

# THE CRUSTACEAN COMMUNITIES OF RIVER TAGUS RESERVOIRS. ZOOPLANKTON STRUCTURE AS RESERVOIR TROPHIC STATE INDICATOR

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## ABSTRACT

Ten reservoirs of the Tagus River Basin were studied during three years to assess their trophic state. Seasonal abundance of zooplankton was followed. Species composition and food web structure were analysed to relate abundance and proportion of certain species or groups of species to reservoir trophic state. Low zooplankton concentration and high water transparency values were associated with high ratio of calanoids to cyclopoids and the presence of large *Daphnia* populations. High *Acanthocyclops robustus* density was associated with large populations of *Bosmina* in the most eutrophic reservoirs.

Key words: *Copidadiaptomus numidicus*, *Thermocyclops dybowskii*, *Acanthocyclops robustus*, Calanoid-Cyclopoid interactions, zooplankton, crustaceans, reservoirs, trophic state index, seasonal dynamics.

## RESUMEN

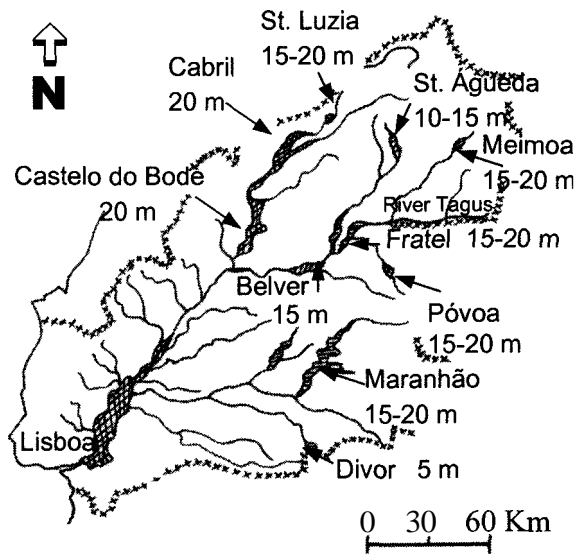
Durante tres años se ha estudiado los cambios estacionales en la abundancia del zooplancton de diez embalses de la cuenca del río Tagus con la finalidad de establecer su estado trófico. Para ello se ha estudiado la composición de especies y la estructura de la cadena trófica. Los resultados obtenidos han permitido relacionar la abundancia de ciertas especies o grupos de especies con el estado trófico de los embalses. Así, la baja concentración de zooplancton y la elevada transparencia del agua están asociados a un cociente calanoides/ciclopídeos elevado y a la presencia de grandes poblaciones de *Daphnia*. Igualmente, en los embalses más eutróficos, una gran densidad de *Acanthocyclops robustus* se asocia a una gran abundancia de *Bosmina*.

Palabras clave: *Copidadiaptomus numidicus*, *Thermocyclops dybowskii*, *Acanthocyclops robustus*, Calanoid-Cyclopoid interactions, zooplankton, crustáceos, embalses, índice de estado trófico, dinámica estacional.

## INTRODUCTION

In Tagus River Basin as well as in the Iberian Peninsula, lakes are virtually nonexistent and reservoirs are the most important water bodies (Armengol, 1980). The studied reservoirs are located in distinct areas and are subjected to different climatological and anthropogenic influences. These influences along with different age result in different reservoir trophic state. The seasonality and nature of zooplankton assemblages may constitute important sources of information to assess reservoir trophic state.

The ratio of calanoid to cyclopoid copepods frequently declines with eutrophication (Gannon & Stemberger, 1978; Hurlbert & Mulla, 1981; Gulati, 1984; Muck & Lampert, 1984; Maier, 1996; Adrian, 1997). Considering the possible interactions between cyclopoids and calanoids, competition is probably dominant among naupliar stages while among copepodid stages competition, predation and cannibalism may be all influential (Soto & Hurlbert, 1991a). Calanoid *nauplii* have been referred to endure starvation more adequately than cyclopoid *nauplii* (Soto & Hurlbert, 1991a, b) and both cala-



**Figure 1.** Reservoir location, and depth of sampling tows. *Situación de los embalses y profundidad de las pescas verticales.*

noid *nauplii* and adults have lower food threshold concentrations than cyclopoids (Santer, 1994; Hansen & Santer, 1995). The abundance of predaceous cyclopoid adults is thus dependent on the survival of herbivorous developmental stages competing with calanoids for edible phytoplankton. Furthermore, when food is scarce, calanoids may reduce phytoplankton availability to rotifers and indirectly reduce cyclopoid prey (Soto & Hurlbert, 1991b). Rotifer species composition and abundance have been considered good indicators of water quality (Gannon & Stemberger, 1978; Pejler, 1983; Karabin, 1985) and Matveeva (1991) considered that the trophic state of a lake may be reflected on the total summer rotifer density.

Our purpose is to investigate the organization and seasonality of zooplankton assemblages during a three year seasonal survey in 10 reservoirs located in the Tagus River Basin. The geographical distribution of species is compared with previous references for Spain (Armengol, 1978, 1980, Margalef *et al.*, 1976, Toja, 1980). Considering that the abundance pattern of species and the food web structure may be altered by eutro-

phication (Schindler 1987; Carpenter *et al.* 1993) part of this study was directed to the relationship between the crustacean type of community and the trophic state of the reservoir. Comparisons with literature are discussed.

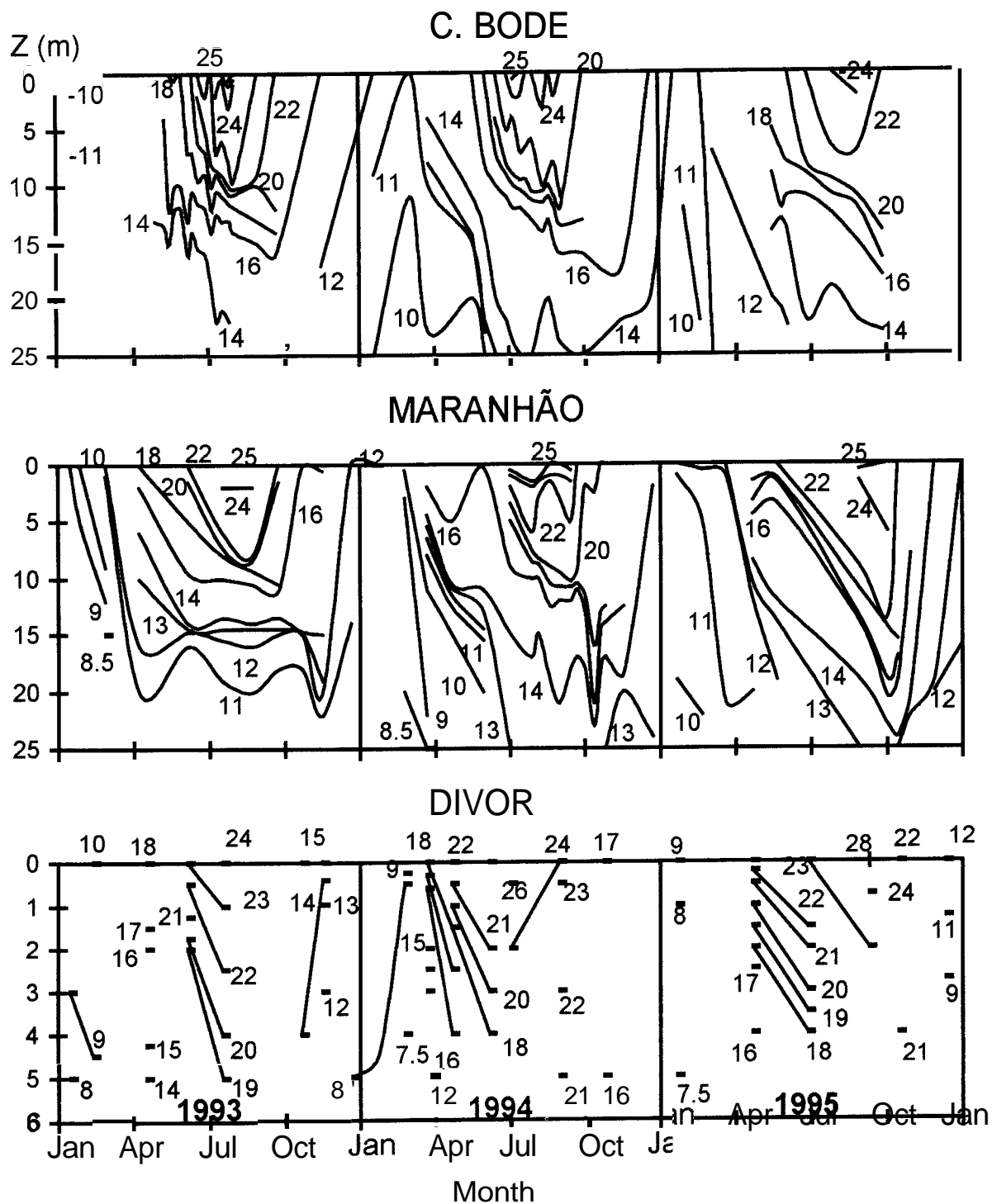
## MATERIAL AND METHODS

### Reservoirs and Environmental data

The reservoirs sampled are located in the Tagus River Basin (Fig. 1). Three of the reservoirs, St. Luzia, Cabril and Castelo do Bode (C. Bode) are an example of chain reservoirs on Zêzere River. These reservoirs, along with Meimoa and St. Agueda (or Marateca) are located at the North side of Tagus River and Divor, Maranhão and Póvoa are located on the southern side. Fratel and Belver are two reservoirs resulting from dams on Tagus River.

