but with a marked salinity gradient along its length. Samples were taken at mid-depth. (2) "Cullera" is also a eutrophic elongated lagoon (3.5 × 0.25 km, Fig. 2) perpendicular to the sea, 35 km south of Valencia, with a maximum depth of 7.5 m. At the time of the study it was stratified due to a marine saline wedge underneath the flowing fresh-water. Samples were taken at several depths of the vertical profile at three points: source, centre and mouth of the lagoon, which had depths of 3.5, 7.3 and 5 m, respectively. (3) "Albufera of Valencia" is the largest coastal oligohaline lagoon of Mediterranean Spain (2.3 km^2), rounded in shape and very shallow (mean depth 0.75 m). It is hypertrophic and dominated by cyanobacteria. Samples were taken at five stations (Fig. 3) from mid-depth.

Abundance of *Brachionus* species was estimated from samples taken with a 8 liter VAN DORN bottle at different depths and times of the year and filtered on 54 μm mesh Nytal. These samples were counted with an inverted microscope at 100 or 200 × magnification. Other limnological parameters were determined by classical methods (GOLTERMAN et al. 1978).

Results

La Ricarda

At the time of the study (13 November 1973) a salinity gradient caused by mixture of different proportions of fresh and marine waters was observed (Fig. 1). Salinity varied from 2.8 ‰ at the sampling point farthest from the sea, to 4.5 ‰ at the nearest. The ratios $Cl^{-1} : SO_4^{=} :$ Alk were respectively 8.5 : 2 : 1 and 13.5 : 1.5 : 1 at these two points and the ratios $Na^+ : Mg^{2+} : Ca^{2+}$ were respectively 8 : 2 : 1 and 10 : 2 : 1. Other parameters

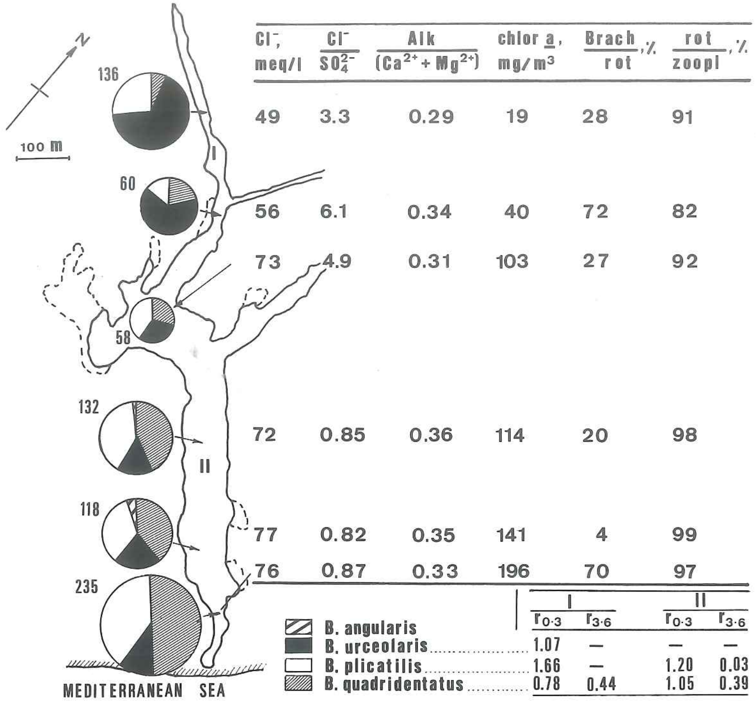

Fig. 1. Outline of La Ricarda lagoon indicating the relative proportion of each *Brachionus* species, at the different sampling stations. The surface of the circles is proportional to the number of individuals/l of the genus *Brachionus* which is indicated at their left side. Chloride and chlorophyll-a concentrations and the ratios chloride to sulphate, alkalinity to alcaline earths, *Brachionus* total number of rotifers and rotifers to total number of zooplankters (except ciliates) are also indicated. At the bottom, a table shows the growth rates of three coexisting species enclosed in limnocorrals, located in the sites symbolized by I and II in the map. Growth rates were calculated from

$$r_{0-3} = \frac{\ln N_{t3} - \ln N_{t0}}{t_3 - t_0},$$

$$r_{3-6} = \frac{\ln N_{t6} - \ln N_{t3}}{t_6 - t_3}$$

where t_0, t_3, t_6 are respectively the enclosure initial time and 3 and 6 days after; and N_{t0}, N_{t3}, N_{t6} the corresponding number of individuals at those times. (–) indicates that rates are zero or negative.

