UNIVERSITAT DE VALÈNCIA
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CARACTERIZACIÓN ESTRUCTURAL DEL ZOOPLANCTON DE LAS LAGUNAS CÁRSTICAS DE CUENCA, CON ESPECIAL ATENCIÓN A SU DISTRIBUCIÓN VERTICAL

Javier Armengol Díaz
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789 East Eisenhower Parkway
P.O. Box 1346
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Firmado: Javier Armengol Díaz

Biológicas

Tesis dirigida por Maria Rosa Miracle Solé
Dra. en Ciencias Biológicas y Catedrática de Ecología en la Universitat de València

Fdo:Maria Rosa Miracle Solé

A mis Padres

A Carmina

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I.- INTRODUCCIÓN GENERAL

INTRODUCCIÓN GENERAL

Nuestro país no cuenta con gran número de lagos, en especial si lo comparamos con los países europeos de nuestro entorno (Pardo, 1910); pese a la escasez cuantitativa de lagos, en nuestro país sí que se presenta una gran diversidad de humedales. Por otra parte, es destacable el escaso bagaje que presentan los estudios limnológicos en la península ibérica, esto puede tener relación con el escaso número de lagos, pero como señala Margalef, este hecho debería incentivar el estudio de los mismos, pues es en países como el nuestro donde los problemas relacionados con el agua tienen mayor interés, ya que en muchos casos es un factor limitante debido a los prolongados periodos de sequía. La demanda de agua de la sociedad actual unida a las condiciones de aridez de nuestro país confieren un factor de estres adicional al ya de por sí escaso número de lagos, por un aumento de la presión humana sobre estos sistemas.

Dentro de este contexto, en la provincia de Cuenca, encontramos una gran cantidad de lagos de origen cárstico, en particular aquellos de tipo pluvial y pluvio-nival (Llopis, 1971), algunos de ellos se agrupan en sistemas de dolinas próximos entre sí y que están formadas por disolución de un mismo tipo de sustrato, pudiendo encontrar distintos grupos de dolinas con agua formadas sobre diferentes tipos de sustratos. Pese a su proximidad espacial y al hecho de compartir un mismo sustrato, estos lagos presentan notables diferencias en cuanto a la composición química de sus aguas y a sus características limnológicas; además hemos de tener en cuenta que el fenómeno cárstico es un fenómeno "vivo" por lo que existen algunos de estos lagos de muy reciente formación (una de las dolinas del sistema cárstico de Arcas-Ballesteros se formó en 1978, cuando un agricultor se encontraba trabajando un campo), mientras que otros son más antiguos; también la morfometría de las cubetas presenta una gran variabilidad reflejada en los diámetros, superficies, perímetros, profundidades y pendientes de sus orillas principalmente. Todas estas características conllevan diferencias en el estado trófico de los lagos (Hakanson, 1990), así como en la comunidad del zooplancton que los habita, cuyo estudio es el principal objetivo de este trabajo.

Las peculiaridades morfométricas de alguna de estas dolinas, junto con otras características del sustrato o de su particular ubicación, determinan fenómenos de estratificación vertical de sus aguas. En la mayoría de las dolinas profundas esta estratificación tiene carácter temporal pero es muy marcada y de larga duración, empezando muy pronto en la primavera. También existe algún caso en que la estratificación de la columna de agua es permanente y constantemente nos encontramos una parte de la columna de agua con características anóxicas. Este fenómeno conocido como "meromixis" (es decir , mezcla parcial de las aguas) tiene gran importancia por su

efecto sobre las características limnológicas así como sobre las poblaciones planctónicas. En esta región se han estudiado dos lagunas con esta característica: la laguna de La Cruz, que presenta una meromixis biogénica (i.e. la meromixis se deriva o refuerza por la descomposición de la materia orgánica), y el lago del Tobar que presenta una cubeta con meromixis crenogénica (i.e. su meromixis se debe a que un manantial de agua salada llena esta cubeta, ya que subyacente a las calizas jurásico-cretácicas se localiza un estrato geológico evaporítico del Keuper).

Una particularidad de los lagos meromícticos consiste en la marcada microestratificación de algunos parámetros físico-químicos que lleva aparejada la microestratificación de las poblaciones de zooplancton y, en particular, las poblaciones de rotíferos que en estas capas alcanzan enormes acúmulos formando picos de densidad muy pronunciados con escasos centímetros de diferencia en el perfil vertical. El estudio de estas capas requiere el empleo de técnicas de muestreo especiales que permitan la laboriosa recolección de muestras en capas muy finas del perfil vertical y gran precisión en la caracterización físico-química de las aguas (Miracle *et al.*, 1992). Las peculiaridades de estas lagunas cársticas ha llevado al descubrimiento de una nueva especie de rotífero, *Anuraeopsis miraclei,* descrito por vez primera en la laguna de La Cruz (Koste, 1991) aunque se había encontrado también en otra laguna próxima, Lagunillo del Tejo, y más tarde ha sido citado en un lago alpino (Jersabeck, 1995).

Además de la estrecha colaboración con el Dr. Koste para la descripción del rotífero en cuestión, desarrollamos un primer trabajo en el que comparamos la distribución de dos especies congenéricas del género *Anuraeopsis, A. fissa* y *A. miraclei*, -que en aquellos momentos no estaba considerado como una especie diferente aunque sus características morfológicas y ecológicas así parecían indicarlo- en dos diferentes lagunas; esto constituye el capítulo V.1 de este trabajo.