Except for Divor, Belver and Fratel, all reservoirs are warm monomictic with stable thermal stratification from May-June until the end of September. In 1994 and 1995 thermal stratification was in progress after mid-April due to higher air temperatures in the first months of these years relatively to 1993 (Fig. 2). The warmest year was 1995 with an annual average of 16.2 °C and the highest monthly average temperatures with an exception for September (Meteorological Institute, Portugal). Divor is a shallow reservoir (maximum depth 8 m) in an open landscape. In Divor the weak thermal gradient is easily broken by the wind and in Belver and Fratel thermal stratification can only be established in periods of small river flow.

The reservoirs north to the river Tagus are characterised by soft waters, being the minimum value of 18.5 mg CO<sub>3</sub><sup>2-</sup>/l recorded for Meimoa Reservoir in the summer of 1995 and the maximum of 33.8 mg CO<sub>3</sub><sup>2-</sup>/l for C. Bode in the summer of 1994. The reservoirs located on Tagus River had soft to moderately soft waters (40 to 120 mg CO<sub>3</sub><sup>2-</sup>/l) and the three reservoirs south to Tagus had hard waters (minimum of 158.5 mg CO<sub>3</sub><sup>2-</sup>/l for Maranhão).



**Figure 2.** Thermal stratification in deep reservoirs to the North of Tagus River (C. Bode), South of the Tagus River (Maranhão) and in a shallow reservoir (Divor). *Estratificación térmica en los embalses profundos al Norte del río Tagus (C. Bode), al Sur (Maranhão) y en un embalse somero (Divor).*

Transparency values were usually high during winter and low at the beginning of summer. Exceptions occurred when the sampling date was preceded by short periods of rainfall, such as during the winter of 1993 when silt was washed to the reservoirs. The highest transparency values were measured at S. Luzia, Cabril, C. Bode and Meimoa reservoirs. However, the seasonal values for Meimoa decreased gradually after the summer of 1994. The lowest transparency values were recorded for the reservoirs south to Tagus River and Agueda Reservoir. All reservoirs showed a tendency for eutrophication during 1994. The lack of rain and higher air temperatures accounted for a general decrease in the water level of the reservoirs, excluding Belver and Fratel. Years 1993, 1994 and 1995 were dry and the reservoirs exhibited the minimum water level in the summer of 1995 (Meteorological Institute, Portugal). The situation was particularly acute in the reservoirs south to Tagus River and was altered only after October 1995.

### Sampling

On each sampling date, two vertical hauls (20 m long or maximum reservoir depth) were taken with a Wisconsin type net of 80 µm mesh size at a central sampling station. Samples were taken in December or January (winter), March (spring), July or August (summer) and October (autumn) during 1993, 1994 and 1995. In order to record the depth distribution of each crustacean population during summer, samples were collected with van Dorn bottles at 2 m intervals. Average chlorophyll-a (CHLa) concentrations were calculated from samples taken at 2 m intervals from surface until 15 m depth or maximum reservoir depth. CHLa was extracted in acetone. Animals were anaesthetised with carbonated water and preserved in sugar saturated formaldehyde (2% v/v). Copepodid stage five and adult copepods (C V and C VI, respectively) and all stages of *Cyclops* spp. and *Macrocyclus albidus* were counted in the whole samples from vertical hauls, whereas copepodid stages one to four (C I to C IV) and *nauplii* of each species were counted in subsam-

ples. When the density of cladocerans was high, two subsamples of 1/5 of the total volume were analysed and rotifers were counted in subsamples of 1/10 or 1/20 of the total sample volume. Since rotifers were collected with a net of 80 µm mesh size, when a finer mesh is appropriate (25-50 µm mesh size, Nogrady, 1993), all rotifer densities should be considered with caution. Some of the *Daphnia* species, henceforth referred as *Daphnia hyalina*, belong to the *Daphnia hyalina-galeata* complex (Flossner & Kraus, 1986) or were later identified as *D. longispina* or close to *D. galeatu* (Schwenk et al., 1998). Copepods were identified according to Kiefer (1978) and Dussart & Fernando (1990).

### Numerical procedures, indices and statistics

All calculations were based on two replicate samples from each reservoir. The method applied to estimate water hardness followed Standard Methods (1992) and values were scaled according to Sawyer (1960 in Standard Methods, 1992). In order to relate zooplankton assemblages to reservoir trophic state, Karabin (1985) index was applied to total summer rotifer density and the ratio of calanoids to cyclopoids was calculated. To estimate the relative proportion of crustacean

**Table 1.** Classification of crustacean species according to nature and mode of food collection (see text for references). *Clasificación de los crustáceos de acuerdo con su estrategia alimentaria (veuseel texto para las referencias).*

COPEPODS	CLADOCERANS
I. CARNIVOROUS <i>Acanthocyclops robustus</i> <i>Cyclops strennus</i> <i>Cyclops vicinus</i> <i>Macrocyclus albidus</i>	IV. MICROFILTERS <i>Diaphanosoma brachyurum</i> <i>Ceriodaphnia</i> sp. <i>Bosmina longirostris</i>
II. FILTER FEEDING <i>Copidodiptomus numidicus</i>	V. MACROFILTERS <i>Daphnia pulex</i> <i>Daphnia hyalina</i> x <i>galeata</i> <i>Daphnia parvula</i> <i>Daphnia cucullata</i>
III. HERBIVOROUS NON-FILTRATING <i>Thermocyclops dybowskii</i> <i>Tropocyclops prasinus</i>	

groups with particular feeding requirements to total crustacean population, species were grouped according to the nature and collection of food as classified by Margalef (1953), Fryer (1957), Brooks and Dodson (1965) and Hutchinson (1967) (Table 1).

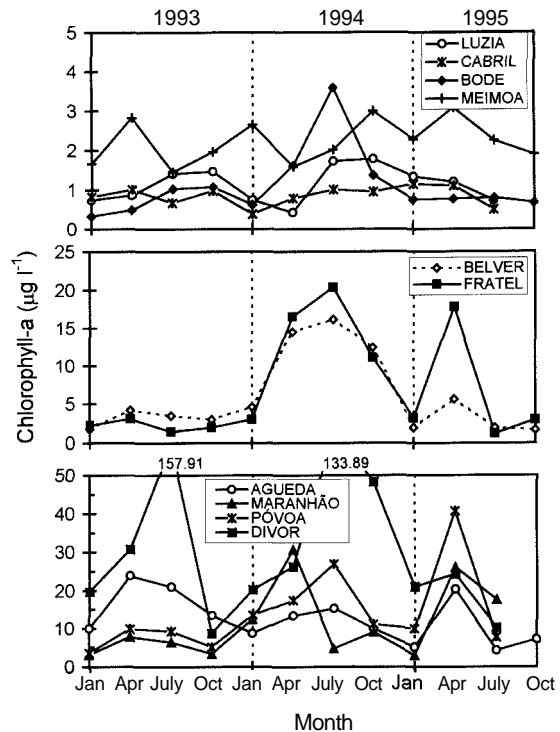
Spearman's correlation coefficient was used to measure the degree of association: (i) among reservoirs using chlorophyll-a (CHLa) values; (ii) between rotifer densities and CHLa; (iii) between rotifer densities and proportion of crustacean classes; (iv) between the proportion of classes II to IV and CHLa; (v) among proportion of classes II to V, also considering the proportion of class I to be constant and (vi) between clutch size (CLS) of *Acanthocyclops robustus* and CHLa. Secchi disk transparency values were regressed on CHLa values to investigate the dependence of reservoir transparency on the amount of CHLa. Appropriate probability values were adjusted for the number of simultaneous tests according to the sequential Bonferroni technique (Rice, 1989).