and ratios are shown in Fig. 1. Along with this variation in salinity and ionic relationships there was a flow gradient, with the flow being substantial at the source of the lagoon and becoming much reduced as water approached the mouth. Associated with those gradients there is a striking replacement of *Brachionus urceolaris* by *Brachionus plicatilis* and *Brachionus quadridentatus*, from the source to the mouth of the lagoon (Fig. 1).

In previous work (Miracle & Guiset 1977) duplicate 10 l experimental cages of Nytal were placed (June 20, 1975) at two opposite ends of the lagoon. These were removed after three, six and twelve days. The three coexisting species of *Brachionus* experienced a great ncrease in population density inside the cages during the first days, reaching values 20—100 times higher than in the open water. This increase was followed by a substantial decrease and mixis, while in the open water populations were more or less uniformly maintained. From this data we have calculated the growth rates of the species in Fig. 1, from the beginning of the experiment to day 3 and from day 3 to day 6 (from six to twelve growth was negative for all species and sites).

Enclosed *B. plicatilis* had the highest densities and growth rates; maximum density reached by this species (ca. 13,000 ind/l, in contrast with the mean of 430 ind/l in the open water) was nearly the same in the cages located at the two opposite ends, but growth was slower in the cages near the mouth where flow was also slower. *B. urceolaris* had some growth onyl upstream and *B. quadridentatus* was more favored at the mouth. *B. quadridentatus* rate of increase was lower than that of *B. plicatilis* at the beginning, but the species could be growing during longer time, even coexisting with the high densities of *B. plicatilis*; *B. quadridentatus* was, by the end of the experiment, more favored inside the cages than the other species.

The lagoon of Cullera

This lagoon showed an estuarine circulation and, due to a marine water intrusion below the freshwater runoff, a halocline and an oxycline were established throughout the year of the study. A marked seasonal fluctuation characterized the lagoon (Table 1, Fig. 2) subject to the interaction between salt- and fresh-water masses. A period of high marine influence and vertical mixing in winter contrasts with a period of inland influence and stability in summer; this leads to a sharp stratification of the waters and a succession of planktonic communities. Phytoplankton dominance changed from centric diatoms in winter (*Stephanodiscus subsalsus*) and spring (*Cyclotella atomus*) to dominance of Chlorophycea (*Chlamydomonas* sp., *Chlorella homosphera*) in summer, ending with a high proportion of Cryptophycea in late summer (Rojo & Miracle 1984).

Data on the variation of *Brachionus* species in the years 1980—1981, corresponding to the conditions described in Table 1 are shown in Fig. 2. In mid October 1980, vertical mixing began, the halocline rose and the former summer stratification was disrupted; the zooplankton community became totally dominated by *B. plicatilis*. As autumn advanced, a brief period of stability followed, the halocline got deeper, and salinity diminished. *B. plicatilis* disappeared except in the centre of the lagoon arround the level of the oxycline. Several populations of other *Brachionus* developed, although with much reduced densities and localized at the surface. Species of *Synchaeta* and *Notholca* dominated the plankton. In the centre of the lagoon, more deep and stable than the other two sampling stations, four *Brachionus* species coexisted: *B. urceolaris*, *B. quadridentatus*, *B. bidentatus* at the surface and *B. plicatilis* at the oxycline. Greater mixis in winter and marine influence favored marine and brackish water species such as *Synchaeta grimpei*. *Brachionus* populations vanished except for a small population of *Brachionus leydigi*. This mixed condition persisted in spring with brackish water species and larvae of marine benthic invertebrates in the plankton. Later *Brachionus* species started again to show population growth initiated by *B. plicatilis* which, by May, was abundant in the lower half of the lagoon, especially at the mouth where mixing is always more important. Again the centre had a higher diversity with with 5 coexisting *Brachionus* species. At this time stratification began to establish and in summer the halocline and the oxycline were at the same depth.