En el capítulo V.2 se estudió el ciclo anual (1987-1988) del zooplancton, en particular de los rotíferos por ser el zoplancton dominante, en la laguna de La Cruz. En este estudio se utilizó por primera vez un muestreador de capa fina con el que se recogían muestras a intervalos de 20 cm en la columna de agua, lo que permitió la detección de una marcada estratificación en las poblaciones de rotíferos situadas en la zona de la oxiclina. El capítulo V.4 recoge el estudio del zooplancton realizado en la laguna Arcas-2 durante los años 1990-1991, en este caso el estudio se centró en la comparación de dos especies de rotífero que desarrollaban máximos de densidad en la zona de la oxiclina, se observó que tenían una microdistribución diferente y que además, sus estrategias reproductivas y de colonización del ambiente planctónico también eran diferentes y peculiares para cada una de las especies; en este trabajo también se empleó una metodología especial con el fin de estudiar con detalle la microestratificación.

Otro centro de interés para nuestros estudios lo constituye el lago del Tobar, situado al N de la provincia de Cuenca, en el límite con Guadalajara; este lago, también de origen cárstico, presenta algunas peculiaridades como son su tamaño relativamente grande comparado con los otros lagos de la zona, pues tiene casi un kilómetro de longitud máxima y la presencia de una cubeta meromíctica, que en este caso debe su meromixis a una capa hipersalina situada a partir de los 12 m (Vicente *et al.*, 1993); estas características confieren gran peculiaridad a sus poblaciones planctónicas constituyendo el estudio de las mismas el capítulo V.3 de la presente Tesis. En este lago se desarrolló también un estudio sobre la migración vertical coetáneo con la Tesis (King y Miracle, 1995).

La laguna de La Cruz, como se ha comentado anteriormente es de carácter meromíctico y posee una marcada estratificación físico-química que se corresponde con una marcada estratificación de sus poblaciones zooplanctónicas, estas características, junto con su pequeño tamaño y su ubicación en el interior de una cubeta con paredes casi verticales de 25-30 m, contribuyen a la gran estabilidad de sus aguas al protegerla de los vientos, impidiendo la mezcla de toda la columna de agua. Estas características nos llevaron a diseñar una experiencia encaminada a determinar los movimientos migratorios del zooplancton en la columna de agua, y en especial, si las densas poblaciones que observábamos en la oxiclina eran activas y si existían movimientos migratorios entre la oxiclina y otras capas superiores de agua que permitieran a los organismos del zooplancton epi-metalimnéticos el aprovechamiento de los importantes recursos nutricionales que se acumulan en estas capas profundas. La experiencia se realizó en septiembre pues es al final del verano cuando las poblaciones de rotíferos en estas capas son más densas, probablemente debido a la acumulación de la materia orgánica procedente de la biomasa generada en las capas superiores durante el verano. Los resultados de esta experiencia se recogen en el capítulo V.6.

El estudio de la relación de los parámetros físico-químicos con las poblaciones del zooplancton en un ciclo anual se ha abordado mediante el Análisis de las Componetes Principales (PCA), esta técnica de estadística multivariante nos ha permitido identificar las interacciones de las poblaciones zooplanctónicas entre si y con aquellos parámetros abióticos que explican una mayor varianza en nuestros datos espacio-temporales, y conocer por tanto qué parámetros son responsables de los principales cambios en el ciclo anual y en la columna de agua a los que se asociarían las variaciones de la distribución del zooplancton en el espacio y en el tiempo. Esta técnica se aplicó al estudio de muestras obtenidas entre junio de 1987 y octubre de 1988 en la laguna de Arcas-2 y los resultados obtenidos se describen en el capítulo V.5.

Finalmente se realizaron muestreos en todas las lagunas permanentes de los sistemas cársticos de Arcas-Ballesteros, Fuentes y Cañada del Hoyo en dos épocas: primavera y principios del otoño de 1992. En estos muestreos se tomaron datos de la mayoría de parámetros físico- químicos, y se tomaron muestras del zooplancton en el perfil vertical. Como complemento se realizó una campaña al final del invierno de 1993 en la que se realizaron estudios batimétricos de la mayoría de lagunas estudiadas en el año 1992. Con estos datos se aplicaron técnicas de estadística multivariante como son: correlaciones, el Análisis de Componentes Principales (PCA), ya utilizado en el capítulo V.5, y técnicas de clasificación y agrupamiento de los datos mediante los programas TWINSPAN y DECORANA (Hill, 1979); estas técnicas nos permitieron identificar las principales fuentes de variación en nuestros datos, también se calcularon diversos parámetros bióticos que caracterizaban a las diferentes lagunas y se observó como estos parámetros se ven afectados por los parámetros físico-químicos. Con todo ello se realizaron agrupamientos de las distintas lagunas por sus semejanzas en cuanto a las comunidades zooplanctónicas que las poblaban, además el programa TWINSPAN a la vez que realiza estas agrupaciones determina las especies indicadoras o características de cada agrupación. Esto conecta con la utilización cada vez más extendida de los organismos como bioindicadores de diferentes condiciones ambientales y en especial de los distintos tipos y niveles de contaminación.

Como resumen se podría indicar que se ha procedido a la caracterización del zooplancton en una serie de lagunas cársticas conquenses, y al estudio en algunas de estas lagunas de los fenómenos asociados con la distribución vertical de las poblaciones planctónicas poniendo de manifiesto las microestratificaciones y los ingentes acúmulos de organismos que tienen lugar en las interfases oxico-anóxicas de estas lagunas. Esta caracterización es importante para profundizar en el conocimiento de estos sistemas de gran fragilidad e interés para nuestro patrimonio cultural, hay que destacar que estas lagunas actualmente están incluidas por la Junta de Comunidades de Castilla La Mancha en el Plan de Ordenación de los Recursos Naturales (PORN) de los humedales Castellano-Manchegos con vistas a la protección de los mismos. Finalmente debo reseñar que algunas de estas lagunas han sufrido algunas transformaciones desde que estos estudios fueron realizados, confío en que estas transformaciones no sean irreversibles y que éste y otros estudios contribuyan a la conservación de estos sistemas sometidos a una fuerte presión humana.