Carlson's (1977) trophic state index (TSI) was applied to chlorophyll (CHLa) values using the formula:

$$TSI(CHLa) = 10 * \left( 6 - \frac{2.04 - 0.68 \ln(CHLa)}{\ln 2} \right)$$

TSI applied to Secchi disk transparency data was not calculated since reservoirs received, periodically, high amounts of non-algal particulate organic matter (*pers. obs.*). Moreover, in some reservoirs turbidity of the water may be controlled by light absorbing compounds other than chlorophyll (Caramujo & Boavida, 1998).

Cluster analysis was performed on the full data set of crustacean taxa abundances comprising each season sets in the total number of reservoirs, using the Manhattan dissimilarity measure and Ward's sum of squares clustering algorithm. The same method of cluster analysis was applied to CHLa concentration, density of *A. robustus* and species abundance. Data were  $\log_{10}(n+1)$  transformed prior to analyses. The STATISTICA pattern analyses package (1995) was used.



**Figure 3.** Average Chlorophyll-a values in reservoirs with transparency values higher than 4 m (St. Luzia, Cabril, C. Bode Meimoa); transparency values between 2 and 4 m (Belver, Fratel) and in reservoirs with transparency values lower than 2 m (St. Águeda, Maranhão, Póvoa, Divor). *Media de las concentraciones de clorofila a en embalses con transparencias mayores a 4 m (St. Luzia, Cabril, C. Bode); transparencias entre 2 y 4 m (Belver, Fratel) y en embalses con transparencias menores a 2 m (St. Águeda, Maranhão, Póvoa, Divor).*

## RESULTS

### Chlorophyll

For the year of 1993 most reservoirs with average transparency values below 2 m showed maxima in chlorophyll-a (CHLa) average values during spring (Fig. 3). In 1994, except for Maranhão reservoir, high values of CHLa were registered mainly during the summer when blooms of algae developed. Diatom blooms were observed in S. Luzia, Cabril, C. Bode and Meimoa and blooms of *Aphanizomenon flos-aquae* and *Microcystis aeruginosa* were observed in the other reservoirs.

**Table 2.** Trophic state index (TSI, from CHLa values) of the reservoirs belonging to the Tagus River system. *Índices de estado trófico (TSI según las concentraciones de clorofila) de los embalses pertenecientes al sistema del río Tagus.*

Reservoir	1993	1994	1995
Belver	Mesotrophic	Meso-Eutrophic	Mesotrophic
Cabril	Oligotrophic	Oligotrophic	Oligotrophic
C. Bode	Oligotrophic	Mesotrophic	Oligotrophic
Divor	Eutrophic	Eutrophic	Meso-Eutrophic
Fratel	Mesotrophic	Eutrophic	Meso-Eutrophic
Maranhão	Meso-Eutrophic	Meso-Eutrophic	Mesotrophic
Meimoa	Mesotrophic	Mesotrophic	Mesotrophic
Póvoa	Meso-Eutrophic	Meso-Eutrophic	Eutrophic
St. Agueda	Eutrophic	Meso-Eutrophic	Mesotrophic
St. Luzia	Oligotrophic	Oligotrophic	Oligotrophic

In 1995 CHLa values peaked in spring and the species which formed blooms in previous summers were observed in small quantities with the exception of Meimoa. The seasonal fluctuations in CHLa values were not correlated among reservoirs (highest  $r = 0.590$  for C. Bode  $\times$  Divor; d.f.= 11;  $p = 0.057$ ) and transparency values were not dependent on CHLa values (highest adjusted  $r^2 = 0.153$  for C. Bode with  $F_{1,10} = 2.99$ ,  $p = 0.12$ ). CHLa was generally in higher concentrations at 5 to 10 m depth in the clear water reservoirs and at 3 to 5 m depth in more turbid reservoirs (transparency values of less than 2 m).

Carlson's trophic state index (TSI) calculated from summer CHLa values allowed the classification of Cabril and St. Luzia as oligotrophic reservoirs and C. Bode as mesotrophic in 1993 and 1994 and oligotrophic in 1995 (Table 2). All other reservoirs were either mesotrophic or eutrophic.

### Zooplankton Abundance Patterns

The largest zooplankton densities were recorded in the southern reservoirs. Maximum was recorded in Divor where densities over 1000 ind./l were observed during the summers. Minima abundances were observed in St. Luzia, Cabril, C. Bode and Meimoa reservoirs.

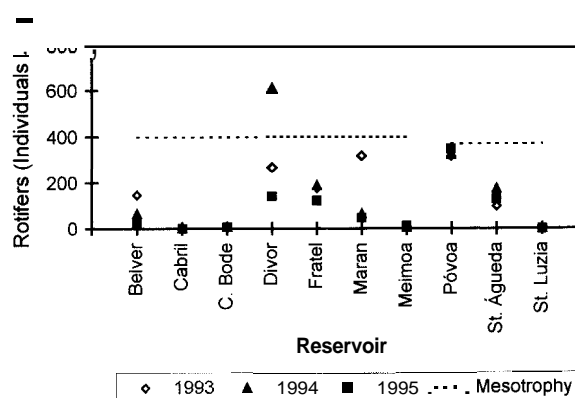
### Rotifers

In all reservoirs rotifer maxima were recorded during summer. St. Luzia had the lowest rotifer

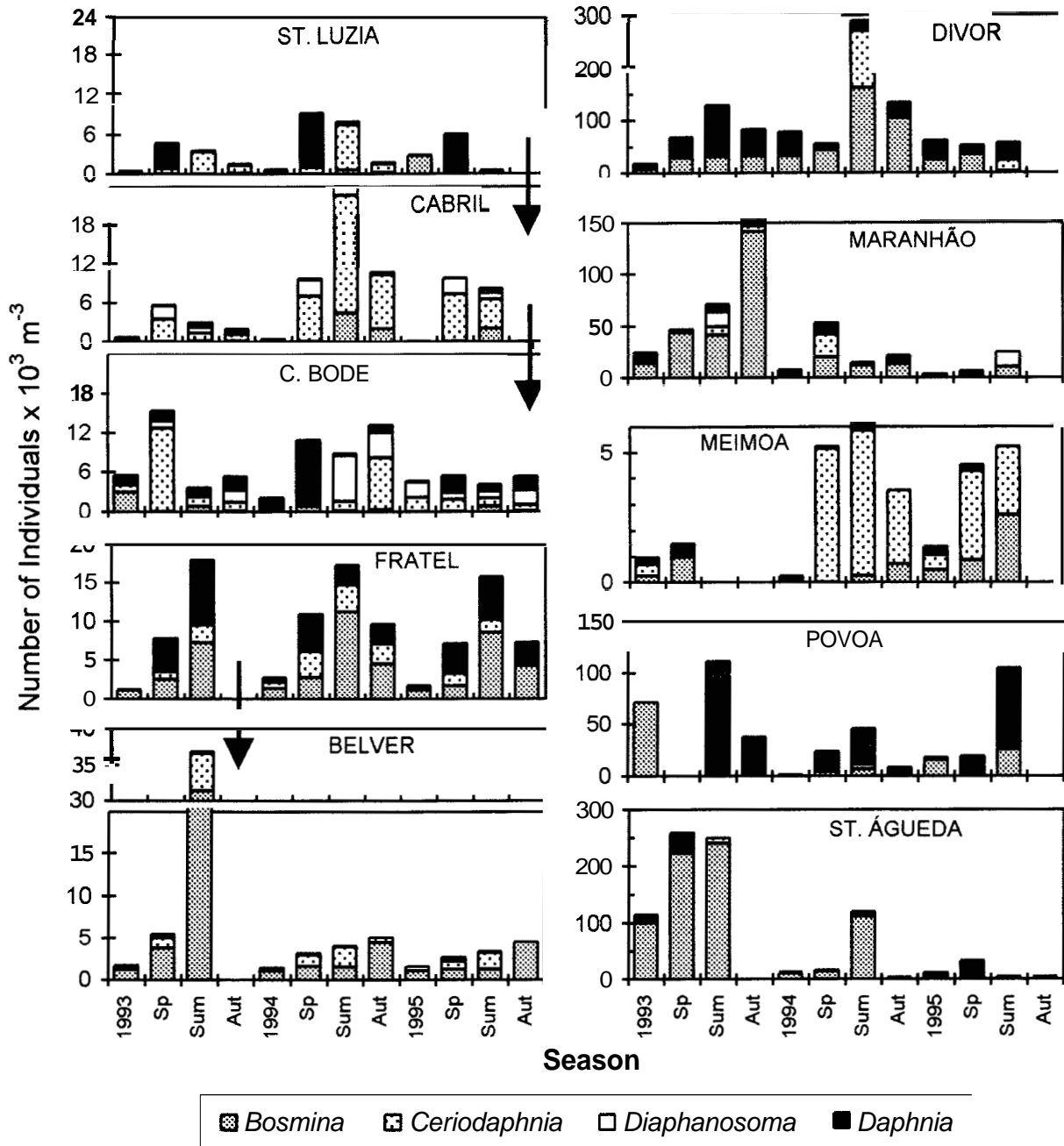
density (minimum of 88 individuals/m<sup>3</sup>) and the highest values were recorded in Divor and Póvoa ( $613 \times 10^3$  and  $352 \times 10^3$  ind./m<sup>3</sup>, respectively). Rotifer summer density indicated Divor as a mesotrophic reservoir (Fig. 4). Both in Póvoa and Divor reservoirs, rotifera abundances were correlated to CHLa (lowest value for Divor with  $r = 0.738$ ; d.f.= 8;  $p = 0.04$ ).