Table 1. Mean values of several features characterizing two layers of Cullera lagoon: the upper flowing freshwater and the gradient stratum to the monimolimnion. Their respective depth limits are given for each date and sampling station (1 to 3 from mouth to source). Heading abbreviations as in Fig. 1.

Date	Stat.	Depth, m	Temp, °C	Cond, µS/cm	Alk, meq/l	$Cl^-/SO_4^=$, (in eq)	O_2, ml/l	Chl-a µg/l	Brach, % rot.	rot, % zoopl.
18–Oct–80	1	0 – 0.50	17.5	7,475	–	–	6.4	–	56.6	99.0
		0.50 – 1.25	18.8	29,720	–	–	7.6	–	57.8	97.2
	2	0 – 0.50	18.9	7,807	–	–	3.8	–	75.4	95.1
		0.50 – 1.50	19.5	29,970	–	–	3.9	–	70.1	92.1
	3	0 – 0.65	18.2	4,179	–	–	6.5	–	80.7	85.9
		0.65 – 1.25	19.6	33,570	–	–	5.7	–	74.6	90.4
29–Nov–80	1	0 – 2.45	7.5	2,055	2.9	5.3	6.3	4.4	1.1	89.7
		2.45 – 3.05	12.2	26,820	4.0	49.3	0	0	0.7	90.4
	2	0 – 2.25	7.3	2,079	2.9	3.2	7.9	4.1	1.1	89.6
		2.25 – 3.30	12.8	25,220	4.3	67.9	0	0	0.8	70.7
	3	0 – 2.25	9.2	3,572	2.8	2.4	2.8	2.8	0.09	86.6
		2.25 – 3.30	14.8	23,240	3.4	39.8	3.4	4.0	0.05	85.7
27–Feb–81	1	0 – 1.00	14.1	5,450	4.4	72.1	15.9	65.1	0	93.2
		1.00 – 3.75	13.0	33,540	4.0	89.5	12.2	100.1	0	80.2
	2	0 – 1.00	14.8	5,664	4.5	42.9	12.6	53.1	0.8	79.9
		1.00 – 4.50	13.5	38,450	4.3	100.0	9.6	36.4	0.03	89.7
	3	0 – 1.10	15.5	2,176	4.6	3.6	5.9	53.5	0	82.0
		1.10 – 3.25	14.1	33,890	4.3	–	3.6	30.8	0	93.3
2–May–81	1	0 – 1.25	18.0	2,280	3.6	0.9	8.7	82.7	4.5	77.8
		1.25 – 3.75	17.1	24,060	4.1	13.4	3.5	29.6	2.7	74.3
	2	0 – 1.65	19.2	2,668	3.2	1.7	9.4	86.0	12.4	70.3
		1.65 – 3.70	16.9	28,150	4.8	19.2	2.0	32.0	3.7	43.8
	3	0 – 1.75	21.8	1,760	2.6	0.4	7.5	40.9	12.8	53.6
		1.75 – 3.25	17.1	28,920	3.4	12.9	2.9	26.5	0.6	57.9
1–Jul–81	1	0 – 3.65	22.8	2,524	3.0	0.7	6.3	9.3	0.3	44.3
		3.65 – 4.00	22.8	16,040	7.4	9.5	0	0	28.5	4.1
	2	0 – 3.55	24.5	2,503	2.9	1.6	4.5	10.8	1.8	31.3
		3.55 – 4.13	23.5	16,000	5.9	9.1	0	0	0.4	52.3
	3	0 – 2.50	24.5	1,501	3.0	0.6	6.8	14.3	4.4	14.7
		2.50 – 3.25	22.8	4,345	3.0	2.5	3.0	11.0	1.0	15.0
8–Sep–81	1	0 – 4.15	25.3	1,387	3.3	0.7	5.3	–	47.2	44.5
		4.15 – 4.50	23.6	23,400	3.3	1.3	3.3	–	37.3	28.2
	2	0 – 4.15	24.8	1,351	3.2	0.7	4.8	–	51.2	45.5
		4.15 – 4.35	24.0	15,300	10.0	9.4	0	–	43.9	21.8
	3	0 – 3.50	26.0	1,190	3.5	0.5	6.3	–	0.3	46.5