II.- MATERIAL Y MÉTODOS

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II.1.- LUGARES Y PERIODOS DE MUESTREO

Tanto el calendario como las diferentes profundidades a las que se realizaron los muestreos se detallan en cada uno de los capítulos, sin embargo creemos conveniente dar una visión completa sintetizando la información fragmentaria de los mencionados capítulos.

La **Laguna de la Cruz** fue muestreada desde junio de 1987 hasta octubre de 1988 (capítulos IV.1 y IV.2), en el centro de la cubeta. Las muestras se tomaron mensualmente en la época de mayor estratificación del año 1987 y, aproximadamente cada dos meses, en el resto del periodo estudiado. Las profundidades de muestreo variaban en función de las características limnológicas de la columna de agua durante las diferentes visitas pero, en general, se tomaban las muestras al principio y al final del epilimnion, varias en el metalimnion, según el gradiente de temperatura y oxígeno (se recogía una muestra en el máximo de oxígeno y otra en el inicio de la disminución), y se realizaba un muestreo más exahustivo en la oxiclina, donde se tomaron muestras cada 10 ó 20 cm.

En esta misma laguna se tomaron muestras para la descripción del ciclo diario y el estudio de la migración vertical del zooplancton (capítulo IV.6) durante los días 15 y 16 de septiembre de 1989. Se realizaron cinco muestreos a diferentes horas de un ciclo diario (0, 7, 12:30, 18 y 22 h); en todos los casos se tomaron muestras en 8 profundidades (0.5, 4.5, 8.5, 10.5, 12, 12.5, 13 y 13.7 m). También se dispusieron unas trampas de migración vertical durante tres periodos que abarcaban aproximadamente el ciclo diario (noche, de 22 a 6 h aprox.; mañana, de 6 a 14 h aprox. y tarde, de 14 a 21 h aprox.), situadas en 4 profundidades diferentes (4.5, 8.5, 12.5 y 13.7 m).

Arcas 2 fue muestreada durante el ciclo anual 1987-1988 de manera semejante a como lo fue la laguna de La Cruz (dada la proximidad entre una y otra zona se aprovechaba el mismo viaje para muestrear ambas lagunas), también en este caso se puso un mayor énfasis en los muestreos de la zona de la oxiclina (capítulos IV.1 y IV.5).

Esta laguna se volvió a muestrear durante el periodo noviembre 1989/diciembre 1991. En este ciclo los periodos de muestreo estuvieron próximos a los 15 días en la época de estratificación y cada dos meses aproximadamente en la época de mezcla. De nuevo se realizó un muestreo de la columna de agua, más exahustivo en el gradiente de oxígeno del meta-limnion que en las aguas superficiales (capítulo IV.4).

La **Laguna grande del Tobar** se visitó en diferentes fechas entre 1991 y 1992, se tomaron muestras aproximadamente cada metro en el mixolimnion de la cubeta

meromíctica, durante este periodo también se realizaron muestreos diurnos y nocturnos de la columna de agua (capítulo IV.3).

En 1992 se muestrearon **todas las lagunas** permanentes de los sistemas cársticos de Cañada del Hoyo, Arcas-Ballesteros y Fuentes. Se realizaron dos campañas de muestreo, la primera empezó a finales de abril y se dilató durante la mayor parte del mes de mayo, la segunda comenzó al final de septiembre prolongándose durante el mes de octubre. Las muestras se tomaron anclados sobre la zona más profunda de la laguna, y en función de las características limnológicas se seleccionaron varios puntos de muestreo en el perfil vertical. El número de puntos osciló entre 1 y 5, dependiendo principalmente de la profundidad de la columna de agua y de su grado de estratificación (capítulo IV.7). Posteriormente, durante el mes de marzo y principios de abril de 1993, estas mismas lagunas se visitaron para realizar un estudio detallado de sus características morfométricas (capítulo II.5).

II.2.- PARÁMETROS FÍSICO-QUÍMICOS

a) Parámetros físico-químicos medidos "in situ"

Estos parámetros fueron medidos desde una barca fijada mediante cables en el centro del lago, en la zona más profunda, utilizando sondas que permitían situar los sensores en las profundidades deseadas (temperatura, conductividad, oxígeno disuelto y medida de la penetración de la luz), o mediante la elevación del agua de distintas profundidades con una bomba y medida de determinados parámetros (Potencial de oxidación-reducción y pH) en un recipiente (Fig. II.1) especialmente diseñado a tal efecto.

La medida de la **Temperatura** se llevó a cabo a pequeños intervalos de profundidad en la columna de agua para definir el perfil de temperaturas hasta el fondo de las lagunas; ya que la selección de los puntos de muestreo dependía sobre todo del estado térmico de la laguna. La temperatura se media por lo general cada medio metro, aunque en casos de fuerte estratificación el intervalo era menor y, cuando la homogeneización de la columna era grande, el intervalo fue mayor. Estas medidas se realizaron mediante termopares (ATC) instalados tanto en el oxímetro como en el conductímetro. Se constató una pequeña diferencia en la medida registrada por ambos aparatos por lo que para este trabajo únicamente se han considerado las medidas obtenidas con el oxímetro.

El perfil de **conductividad** se obtuvo de manera similar al de temperatura, utilizándose para ello un conductímetro WTW modelo LF 91.

El **oxígeno disuelto** se midió utilizando un oxímetro polarográfico WTW modelo OXY 92 con un electrodo de plata-oro. La medida de los perfiles verticales de oxígeno se realizó con gran detalle y a intervalos muy pequeños de profundidad (10 cm) en las zonas de la oxiclina; esto se debe al gran interés que presenta para este trabajo la microestratificación de las poblaciones de rotíferos, microestratificación que se correlaciona en gran medida con el marcado gradiente que presenta este parámetro. Los valores de oxígeno disuelto se midieron en mg/l así como en porcentaje de saturación. En algunos trabajos las medidas fueron contrastadas analizando diversas muestras por el método de Winkler (Golterman *et al.*, 1978).