### Cladocerans

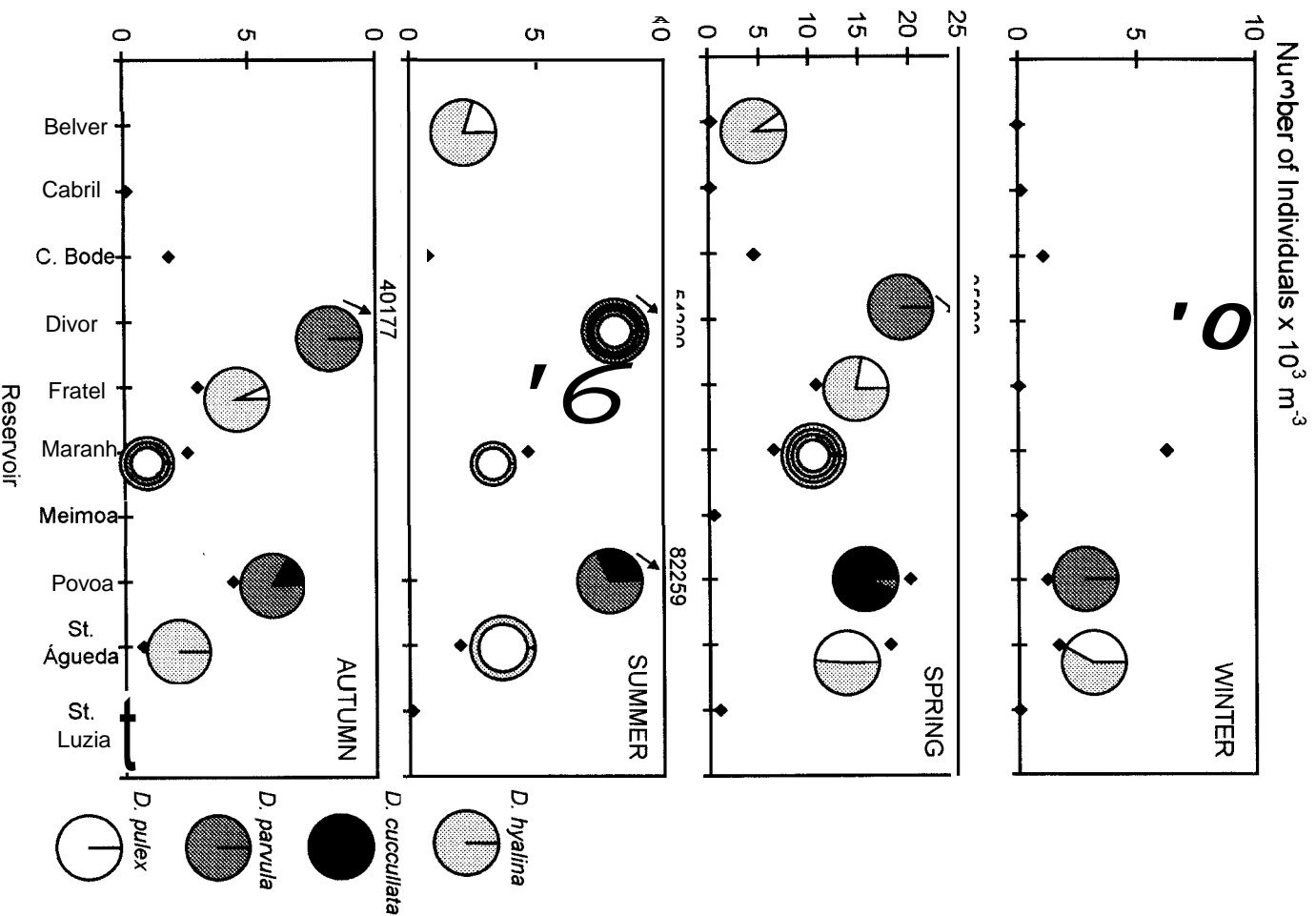
Daphnia and Diaphanosoma dominated the cladoceran community in reservoirs of larger transparency values (more oligotrophic) while *Bosmina* dominated in the other reservoirs (Fig. 5). Both *Daphnia hyalina* and *Diaphanosoma bra-*



**Figure 4.** Summer rotifer densities during the sampling years. Values above 400 ind/l indicate mesotrophy (Karabin, 1985). *Densidad de rotíferos en verano durante los años muestreados. Valores superiores a 400 ind/l indican mesotrofia (Karabin 1985)*



**Figure 5.** Seasonal cladoceran densities in each reservoir. Winter from each year is represented by the year cardinal number, spring as "Sp", summer as "Sum" and autumn as "Aut". Arrows indicate water flow direction in chain reservoirs. *Densidades estacionales de cladóceros en cada embalse. El invierno se representa por el número del año, primavera como "Sp", verano como "Sum" y otoño como "Aut". Las flechas indican la dirección del agua en la cadena de embalses.*



**Figure 6.** *Daphnia* spp. densities in each reservoir (black diamonds) and specific composition of *Daphnia* populations (pies). Rings indicate annual variation of species composition. Innermost ring represents 1993 and the outermost, 1995. When *Daphnia hyalina* is the only species present, the populations are indicated only by black diamonds. *Densidades de Daphnia spp. en cada embalse (Símbolo diamantes negros) y composición específica de las poblaciones de Daphnia (diagrama en pastel).* Los anillos indican la variabilidad anual en la composición de especies. El círculo interno representa 1993 y el externo, 1995. Cuando *Daphnia hyalina* es la única especie presente, las poblaciones se indican solo por diamantes negros.



*chyurum* were not observed in Divor and Póvoa reservoirs, and *Diaphanosoma* was absent from Meimoa reservoir. *Daphnia hyalina* exhibited larger populations during spring while *Diaphanosoma* had larger summer populations. In Maranhão, the inverse relationship between *Daphnia* and *Diaphanosoma* abundances reached a maximum when *Daphnia* disappeared altogether during the summers of 1994 and 1995 only to recover in autumn of 1995. Divor and Maranhão reservoirs presented seasonal and annual differences in *Daphnia* species composition. *D. pawula* was present in Maranhão during the spring of 1993, being replaced during summer by *D. hyalina*, and was the dominating *Daphnia* species in autumn of the same year (Fig. 6). In Divor the largest population of *Daphnia* belonged to the species *D. pawula* and in the winter of 1993 *D. cucullata* was represented by a small population. In the summer of 1994, *D. cucullata* was represented by a large, dominating population that disappeared afterwards. In Póvoa *D. pawula* and *D. cucullata* alternated according to the season. *D. pawula* was the only species present during the winter while *D. cucullata* was clearly dominating during spring and was subsequently

replaced by *D. parvula* during summer and autumn.

*D. pulex* was present in Agueda, Belver and Fratel reservoirs (Fig. 6). The largest populations were recorded in Agueda during winter and spring. In autumn, small populations of *D. hyalina* were present. During the summer, both *Daphnia* populations were suppressed in St. Agueda in 1993 and 1994, while in 1995 a small population of *D. hyalina* was present. In Belver and Fratel *D. pulex* started to develop in spring and increased in numbers during the summer, followed, in Fratel, by *D. hyalina* population that dominated in autumn (Fig. 6).