Summer stability promoted a succession of plankton communities, diversity increased and *Brachionus calyciflorus* became the dominant rotifer species. *B. plicatilis* could again maintain some population near the oxycline, although, at this depth, *Hexarthra* was the most important rotifer. During this period the copepod *Calanipeda aquaedulcis* showed a maximum and the cladoceran *Moina micrura* was important (Miracle & Vicente 1983). In October 1981 and October 1982, the same conditions of October 1980 were repeated with *B. plicatilis* dominance. Samples from summer 1980 (Miracle & Vicente 1983) and from summer 1982 (unpubl. data), showed the same patterns as those described here fore 1981; in those years *B. calyciflorus* dominance was even more evident.

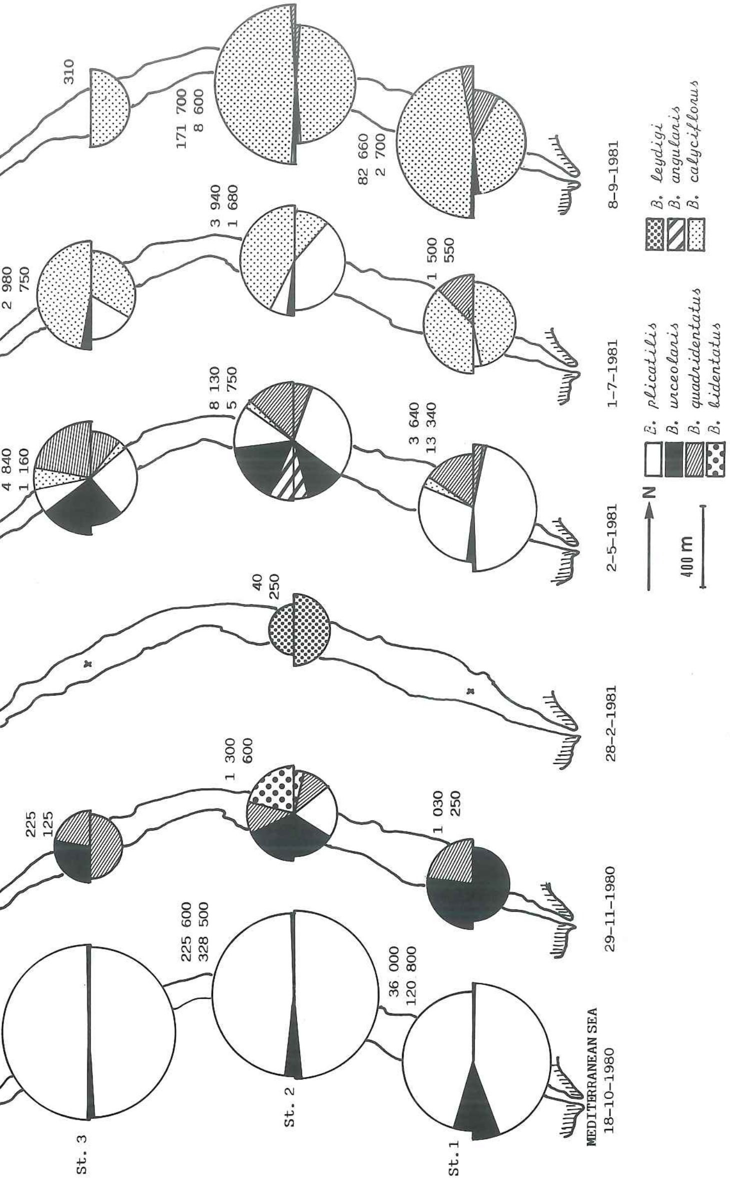

Fig. 2. Outlines of Cullera lagoon showing the relative proportion of each *Brachionus* species, at the same sampling stations (1 to 3) dates and for the two layers of the water column specified in Table 1. Two semicircles are indications of the integrated number of *Brachionus* found in each layer. This number (individuals/m^2) is given near each semicircle whose diameter is proportional to the log transform of that number. Top semicircle correspond to upper flowing layer (limiting depths given in Table 1) and bottom semicircle to the remainder of the water column; rotifers of this layer occur almost exclusively in the gradient stratum.