La **penetración de la luz** en el agua se midió utilizando un radiómetro Crump Sci. Ins. mod. 550 y una medida indirecta de la penetración de la luz se obtuvo de la profundidad de desaparición del disco de Secchi. El disco de Secchi utilizado fue un disco de PVC de color blanco contrapesado y con un diámetro de 20 cm. El coeficiente de extinción de la luz se obtiene de la siguiente expresión:

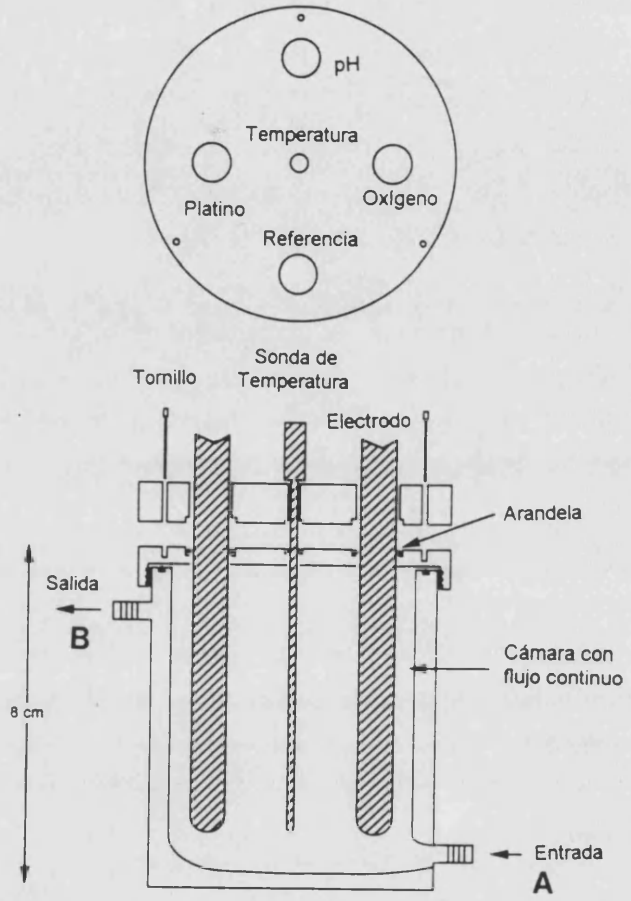
$$\eta = (\log I_1 - \log I_2)/(z_1 - z_2)$$

donde I_1 e I_2 son las intensidades luminosas obtenidas a las profundidades z_1 y z_2. Entre este coeficiente (η) y la profundidad de desaparición del disco de Secchi (D) existe una relación constante que se muestra según la expresión (Wollenweider, 1974):

$$\eta \times D = C$$

El **potencial de oxidación-reducción** y el **pH** se midieron de manera simultánea, bombeando agua y midiéndola en un recipiente que permitía el flujo contínuo del agua en donde estaban instalados los electrodos (de la marca Orion) para la determinación de pH y potencial redox además de un sensor de temperatura (Fig. II.1). Posteriormente los valores del redox se transformaron para referirlos al potencial del electrodo estándar de hidrógeno (Eh).

Las medidas del pH se tomaban midiendo el pH en muestras de agua recogidas con una botella hidrográfica del tipo Ruttner del capítulo IV.



(Fig. II.1) Esquema del recipiente de flujo continuo utilizado para la medida *in situ* del pH y del redox.

b) Análisis químicos realizados en el laboratorio

En la Tabla II.1.b se resume la metodología empleada para la realización de los análisis químicos realizados en el laboratorio, previamente se había realizado la toma y fijación de las muestras, utilizando la metodología de la Tabla II.1.a.

Tabla II.1.a

ANÁLISIS	BOTELLA	VOLUMEN (ml)	TRATAMIENTO PREVIO	FIJACIÓN
Alcalinidad	vidrio	100	-----	HCl valorado
Amonio	vidrio	125	-----	1 ml HCl 6N
Cationes	polietileno	50	-----	-----
Cloruro	polietileno	variable	Filtración GF/F	cloroformo
Fósforo soluble	polietileno	50	Filtración GF/F	cloroformo
Fósforo total	vidrio	125	-----	0.8 ml H_2SO_4 1:2
Nitrato	polietileno	250	Filtración GF/F	2 ml ácido bórico
Nitrito	polietileno	50	Filtración GF/F	0.5 ml sulfanilamida
Oxígeno[1]	vidrio	250	-----	2 ml KOH y KI 1 ml CdCl
Pigmentos	polietileno	1000	Filtración GF/F	-----
Silicato	polietileno	50	Filtración GF/F	cloroformo
Sulfato	polietileno	variable	Filtración GF/F	cloroformo

[1] Método Winkler

Tabla II.1.b

ANÁLISIS	MÉTODO EMPLEADO	REFERENCIA
Alcalinidad	Acidimétrico; valoración con NaOH	Método de Watemberg
Amonio	Electrodo selectivo Orion mod. 95-12	
Cationes	Absorción atómica	
Fósforo soluble	Volumétrico; argentimetría	APHA, 1976
Cloruro	Colorimétrico; fosfomolibdato y reducción a azul de molibdeno	Murphy y Riley (1962)
Fósforo total	Hidrólisis ácido-persulfática en caliente	Golterman, 1978
Nitrato	Colorimétrico previa reducción a Nitrito	Morris y Riley, 1963
Nitrito	Colorimétrico, reacción de Griess	Wood et al., 1967
Oxígeno	Winkler; iodometría e indicador de almidón	Golterman et al., 1978
Pigmentos	Espectrofotométrico en extracto acetónico	Striklands y Parsons, 1972
Silicato	Colorimétrico; formación de silico-molibdato en medio reductor ácido	Mullin y Riley, 1955
Sulfato	Nefelometría	Rodier, 1984

II.3.- MÉTODOS DE MUESTREO DEL ZOOPLANCTON

Aunque cada uno de los capítulos lleva una descripción de la metodología empleada, se ha considerado conveniente compendiar y explicar con más detalle en este capítulo los diferentes métodos de muestreo del zooplancton utilizados en este trabajo.