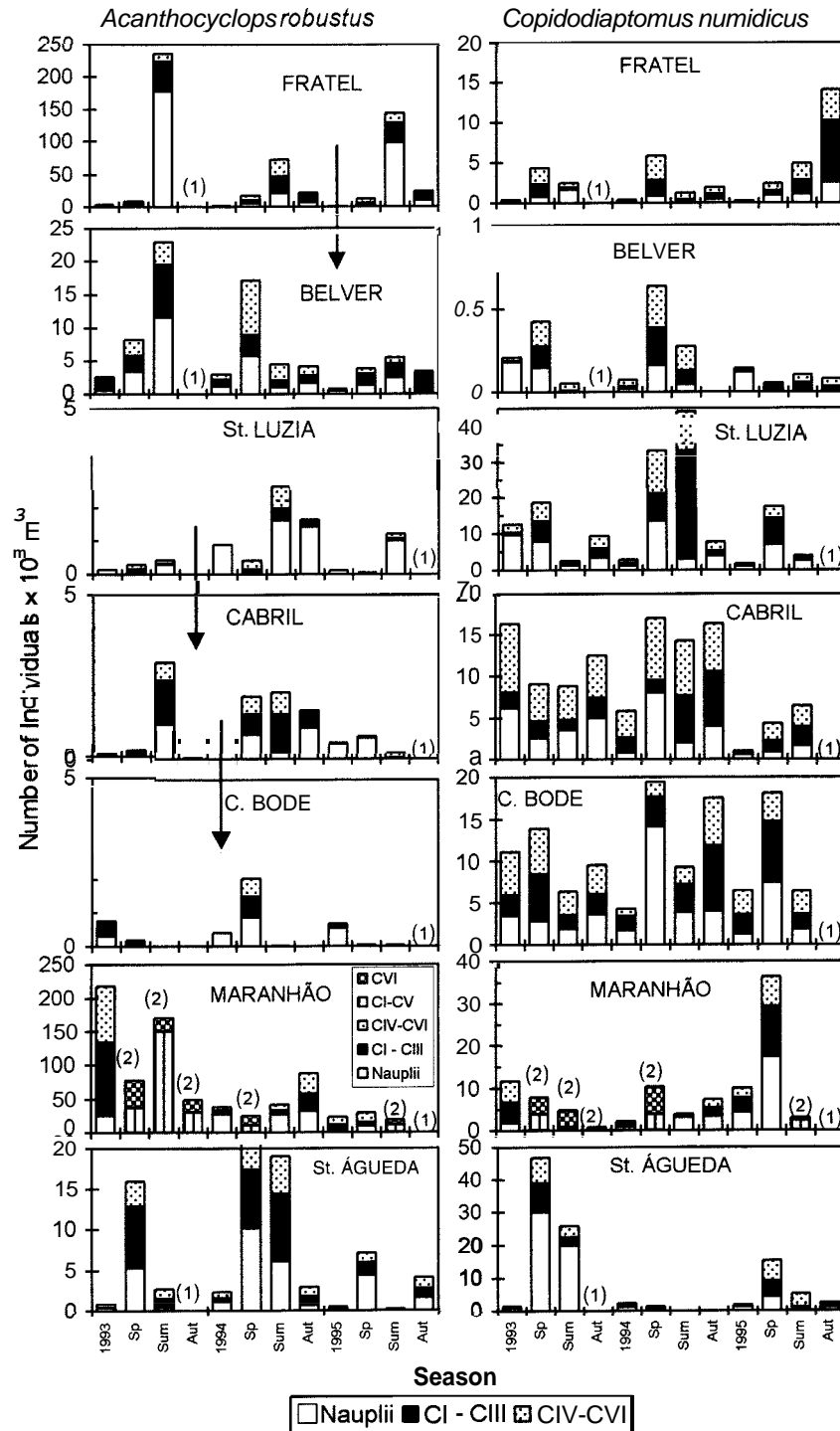
#### Copepods

A total of 9 copepod species was recorded for the reservoirs of Tagus River Basin during the 3 year survey (Table 3).

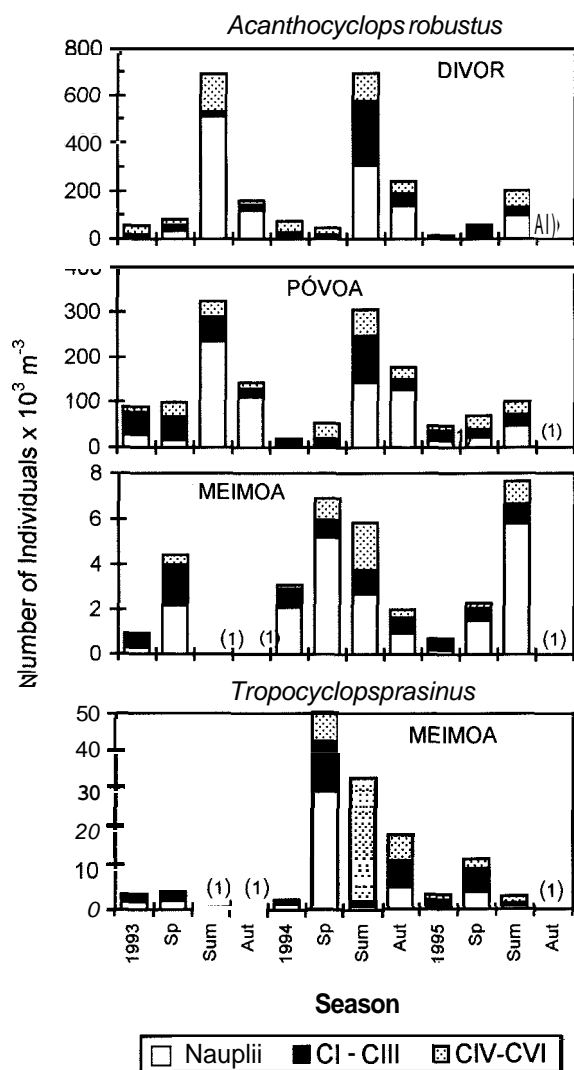
*Copidodiaptomus numidicus* dominated the communities where transparency values were larger, usually accompanied by *Daphnia* (either from *hyalina* × *galeata* group or *pulex* group) and *Ceriodaphnia* sp. (Fig. 7). *C. numidicus* was absent in Póvoa, Meimoa and Divor and was represented by low number of individuals in Fra-

**Table 3.** Species of copepods present in the reservoirs of Tagus River Basin. Reservoirs are indicated by the first two letters of their names. Copepod species that occurred only occasionally are marked with an asterisk (\*). *Especies de copépodos presentes en los embalses de la cuenca del río Tagus. Los embalses se indican por las dos primeras letras de su nombre. Las especies de copépodos que solo aparecen ocasionalmente están marcadas con un asterisco (\*).*

Copepoda	Ág	Be	Ca	Bo	Div	Fra	Ma	Me	Pó	Lu
<b>Calanoida</b>										
<i>Copidodiaptomus numidicus</i>	+	+	+	+		+	+			+
<b>Cyclopoida</b>										
<i>Acanthocyclops robustus</i>	+	+	+	+	+	+	+	+	+	+
<i>Cyclops strenuus</i>			+	+						
<i>Cyclops vicinus</i>		+				+				
<i>Macrocyclus albidus</i>								+		+
<i>Thermocyclops dybowskii</i>		+	+	+		+	+			+
<i>Tropocyclops prasinus</i>								+		
<i>Paracyclops fimbriatus</i> *		+				+				
<i>Eucyclops serrulatus</i> *		+								
<b>Harpacticoida</b>										
<i>Canthocamptus</i> sp. *				+						



**Figure 7.** Densities of main copepod populations in reservoirs where the calanoid *C. numidicus* was recorded. See legend of figure 5 for further details. *Densidades de las principales poblaciones de copépodos en embalses donde se capturó el calanóide C. numidicus.* (Ver leyenda de la figura 5 para más detalles).



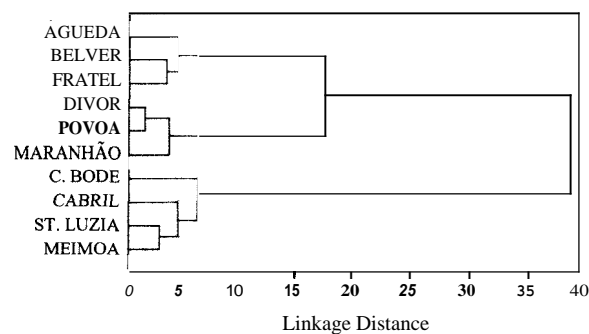
**Figure 8.** Cyclopoid densities in reservoirs without calanoid populations. *Densidades de ciclopoides en embalses sin poblaciones de calanoides.*

tel and Belver (Fig. 7). *Thermocyclops dybowskii* occurred mainly during the warmest seasons and during the winter was absent or represented mainly by adults and nauplii. *7: dybowskii* never co-occurred with *Tropocyclops prasinus* (Meimoa reservoir) and was never observed in Águeda, Divor and Póvoa reservoirs. *A. robustus* was the dominant copepod in the zooplankton communities of the most eutrophic reservoirs. Population peaks were observed during spring or sum-

mer (Fig. 7 and 8). In the reservoirs of lower CHLa concentration *A. robustus* almost disappeared during the coolest months. Considering *A. robustus* abundances at all seasons, three groups of reservoirs were obtained (Fig. 9): reservoirs (i) with *A. robustus* at low densities (Meimoa, St. Luzia, Cabril and C. Bode); (ii) with *A. robustus* intermediate densities (Águeda, Belver and Fratel) and (iii) with high densities of the cyclopoid (Divor, Póvoa and Maranhão). *Macrocyclus albidus* was present in St. Luzia and Meimoa. The largest population was recorded in Meimoa where 1390 ind./m<sup>3</sup> were found in spring. During the winter, only earlier nauplii and later copepodid stages could be observed. The populations always peaked during spring and autumn. *Cyclops strenuus* was observed in small numbers in C. Bode and Cabril and *Cyclops vicinus* was sporadically observed in Fratel and Belver.