Albufera of Valencia

The Albufera of Valencia is an oligohaline hypertrophic lagoon. During the year of the study, July 1982—July 1983, conductivity varied from 1500 to slightly over 3000 μS/

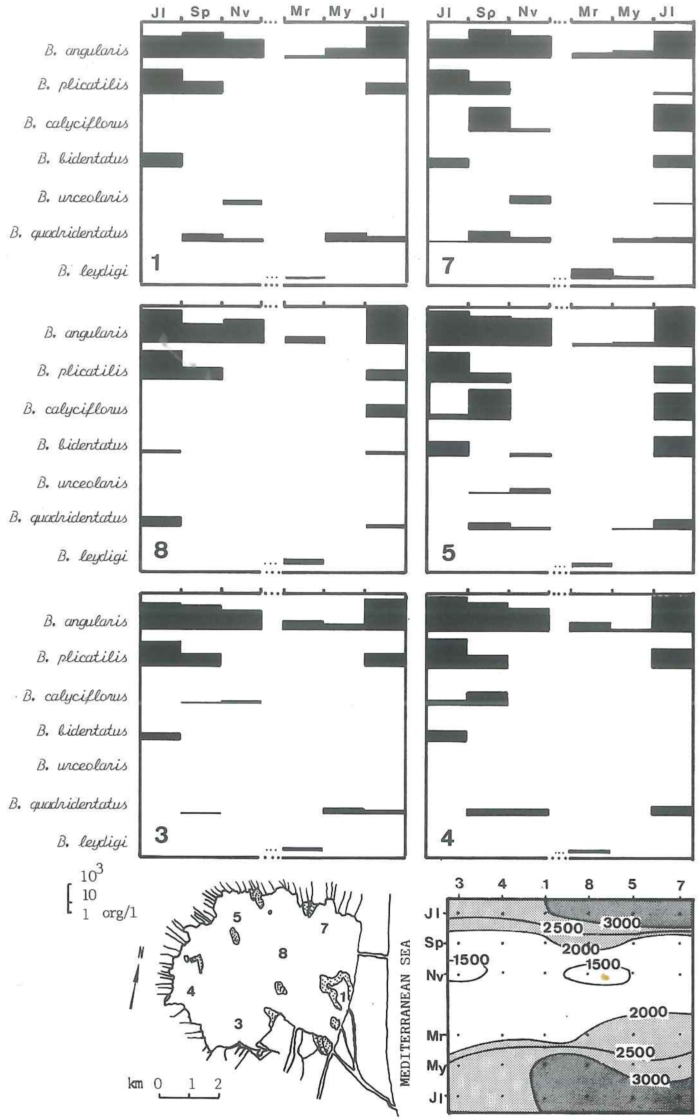

Fig. 3. Abundance in number of individuals/l (logarithmic vertical scale) of the different *Brachionus* species in the Albufera of Valencia, during an annual cycle in the six sampling stations indicated in the map. Conductivity in μS/cm is also indicated by isolines in the bottom graph between sampling stations and months.

cm (Fig. 3) and chlorophyll-a concentrations varied from 200 mg/m^3 in autumn and winter to over 400 mg/m^3 in spring and mid summer. Maxima in spring exceeded

00 mg/m^3 (MIRACLE et al. 1984). Human manipulation of the lagoon, which is used as regulator for rice field irrigation, amplifies the annual variation; dams are partially losed from April to August during rice growth and completely closed from No-ember to January. On the other hand, water flow to the sea is important in Sep-ember when dams are open and rice fields are dried for harvest. Dams are partially pened also from January to April, with substantial flow in spring. Torrential rains are ommon at this latitude in autumn and, during the present study, floods contributed a najor flow of water. Conductivity diminished from July to November as did the Cl^-/$O_4^=$ ratio, which decreased from values of 1.1—1.5 (depending on the sampling sta-on) in July to values near 1, in September, and to 0.6—0.7, in November (MIRACLE et l. 1984).