En función de los diferentes aspectos del zooplancton estudiados en cada capítulo se han utilizado diferentes metodologías. A continuación se comentan las principales características de cada una de ellas, concretamente de la toma de muestras mediante: bomba peristáltica, botellas hidrográficas, trampa de Patalas, red de plancton y trampas para el estudio de la migración vertical.

a) Muestreo con bomba peristáltica

Esta técnica de muestreo consiste en la utilización de una bomba peristáltica que, en nuesto caso, estaba conectada a un muestreador en forma de doble cono, descrito en Miracle *et al.*, 1992 (Fig II.2) y que permite succionar la cantidad de agua requerida de la profundidad deseada. El empleo del muestreador de doble cono permite tomar la muestra con flujo laminar y por tanto con menor perturbación, además al estar conectado a una manguera y a su vez a una cinta métrica inextensible, permite ajustar con gran precisión el punto de muestreo; otra ventaja es que permite tomar una cantidad variable de agua que se ajusta en función de los requerimientos de cada estudio, esto hace esta técnica muy adecuada para el estudio cuantitativo. Como desventajas de esta técnica de muestreo cabe destacar la subestima de los organismos del zooplancton más grandes y con mayor capacidad de natación, así como de aquellos que presenten reacciones de escape reotácticas.

Esta ha sido una de las metodologías más empleadas en este trabajo para la obtención de muestras (capítulos IV.1, 2, 4, 5 y 6) pues el principal objeto de estudio han sido los rotíferos, que por su tamaño y capacidad de natación, son capturados en general con alta eficacia mediante este método. Sin embargo en la mayoría de trabajos se ha combinado esta metodología con el empleo de botellas de muestreo y redes de plancton.

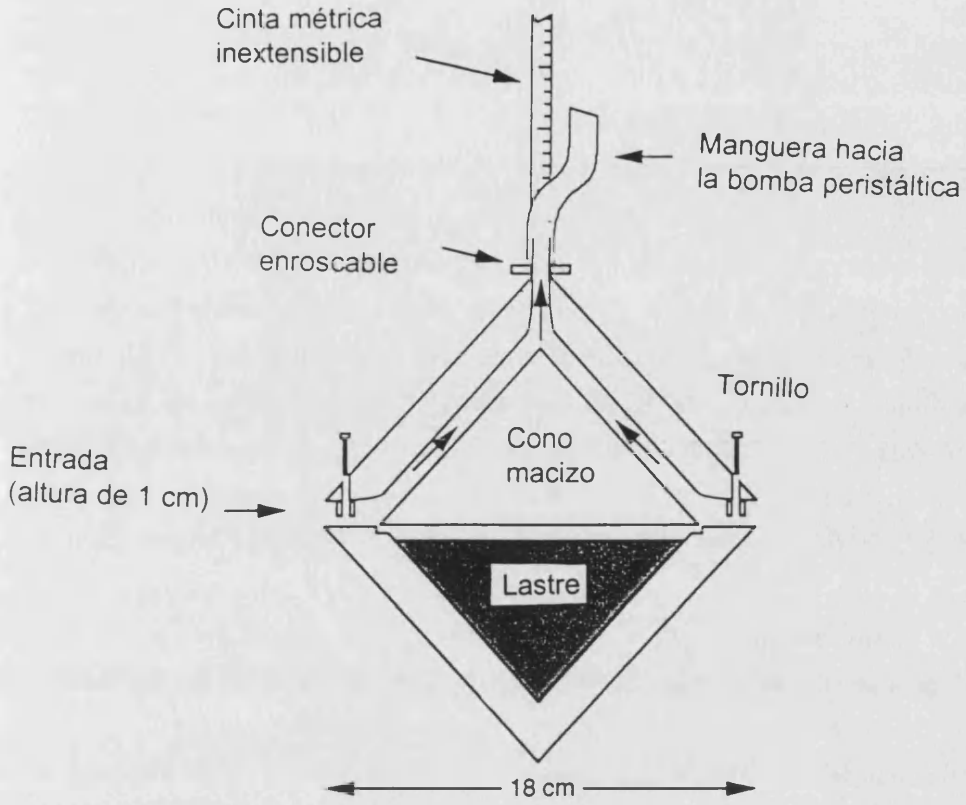


Figura II.2 Esquema del muestreador de doble cono empleado para la toma de muestras con bomba peristáltica.

b) Botellas hidrográficas

Esta técnica complementa a la anterior, en nuestro caso fueron empleadasdas tipos de botellas: botellas Van Dorn y botella Ruttner.

Las primeras (Fig II.3) son dos botellas con un sistema de apertura común, las botellas son de metacrilato transparente con el fin de disminuir las reacciones de escape, al menos las dependientes de la visión; entre las dos capturaban un volumen de 5.4 l. Estas botellas se utilizaron para complementar los estudios de zooplancton, en particular el zooplancton más grande y con mayor capacidad natatoria, y también fueron utilizadas en épocas de mezcla y de bajas densidades de zooplancton. En los muestreos del capítulo IV.7 fue la técnica utilizada para la determinación cuantitativa.

La botella Ruttner (Lámina I), es también transparente y posee una capacidad de 3 l, fue utilizada principalmente para la toma de agua para los análisis químicos en periodos de mezcla o en aquellos en los que no se utilizó bomba (como en los muestreos del capítulo IV.7). Este tipo de botella fue menos empleado para el estudio del

zooplancton pues debido a su sistema de cierre ocasiona turbulencias que pueden afectar a la captura del zooplancton de mayor tamaño.