Copepodid stages of the calanoid *C. numidicus* exceeded cyclopoid copepodid stages in reservoirs with higher transparency (Fig. 10). A decrease in the proportion of calanoids to cyclopoids was observed in summer samples when *7: dybowskii* was present in the reservoirs. The proportion of calanoid nauplii to cyclopoid nauplii was lower than the relation evidenced by copepodid stages.

Relatively to the vertical distribution of species during the summers, only in Cabril reservoir a clear decrease in mean population depth of *Daphnia* and later copepodid stages of all cope-



**Figure 9.** Dendrogram depicting groups of reservoirs according to *A. robustus* densities at all seasons. *Dendrograma mostrando los grupos de embalses según las densidades de A. robustus en todas las estaciones.*

pod populations during summer was observed (except for *nauplii*, only 10% of total zooplankton in the upper 10 m). Later copepodid stages of *T. dybowskii* were always observed below 10 m and this vertical distribution was particularly clear in Maranhão where 90% of all copepodid stages could be found between 8 and 20 m in summer samples. All other species were observed to dwell in the first 10 m of the reservoirs with occasional population peaks between 5 and 7 m depth. In shallow reservoirs and reservoirs without thermal stratification the populations had a roughly even distribution among depths.

### Zooplankton communities

In order to reveal the structure of zooplankton communities the various crustacean species were grouped according to Table 1. We have therefore distinguished carnivores from herbivores and, within this last class, copepods were separated from cladocerans. Carnivorous copepods dominated in the more eutrophic reservoirs and herbivorous copepods dominated the communities of the least eutrophic reservoirs (Fig. 11). Microfiltering cladocerans generally dominated over macrofilter cladocerans in more eutrophic reservoirs. However, population peaks for the latter were recorded during spring.

Except for St. Luzia, none of the classes varied with CHLa in a significant way. In St. Luzia the abundance of class IV was significantly correlated to CHLa ( $r = 0.742$ ; d.f.= 11;  $p < 0.05$ ) although this significance disappeared when the predator density (class I) was held constant ( $r = 0.417$ ; d.f.= 8;  $p > 0.05$ ). The importance of predators is further emphasized when the pair of classes II and IV and the pair of classes IV and V were only significantly correlated at constant predator density. In C. Bode and Cabril cyclopid predators had a reduced influence on the other zooplankton classes (Table 4) although the significant correlation between classes II and IV was lost when predator density was controlled. In Maranhão reservoir the abundance of class I was inversely correlated to the abundance of class 11. In Belver, Fratel and Agueda a similar trend was recorded.

In Divor, rotifer abundances were correlated to class V abundances although that correlation became non-significant at constant predator-copepod densities (Table 4). Copepod predators were significantly correlated to class IV and the relation between macrofiltering and microfiltering cladocerans was only disclosed when the abundance of predator copepods was controlled. *A. robustus* CLS was correlated to CHLa ( $r = 0.757$ ; d.f.= 7;  $p = 0.05$ ) and this correlation was further

**Table 4.** Spearman's correlation coefficients and partial correlation coefficients between trophic classes of crustaceans in the reservoirs. \* indicates significant  $p \leq 0.008$  adjusted for the number of simultaneous tests according to the sequential Bonferroni technique (Rice, 1989). (see Table 1 for information on trophic classes). *Coefficientes de correlación de Spearman y de correlación parcial entre grupos tróficos de crustáceos. \*indica significativa para  $p \leq 0.008$  ajustado al número de tests simultáneos de acuerdo con la técnica secuencial de Bonferroni (Rice, 1989). (ver Tabla 1 para información sobre grupos tróficos de crustáceos).*

	Spearman's correlation coefficient. df = 11	Control for Group I. df = 8
St. Luzia Classes II x IV	- 0.583	- 0.945 *
C. Bode Classes II x III	- 0.946 *	- 0.904 *
Maranhão Classes I x II	- 0.886 *	
Divor Rotifera x Class V	- 0.833 *	- 0.747
Classes I x IV	- 0.891 *	
Classes IV x V	0.236	- 1.000

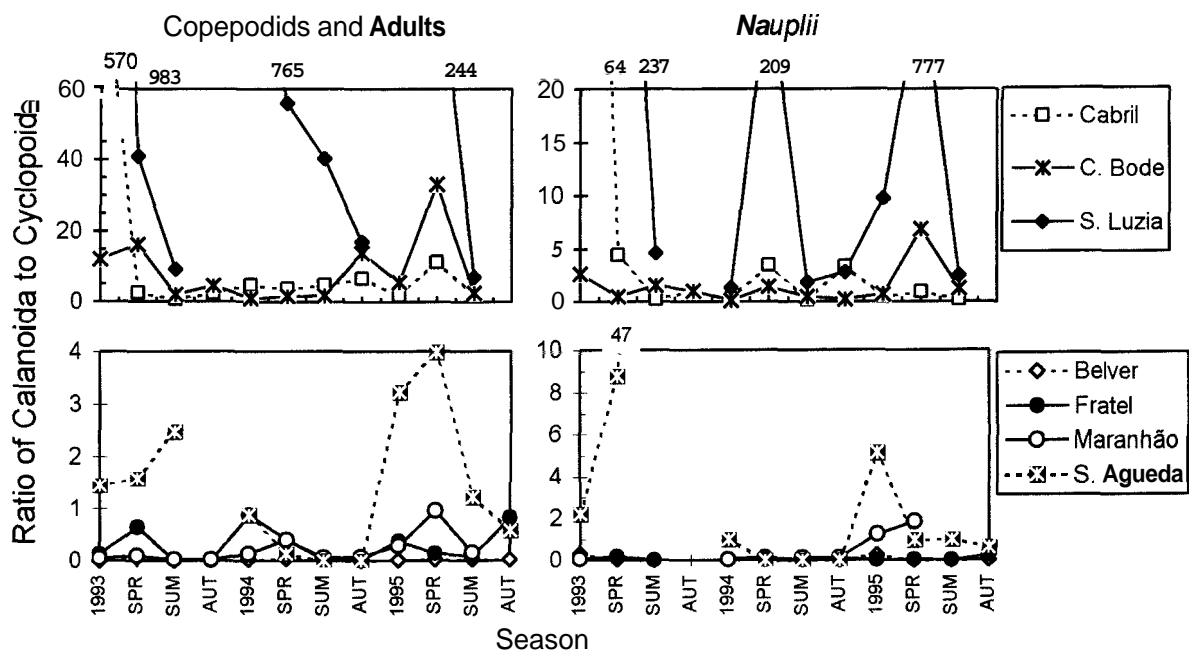
enhanced when the total amount of eggs in the population (i.e. CLS x Ovigerous Females,  $r = 0.984$ ;  $df = 7$ ;  $p < 0.01$ ) was considered.