Zooplankton of the Albufera is dominated by the copepod *Acanthocyclops vernalis* nd *Brachionus angularis* (OLTRA & MIRACLE 1984, in press). The copepod dominated nainly in winter and spring (rotifers/total zooplankton ratio ≃ 0.1—0.7) and the rotifer he rest of the year (rotifers/total zooplankton ratio ≃ 40—78 mid summer, ≃ 13—28 utumn, *Brachionus*/total rotifers ratio >97 mid summer, ≃ 41—92 autumn). Besides *B. ngularis*, with maxima in summer, a succession of other *Brachionus* species occurred, vhich is shown in Fig. 3 for six sampling stations. In stations 5 and 7 diversity of *rachionus* species is greater and succession more complete. *B. leydigi* appeared ex-lusively in winter and early spring, when all other *Brachionus* species were almost non-xistent. In spring and autumn *B. quadridentatus* had small populations. In early summer 1982 and 1983) *B. plicatilis* had strong development (it reached 60 % of total zooplankton July 1981 at station 7, where salinity is higher, apparently to the detriment of *B. angu-aris*), which was succeeded by increase in *B. calyciflorus* (in September 1981, it reached he 56 % of total zooplankton at station 5). In early summer *B. bidentatus* was also of ome importance. A lesser species, *B. urceolaris*, was present exclusively in November at he time of minimum salinity.

Two species of *Brachionus* revealed the striking contrast among sampling stations, be-ause of their absence from some of them. *B. urceolaris*, a lesser species was only found at tation 1, besides the station 5 and 7. More striking is the case of *B. calyciflorus* which pre-ented very high abundance at stations 5 and 7 but was not found in the rest of the la-oon, except for a small population at stations 3 and 4 in summer 1982 and at station 8 in ummer 1983. In mid and late summer, at the time of the high abundance of *B. calycif-orus*, the heterogeneity of the lagoon was greater, and zooplankton had important differ-nces between stations 5 and 7 and the rest; *B. calyciflorus* and the cladoceran *Moina* were nly important in stations 5 and 7 while the others had greater proportions of the Copepoda *Acanthocyclops vernalis* and *Polyarthra*.

Zooplankton differences among the stations correspond to phytoplankton or prey opulation differences. The planktonic fraction of potential food for rotifers is domi-ated by cyanobacteria, mainly species of *Oscillatoria*, and filamentous or large-sized bac-eria, constituted around the 90 % of this planktonic fraction in summer and the 70 % in arly spring (stations 5 and 7 had much higher proportions of Chlorophycea and diatoms han the other stations during the whole year). These differences were more marked in ummer, for instance in September 1984, when at other stations procaryote proportions the planktonic fraction were 90 %, the percentage was 70 % at station 5 and 54 % at sta-on 7 (MIRACLE et al. in press).

Discussion

The results presented here indicate that the distribution of *Brachionus* species could be rather well characterized in the lagoons of Mediterranean Spain. Seasonal variation or annual cycles are more important than the spatial distribution. The most characterized species were *B. leydigi*, *B. plicatilis* and *B. calyciflorus* because of their temperature, salinity and trophic restrictions, respectively.

B. leydigi showed, in the present work, as well as in a study of 57 localities in the Spanish Mediterranean wetlands (MIRACLE et al. 1987), a distribution restricted to a winter (sometimes also early spring) occurrence, when no other *Brachionus* species was prominant. In a previous study of Albufera of Valencia (OLTRA & MIRACLE in press), an annual cycle of zooplankton (April 1980—July 1981) was described for sampling station 1 with a higher sampling frequency than the results presented here. *B. leydigi* showed a maximum in January when all other *Brachionus* species, including *B. angularis*, were practically absent. Its occurrence was largely restricted to the months from December to April. Several authors (KLEMENT 1960) have considered this species as cold stenotherm, however POURRIOT (1965) considered it eurytherm because he found it from 5 to 20 °C in the spring. In Spanish latitudes, *B. leydigi* is without any doubt a winter species (which sometimes is found from late autumn to early spring). Although other factors are involved such as salinity parameters or trophic interaction, temperature seems an important factor for the occurrence of *B. leydigi*; in a range of samples with field temperatures up to over 30 °C, the maximum temperature in which it was found was 19 °C (MIRACLE et al. 1987 and the present paper). Furthermore, from the statistical analysis of 57 coastal wetland localities (MIRACLE et al. 1987), temperature proved to be an important factor for the distribution of *Brachionus* species; *B. leydigi* occurred at low temperatures, while the population of all other species had an obvious preference for higher temperatures.