La principal ventaja que presentan las botellas frente a otros métodos es que permiten tomar una cantidad de agua grande y por tanto mitigar las reacciones de escape del zooplancton de mayor tamaño. Las botellas también permiten bastante exactitud en la toma de las muestras tanto en el volumen como en la selección de la profundidad, pero dada su longitud de aproximadamente 35 cm, integran muestras de una columna de agua de esta altura. En el caso de aguas marcadamente estratificadas, en las que en pocos centímetros de agua hay importantes variaciones en las densidades de organismos, la longitud de la botella y la turbulencia que produce el movimiento de los tapones al cerrarse impiden obtener la distribución precisa de los picos de población. Es por ello que en el caso de poblaciones de rotíferos microestratificadas hemos preferido el empleo de la bomba peristáltica. Otra desventaja del sistema de cierre (en particular el de las botellas Van Dorn) es que la turbulencia que produce puede deshacer la estratificación y afectar las muestras que se tomen con posterioridad.

Este sistema de muestreo ha sido utilizado en algunos casos como alternativa y en otros como complemento de la bomba, sobre todo durante periodos de mezcla; cuando ha sido utilizada conjuntamente con la bomba en periodos de estratificación, se tuvo la precaución de utilizarla al final de los muestreos cuando ya se habían tomado las muestras con bomba.

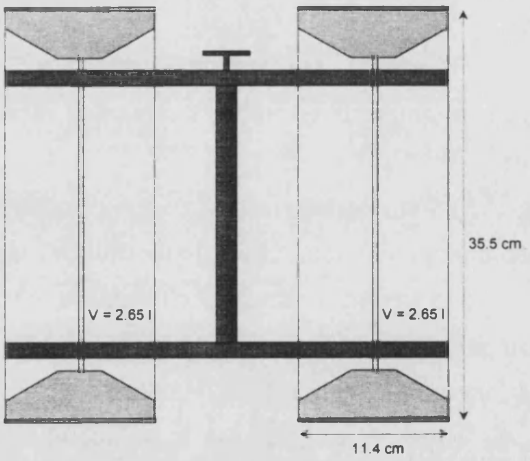


Figura II.3 Esquema de las botellas Van Dorn empleadas en este estudio, indicando sus dimensiones.

c) Trampa de Patalas

La trampa de Patalas empleada en este caso tiene 25 l con una malla de filtración de 100 μm (únicamente se empleó en algunos muestreos del capítulo IV.3). Sus ventajas son el gran volumen de agua que permite filtrar, adecuado en situaciones de oligotrofia, y la efectividad de las capturas debido a su gran volumen, su sistema de cierre y a la transparencia de sus paredes (Lámina I). Es por tanto adecuada para el muestreo del zooplancton de mayor tamaño y mejor capacidad de natación, así como cuando las densidades de organismos son bajas. Por contra, afecta a la estratificación, es de manejo aparatoso y en condiciones de mesotrofia/eutrofia, con densidades elevadas de organismos, presenta problemas para la filtración.

d) Red de plancton

Consiste en la utilización de una red de forma troncocónica (Lámina I) que se arrastra por el agua funcionando como un filtro, en la parte final de la red se sitúa el copo, que recoge los organismos filtrados a lo largo del trayecto recorrido. En nuestro caso la malla utilizada en la confección de la red fue nytal con diámetro de poro de 45 μm, adecuada para los grupos de tamaño igual o superior al de los rotíferos. En nuestro caso se realizaron arrastres verticales y horizontales de la red.

Las redes no son un buen sistema para estudios cuantitativos aunque sí que pueden ser utilizadas para este fin. El cálculo del volumen de agua filtrado por la red se obtiene de la fórmula:

$$V=\Pi r^2 \times d$$

(siendo **r** el radio de la boca de la red y **d** la distancia recorrida)

En este trabajo la red no se ha utilizado para estudios cuantitativos, sino para la obtención de suficientes organismos para su clasificación taxonómica, en especial de copépodos cuyas formas adultas en ocasiones son escasas en las muestras de bomba y de botella, debido a su bajo número y mayor capacidad de natación. Por tanto se ha utilizado para complementar a los otros métodos en el estudio cualitativo del zooplancton.

e) Trampas para la migración vertical

Están inspiradas en las que utilizaron Landon and Stasiak (1983) y Salonen and Lehtovaara (1992), aunque por su tamaño son más adecuadas para la captura de rotíferos, que fue el grupo de organismos para los que se diseñó la experiencia del capítulo IV.6. Constan de un embudo transparente que se introduce en un matraz de 250 ml cerrado por un tapón de goma en el que se ajusta el embudo (Fig II.4). Se colocaron varias de estas trampas por parejas a lo largo del perfil vertical de la laguna, las trampas estaban unidas a una barra metálica con pinzas y esta barra por medio de una cuerda estaba atada a un sistema de boyas y mantenida a la profundidad deseada. Las trampas estaban rellenas de agua previamente sacada de la profundidad donde se colocaban y filtrada por una malla de nytal de 30 μm; la mitad de trampas se colocaron con la apertura del embudo hacia la superficie (para capturar organismos con trayectoria descendente) y la otra mitad con la apertura hacia el sedimento (para capturar organismos en trayectoria ascendente).

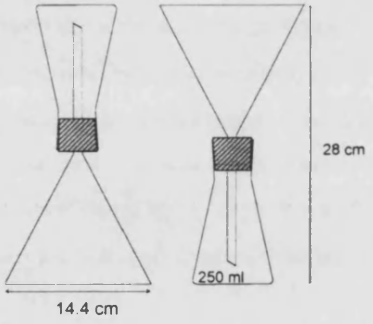


Figura II.4 Esquema de las trampas utilizadas en la experiencia de migración vertical, mostrando sus dimensiones.