Considering the zooplankton classes I, II, III, IV and V at all seasons, three groups of reservoirs were obtained: (i) Cabril, C. Bode and St. Luzia; (ii) Belver, Fratel, Maranhão, Meimoa and St. Agueda and (iii) Divor and Póvoa, in which the dominant copepod groups were respectively (i) herbivores/detritivores; (ii) carnivores/detritivores and (iii) carnivores. The variation of species densities at each season allowed grouping of the reservoirs (Fig. 12). In winter two main groups were formed. Within the first group, Fratel, Maranhão and St. Agueda were farther from Cabril, C. Bode and St. Luzia. Meimoa was the reservoir at a greatest distance from all the others. In spring, Meimoa was grouped with Cabril, C. Bode and St. Luzia. A distinct second group was formed by Belver, Cabril (1994), C. Bode (1994), Fratel, Maranhão and St. Agueda. Divor and Póvoa made a separate group. In summer, Divor

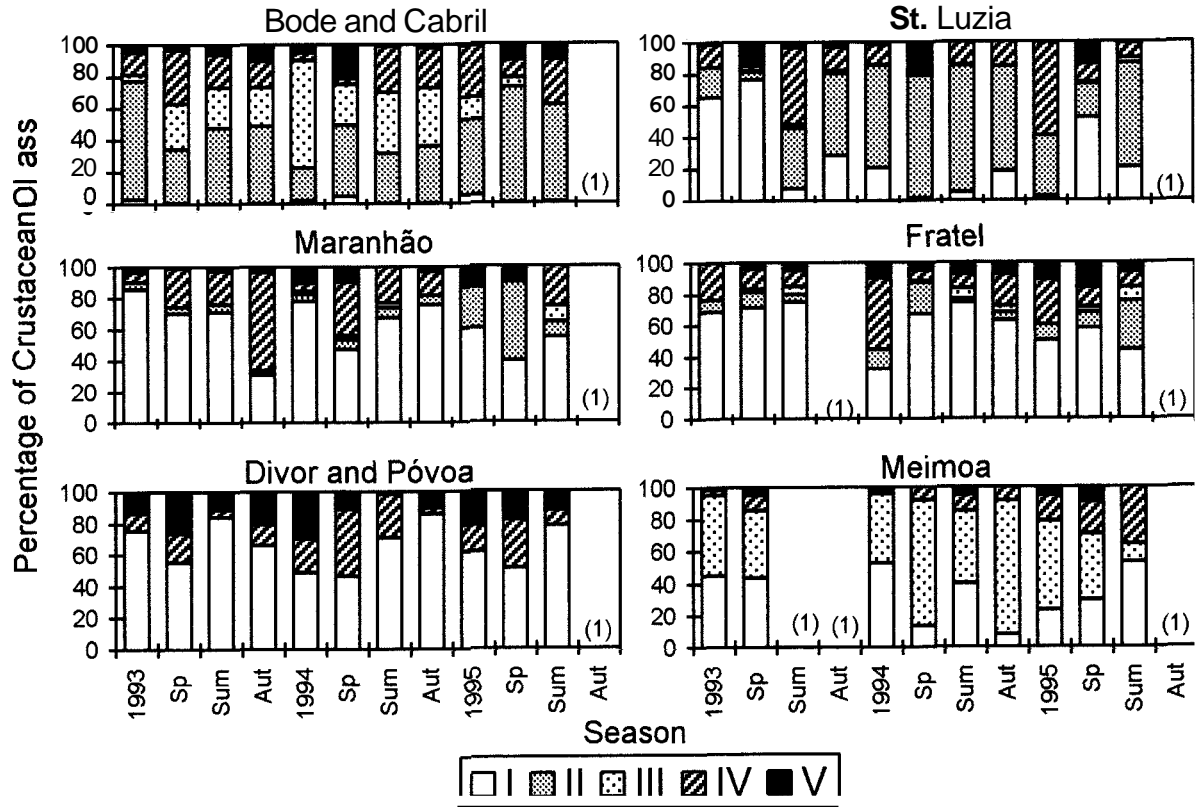
and Póvoa remained closely linked. The other reservoirs were not clearly grouped although Cabril and C. Bode showed a higher connection and Meimoa was placed at a greater distance from these reservoirs. In autumn, Divor and Póvoa remained at a low distance from each other and Cabril, C. Bode, St. Luzia and Meimoa formed a group distinct from Belver, Fratel, Maranhão, Meimoa (1994) and St. Agueda.

## DISCUSSION

The classification of reservoirs according to TSI calculated from CHLa data allowed grouping of the reservoirs as (i) mainly oligotrophic: Cabril, C. Bode and St. Luzia; (ii) mesotrophic: Meimoa; (iii) Mesotrophic to Eutrophic: Belver, Fratel, Maranhão and St. Agueda and (iv) mainly eutrophic: Divor and Póvoa. In 1994, a general increase in CHLa, and in rotifera and cladoceran populations could be observed in the reservoirs.



**Figure 10.** Ratio of calanoids to cyclopoids estimated for the reservoirs at each season. Note the different scales on YY axes. *Relación de calanoides a ciclópodos estimada para cada estación y embalse. Observe que hay diferentes escalas del eje Y.*



**Figure 11.** Proportion of each crustacean class in reservoirs where Class II was the dominant (C. Bode, Cabril, St. Luzia); where Class I dominated and Class II was represented (Maranhão, Fratel) or absent (Divor, Póvoa) and where Class III dominated (Meimoa). *Proporción de cada clase de crustáceos en los embalses donde la Clase II era dominante (C. Bode, Cabril, St. Luzia), en los que la Clase I dominaba y la Clase II estaba representada (Maranhão, Fratel) o ausente (Divor, Póvoa) y donde la Clase III dominaba (Meimoa).*

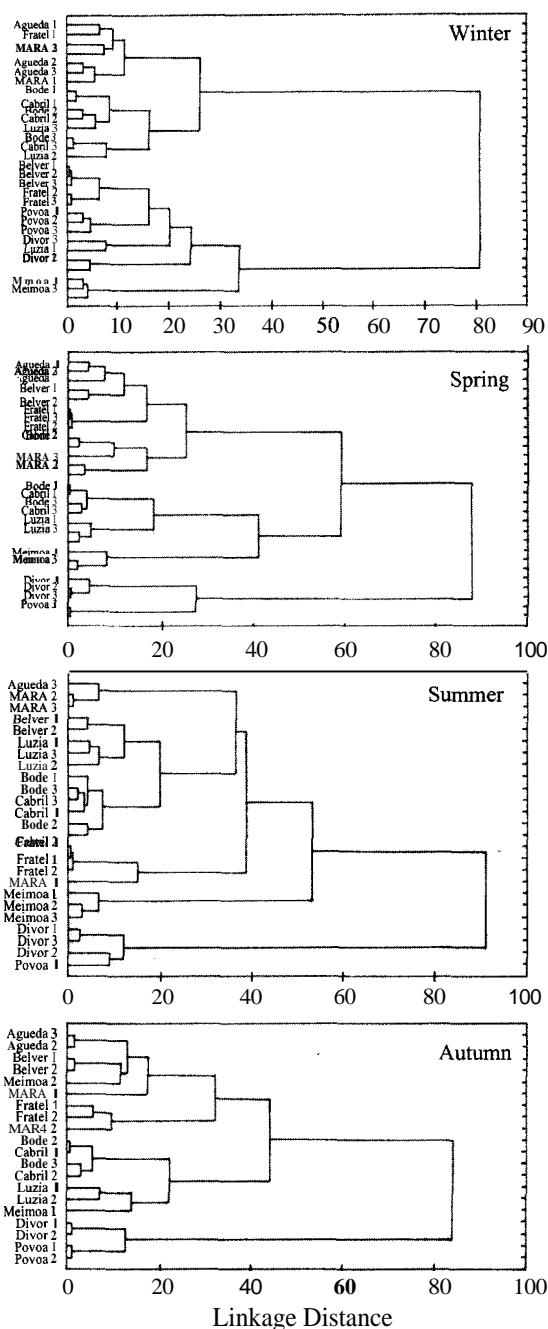
High temperatures, lack of rain and water drainage for human use could all have contributed for this increase in trophic state. This reservoir classification agrees with Marques & Boavida (1997) although these authors in 1991, 1992 and 1993 classified Divor as mesotrophic (so as Cabril) and Fratel as eutrophic taking both chlorophyll and total phosphorus into consideration. However, their samples were mainly collected during summer (com. pers.) and the effect of low water level may have been of importance, especially in the case of Fratel located on Tagus River.

Divor was classified as one of the most eutrophic reservoirs which was confirmed by the highest rotifer density recorded. Karabin (1985) index was, however, inappropriate to ascribe trophic state to the other reservoirs where lower densities

of rotifers were recorded. However, the large mesh size (80  $\mu\text{m}$ ) of the net used to collect the specimens may have prevented the identification of some reservoirs (e.g. Póvoa) as eutrophic by Karabin's (1985) method. In late 70's Cabril, C. Bode and St. Luzia were considered oligotrophic (Cabeçadas *et al.*, 1980; Monteiro, 1982; Oliveira 1982). However, Cabril and C. Bode in early 80's were considered as be approaching mesotrophy (Fernandes, 1985a,b). Belver and Fratel were considered mesotrophic although plankton was recognized as unstable because of river flow (Monteiro, 1977; Oliveira, 1977). Maranhão was considered to be at the edge of eutrophy while Divor and Póvoa were already eutrophic (Monteiro, 1984; Oliveira, 1984). When reservoirs were grouped according to species compo-

sition at each season, groups followed the trend of TSI grouping. However, these results should always be analysed carefully since some communities may be under the influence of peculiar factors as seemed to be the case of Meimoa. The lack of diaptomids in this reservoir apparently was the factor responsible for the placement of this mesotrophic reservoir closer to the most eutrophic reservoirs in winter.