B. plicatilis is clearly restricted by a low salinity limit, and it was never found in the Albufera of Valencia in the above mentioned study of OLTRA & MIRACLE (in press) probably because during the years 1980—81 conductivity limits ranged from 1100 to 1800 μS/cm. In the data from the Albufera presented here, it was found only during periods of higher conductivity (Fig. 3), i.e. in summer, and its was present neither in spring nor in autumn, as in La Ricarda or Cullera (which have higher salinity). Moreover, in the latter lagoons it was usually more abundant near the strand end and near the halocline in stratified waters. RUTTNER-KOLISKO (1971) in a characterization of rotifer associations also places *B. plicatilis* as inhabitant of the more saline waters.

The annual cycle of Cullera demonstrates the character of *B. plicatilis* as pioneer species of the first succession stages; its population growth occurs in the periods of instability and vertical mixing of spring and early autumn, after which it disappears. A small population may, however, persist longer at the central site in the deep, more saline waters of the oxycline, where it has to tolerate very low oxygen concentrations. The high rates of growth (Fig. 1) of this species in experimental enclosures leads to a great increase and the production of resting eggs (MIRACLE & GUISET 1977) and confirms its status as fugitive species or "r" strategist. *B. plicatilis* has a more permanent dominance only in extreme conditions of salinity such as in evaporation coastal lagoons (MIRACLE et al. 1987), in inland saline lakes or near the oxycline in stratified lagoons with saline water at the bottom. WALKER (1981) also points out that its occurrence in high salinities is associated with an ability to tolerate very low oxygen concentrations.

B. calyciflorus may be limited by trophic factors. In Cullera lagoon it occurred only in ummer, being the dominant rotifer species during the period when Chlorophyceae were ominant and euglenoids were present. In Albufera of Valencia the species was abundant nly at stations 5 and 7 when there was a significant percentage of those groups of algae Miracle et al. in press) which seem to be necessary for the development of *B. calyciflorus* Pourriot 1965, 1977); moreover, the proportion of Cyanobacteria and filamentous baceria was much reduced compared with the rest of the lagoon. These organisms, accordng to Starkweather & Kellar (1983) are less suitable than eucaryotic food type in suporting *B. calyciflorus* growth. *B. calyciflorus* preference for flagellates (Volvocales and uglenoids) has been confirmed on many occasions. In waste water treatment plants *B. alyciflorus* showed great developments after a bloom of *Chlamydomonas* and the rotifer ppears to have contributed to the disappearance of this alga (Torrella pers. comm.).

The other species had less well delimited distributions. *B. angularis* is primarily or exlusively a detritivorous species (Pourriot 1969, 1977); so it is a dominant and almost ermanent species in the hypertrophic lagoon of Albufera dominated by Cyanobacteria, rom whose decay the rotifer may grow.

B. bidentatus is a less important species in these lagoons, but has a repetitive ocurrence in early summer in Albufera of Valencia (in the present study, as well as in the ear 1981, Oltra & Miracle in press) and in late spring and late autumn in the central art of Cullera lagoon. *B. urceolaris* and *B. quadridentatus* have a preference for the shalower sites due to their respective benthic and littoral character. For the same reason *B. rceolaris* seemed to be favored in the more oligohaline, flowing or creek influenced wars (it was more favored in the source of La Ricarda and of Cullera in spring, and its ocurrence was restricted to the month of November in Albufera (as well as in 1981, Oltra : Miracle in press). *B. quadridentatus*, on the other hand, preferred more saline and less urbulent waters; it had a slower rate of increase and grew to high densities inside mnocorrals when Nytal mesh was plugged by benthic algae (resulting in much reduced ow).

Results from a more extensive study of Spanish Mediterranean wetlands showed a disibution of *Brachionus* species corresponding mainly to salinity factors variation (Miacle et al. 1987). However, for coexisting species in the same lagoon also other factors e also very important, especially turbulence or flow, temperature and food resources.

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