II.4.- PROCESAMIENTO DE LAS MUESTRAS Y RECUENTO DEL ZOOPLANCTON

En la mayor parte de muestreos con bomba se tomaba una cantidad de agua, entre 2 y 4 litros, que se medía utilizando un bote de plástico graduado, filtrándose a continuación este volumen con tela de nytal de 30 μm. Estos filtros se recogían en tubos de cristal de fondo plano que estaban parcialmente rellenos de formol al 4-5%, de este modo eran almacenados para su posterior recuento y clasificación en el laboratorio, en donde los filtros eran extraídos y lavados cuidadosamente quedando listas las muestras para su

sedimentación y recuento. Las muestras obtenidas de las botellas hidrográficas y las de las trampas de migración vertical fueron filtradas también en la barca y almacenadas del mismo modo. Las muestras de red y trampas de Patalas se transferían a botes de plástico herméticos y se fijaban con formol (quedando la concentración del mismo aproximadamente al 4%) para su posterior estudio en el laboratorio.

Sin embargo las muestras del capítulo IV.4 fueron estudiadas directamente sin filtrar. Se tomaron muestras de un volumen conocido en botellas de cristal, sedimentando después en el laboratorio un volumen determinado y previamente fijado con lugol, en cámaras de sedimentación siguiendo la técnica de Utermöhl, es decir, la misma metodología que se emplea para el estudio del fitoplancton (Utermöhl, 1958).

Todas las muestras cuantitativas fueron estudiadas con posterioridad en el laboratorio realizando los recuentos en cubetas de metacrilato con fondo de cristal del grosor de un cubreobjetos y en un microscopio invertido Nicon TMS utilizando aumentos de 100 ó 200X para los recuentos y de 400 y 1000X para la clasificación de los organismos. Se realizaron recuentos de todos los organismos presentes así como de sus huevos (mícticos y amícticos) y cuando se pudo se contabilizaron los machos que aparecían en las muestras. En la mayor parte de muestras se contaba toda la cubeta y, solo en el caso de densidades muy elevadas que dificultaban el recuento, se realizaron diluciones de las muestras para una más fiable estima de la densidad.

Para la determinación de algunas especies de crustáceos se realizaron disecciones conservadas en glicerina al 10 % y, para la determinación de algunos taxones de rotíferos, se realizó la digestión con NaOH de las partes blandas del organismo lo que permite el estudio del mástax, que es el criterio taxonómico que se emplea para la clasificación de un gran número de especies. Esta misma técnica se utilizó para ver el contenido estomacal del rotífero depredador *Asplanchna girodi* y anotar las especies de rotíferos sobre las que depredaba.

II.5.- REALIZACIÓN DE LAS BATIMETRÍAS Y OBTENCIÓN DE LOS PRINCIPALES PARÁMETROS MORFOMÉTRICOS.

Todas las lagunas de la zona de Arcas-Ballesteros así como de Fuentes fueron visitadas para realizar el estudio batimétrico durante el mes de marzo y los primeros días de abril de 1993. El nivel de agua en las lagunas era similar al observado en 1992.

Para la realización de las batimetrías se utilizó una ecosonda Yazaki modelo YDS-160. En primer lugar se prospectaba el contorno de la laguna y se elegía el diámetro mayor (longitud); éste se señalizaba clavando dos piquetas en ambas orillas, entre estas piquetas se pasaba una cuerda marcada cada metro y seguidamente con la

brújula se anotaba la dirección en la que se extendía este diámetro. A continuación se realizaba la ecosondación de este trayecto comenzando siempre por el punto desde el que se había anotado la dirección, para ello se circulaba en paralelo con el cable y a velocidad constante, realizando marcas en el papel de la ecosonda cada 10 m. Seguidamente se realizaba este mismo trayecto pero esta vez con una pesa atada a una cinta métrica inextensible y se realizaban medidas en distintos puntos de dicho diámetro, de metro en metro en las zonas donde la pendiente era máxima, y cada 2, 5 ó 10 metros en el resto del trayecto, en función de la forma de la cubeta obtenidla previamente por ecosondación.

El siguiente paso consistía en la elección de un segundo diámetro perpendicular al anterior (anchura), que dadas las características del tipo de lagunas (generalmente dolinas casi circulares), normalmente se cruzaba con el anterior en el centro de la laguna. Sin embargo, este segundo diámetro se intentaba hacer pasar por la zona de máxima profundidad de la laguna, y en algunas ocasiones el punto de cruce se situaba algo excéntrico. Una vez elegido este segundo diámetro se seguía el procedimiento descrito anteriormente. En algunas cubetas más complejas o que presentaban pozos o depresiones excéntricos se realizaron otros trayectos para definir mejor la batimetría de la cubeta (Arcas 2 (I), Las Zomas,...).

En el caso de la Laguna Grande del Tobar los datos se tomaron del trabajo realizado por Vicente *et al* (1993).

Posteriormente se realizaron los perfiles de los diámetros escogidos, utilizando los resultados de las pesas cotejados con las profundidades obtenidas en la ecosondación; también se calcularon distintos parámetros morfométricos según Wetzel y Likens (1979) y Timms (1992). Los parámetros morfométricos utilizados en este trabajo fueron:

- **Longitud (L)**: Corresponde a la distancia, en línea recta, entre los dos puntos más distantes del perímetro superficial del lago. En nuestro caso la mayoría de lagos tienen una forma casi circular y en estos casos esta longitud corresponde al diámetro mayor.
- **Anchura (A)**: Máxima distancia entre las orillas perpendiculares a la longitud, corresponde al diámetro menor en lagos de forma casi circular.
- **Diámetro medio (Dm)**: En la mayoría de lagos de forma casi circular se puede definir un diámetro medio como el promedio entre la longitud y la anchura.
- **Superficie (S)**: Superficie encerrada por el perímetro de la laguna medida en metros cuadrados. En la mayoría de estas dolinas cársticas, que son de forma casi circular, se ha aproximado la superficie a la de un círculo, utilizando para ello el diámetro medio.

$$S = \Pi \times (Dm/2)^2$$

Además de esta estima de la superficie también se realizó una estima (que fue la que finalmente se utilizó en los cuadros y para los análisis del capítulo IV.7) mediante análisis de imagen. En primer lugar se calcó el contorno de las diferentes lagunas (figura II.6) de fotografías aéreas (1986). Estos contornos se procesaron mediante un Scaner Hewlett Packard Scanjet IICx y las imágenes fueron analizadas mediante el programa NIH Image 1.58 que permite calcular las superficies y los perímetros de las figuras. Además en el caso de lagunas con formas muy diferentes de la circular, se realizaron diferentes medidas y, utilizando fotografías aéreas, se dibujó el contorno en papel milimetrado contando después los cuadrados para estimar la superficie (Olson 1960).