*Acanthocyclops vernalis* is generally associated with *Copidodiaptomus steueri* and *Daphnia hyalina* in Spanish reservoirs (Margalef *et al.*, 1976). A similar association was found in the reservoirs studied although *Acanthocyclops robustus* and *Copidodiaptomus numidicus* replaced *A. vernalis* and *C. steueri*, respectively. Several authors (Cabeçadas *et al.*, 1980; Oliveira, 1982; Monteiro, 1984, 1988; Fernandes, 1985a, b) have alternatively classified *Copidodiaptomus* species as *steueri* and *numidicus* and *Acanthocyclops* species as *robustus* and *vernal*. Nevertheless, the calanoid and the cyclopoid have been reported to be associated. In clear water reservoirs, *C. numidicus* clearly dominated while *A. robustus* was represented by small populations or was replaced by *Cyclops strenuus* (Cabril and C. Bode) or *Macrocyclus albidus* (Meimoa and St. Luzia). Calanoids were thus favoured over cyclopoids probably as a result of edible phytoplankton scarcity (Soto & Hurlbert, 1991a). *Copidodiaptomus* decreased in numbers in the more eutrophic reservoirs and was utterly replaced by large populations of *A. robustus*. The decline of calanoids has been frequently found in cases of eutrophication (e.g. Patalas 1972, Maier 1996). Under eutrophication processes, calanoids have been reported to be replaced both by cladocerans (Tonolli, 1962; MacNaught, 1975; Edmondson, 1977) and cyclopoid species (Adrian, 1997). The advantage of *Daphnia* over *Eudiaptomus* in eutrophic conditions was related by Muck & Lampert (1980, 1984) to the ability of the cladoceran to increase their feeding rate to a higher level than the calanoid can. Calanoid development stages have lower food threshold concentration relatively to cyclopoids (Santer, 1994) and delays in the duration of the oviductal cycle of cyclopoids were



**Figure 12.** Dendrogram depicting group of reservoirs according to species densities at each season. MARA indicates Maranhão reservoir. 1, 2 and 3 indicate 1993, 1994 and 1995, respectively. Dendrograma mostrando los grupos de embalses de acuerdo con las densidades de especies en cada estación. MARA indica embalse de Maranhão. Los números 1, 2 y 3 indican respectivamente 1993, 1994 y 1995.

observed under strictly herbivorous conditions (Maier, 1989, 1992; Caramujo & Boavida, 1999). In the studied reservoirs the higher proportion of calanoid to cyclopoid copepodid stages relatively to the equivalent proportion of naupliar stages suggested that cyclopoid populations were not being limited mainly by reproductive constraints but rather by the ability of their naupliar stages to develop successfully. These data corroborated the results of Soto & Hurlbert (1991a,b) that ascribe an advantageous position to calanoid *nauplii* over cyclopoid *nauplii* under low feeding conditions. *A. robustus* was the only copepod species inhabiting the more eutrophic reservoirs (Divor and Póvoa) where it was usually accompanied by large populations of *Bosmina longirostris*. Since the abundance of the copepod showed a direct relationship with the increase in rotifers and CHLa, it is highly tempting to relate this species to eutrophication. A proliferation of *A. robustus* was previously associated with eutrophication in the bay of the Helsinki sea area (Purasjoki & Viljamaa, 1984) and in Lake Konstanz (Einsle, 1988). Maranhão was emptied in 1991. After refilling, *A. robustus* was the only copepod species present and *C. numidicus* only reappeared when the water transparency increased (Crispim, 1997). *A. robustus* is primarily an omnivorous species but may utilize algae which are suitable for egg production (Hopp *et al.* 1997). Under suitable feeding conditions, *A. robustus* had the highest reproductive output and adult longevity among four other cyclopoid species (Hopp *et al.* 1997). However, the situation was reversed when on algal diet. The amount of *A. robustus* eggs in Divor was correlated to CHLa but this relation may be the indirect result of better feeding conditions to *A. robustus* prey (i.e. rotifers). In the reservoirs of Tagus River Basin the decrease of the proportion of calanoids to cyclopoids as well as an increase in *A. robustus* density was related to an increase in CHLa concentration.

The proportion of the genus *Daphnia* relative to the cladoceran community also decreased with eutrophication increase. Besides the change in abundance, the genus *Daphnia* was represented by different species in reservoirs at different tro-

phic degrees. Large *Daphnia* species dominated in reservoirs with clearer water (more oligotrophic) and a shift towards small bodied species was observed in more eutrophic reservoirs with *D. pawula* and *D. cucullata* only occurring in the most eutrophic reservoirs. This shift in size could not reflect only the presence of fish since in Maranhão *D. pawula* was present when the fish population was low, after the drastic decrease through reservoir emptying. Furthermore, *D. pulex* was present in Fratel when fish was present in the reservoir (inquiries to fishermen). Adrian and Deneke (1996) also found a shift in warm springs towards the small bodied species (*D. galeata* to *D. cucullata*) ascribed to the change in the food size spectra (Geller & Müller 1981) due to an increase in winter temperatures. CHLa values should be regarded with caution since large cyanobacteria (i.e. over 40 µm) may not be considered edible by cladocerans (e.g. *Daphnia*, Adrian and Deneke, 1996). In Belver, Fratel, St. Agueda and in all southern reservoirs, blooms of cyanobacteria were observed. Filaments of cyanobacteria seriously disturb the filtering process in daphnids which are forced to clean their food groove (Burns, 1968; Gliwicz, 1980). Webster & Peters (1978) and Gliwicz & Lampert (1990) showed that the inhibitory effects of cyanobacteria depend on cladoceran body size, with large species being more affected than small species. Large amounts of phytoplankton allied to cyanobacteria presence seem to have favoured small daphnids and small cladocerans in eutrophic reservoirs. In feeding experiments Crispim (1997) found that *D. pawula* was unable to survive at low food level ( $5 \cdot 10^3$  cells/ml) while *D. hyalina* (and *Diaphanosoma*) established large populations. However, under suitable feeding conditions ( $5 \cdot 10^4$  cells/ml) *D. parvula* rapidly established a population larger than *D. hyalina*. The presence of *D. pulex* and its coexistence with *D. hyalina* is difficult to explain. In coexistence experiments Bengtsson (1986) found that the smallest species was excluded. However, it is accepted that it may be advantageous to be small when food is scarce and daphnids have to endure starvation (Lynch, 1979). It would be interesting



to investigate the process underlying *Daphnia* interactions in Belver, Fratel and St. Agueda.

Classification of crustacean species according to the nature and way of collecting food raises problems because of the different food demands of the several development stages. This difference in food demand is even more acute in the case of raptorial copepods since naupliar and earlier copepodid stages are filter feeding herbivores. Although with limitations, especially in the case of the genus *Daphnia*, the display of the community according to the proportion of crustacean classes offers important information on community organization. Species composition of each class should, however, always be taken into consideration since carnivorous populations in oligotrophic reservoirs were mainly of *Macrocyclops albidus* while in eutrophic reservoirs carnivores were exclusively *A. robustus*. Moreover, the presence of large amounts of cladocerans of class V may be misleading due to large amounts of *D. parvula* and *D. cucullata* in eutrophic reservoirs. Class IV may also be misleading due to the presence of large populations of *Diaphanosoma* and *Ceriodaphnia* in clear water reservoirs, which are replaced by *Bosmina* in more eutrophic reservoirs. Nevertheless, herbivorous calanoids dominated in more oligotrophic waters, while predator copepods dominated in more eutrophic waters. Non predaceous cyclopoids were an important zooplankton class, mainly at summer, in reservoirs with high proportion of diatoms in the phytoplankton. Green algae are poorly assimilated (Horn, 1981) because cyclopoids lack cellulase (Fryer, 1957). Cyclopoids may feed selectively on diatoms and assimilate them efficiently (Toth & Zankai, 1985; Knisely & Geller, 1986; Toth *et al.*, 1987; Hansen & Jeppesen, 1992). Development of *T. dybowskii* in the most oligotrophic reservoirs and the absence of *C. numidicus* in a reservoir with high amounts of diatoms (Meimoa) should be investigated.

The proportion of calanoids to cyclopoids is an efficient method to collect information on trophic state of the reservoirs especially when accompanied by data on the abundance of *A. robustus* and *Bosmina*.

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