- **Perímetro**: Contorno de la laguna medido en metros.
- **Profundidad máxima (Zmax)**: La máxima profundidad de la laguna.
- **Profundidad media (Zmed)**: La profundidad media en nuestro caso se calculó mediante la siguiente fórmula:

$$Zmed = \Sigma Zi/\Sigma i + \Sigma Zj/\Sigma j$$

donde, Zi son las profundidades a la distancia i (i es la distancia a cada metro desde la orilla, en el punto de máxima longitud), y Zj las profundidades a la distancia j (siendo j la distancia de metro en metro desde la orilla, en el punto de máxima anchura).

- **Profundidad relativa (Zr)**: La máxima profundidad expresada como porcentaje del diámetro medio:

$$Zr = 100x\ Zm/Dm = 50\times\sqrt{Zm}/\sqrt{S}$$

- **Volumen (V)**: Hemos realizado una estima del volumen consederándolo como el producto de la superficie y la profundidad media:

$$V = S\times Zmed$$

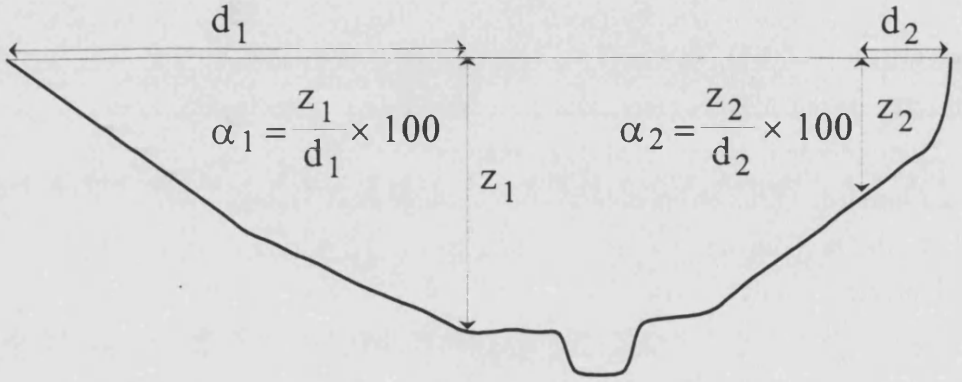
- **Pendiente media (α_{med})**: Se puede calcular despejando de la ecuación:

$$\alpha_{med} = 100\times Zmed/\sqrt{S}/\Pi$$

de manera aproximada también se puede calcular como el número de centímetros en profundidad por cada metro de distancia horizontal.

- **Pendiente del talud (α)**: Es el cociente entre la profundidad que alcanza el talud y la longitud recorrida en superficie para llegar a esta profundidad, expresada como porcentaje. Debido a la dificultad de delimitar el final del talud, en nuestro caso se ha

medido la pendiente en los 5 primeros metros y en los 10 metros de profundidad. Como en todos los casos se realizaron batimetrías en al menos dos de los diámetros de la laguna, se ha estimado la pendiente de los cuatro taludes correspondientes. Con estos datos se ha calculado una pendiente media en los 5 primeros metros (α_5, z_2 = 5 m) y otra en los 10 m (α_{10}, z_1 = 10 m) así como la desviación estandard en esta medida.



- **Desarrollo del perímetro (DP)**: Mide el grado de irregularidad del perímetro, es una medida morfométrica común pero en este caso por presentar muchas de nuestras lagunas perímetros de gran regularidad los valores de todas las lagunas estaban muy cercanos a uno, por lo que no se presentan los resultados.

II.6.- DESCRIPTORES BIOLÓGICOS UTILIZADOS

Para la comparación con los parámetros físico-químicos y el estudio del zooplancton se han utilizado algunos descriptores biológicos de las comunidades estudiadas.

La **diversidad** (H') ha sido calculada en cada una de las profundidades estudiadas y posteriormente promediada para obtener así una diversidad media (H'med), también fue calculada la diversidad conjunta de toda la columna de agua, es decir integrando las distintas muestras para una misma laguna (H'); para su cálculo se utilizó la fórmula de Shannon-Wiener (Shannon and Weaver, 1949):

$$H' = - \Sigma p_i \log_2 p_i$$

La **equitatividad** (E%) fue calculada como 100 H'/H'max, donde H'max = $\log_2$ S. (S = número de especies). También se utilizó un índice, llamado Índice de

Originalidad Floral o **IFO** (Puchalski, 1987), utilizado para evaluar la diferente composición de la fauna zooplanctónica existente entre los diferentes lagos estudiados:

$$IFO = \frac{\Sigma(1/M)}{S}$$

donde M = número de muestras en que se da una especie y S = número de especies en una muestra.

Junto a estos descriptores también se utilizaron: el **número de especies de zooplancton** (S), la **abundancia de zooplancton** el **número de huevos de los rotíferos** y la **abundancia de rotíferos planctónicos y litorales.**

II.7.- MÉTODOS ESTADÍSTICOS

Además de utilizar métodos estadísticos descriptivos como la media, varianza, frecuencia, ocurrencia, etc... Se han utilizado algunos programas de estadística multivariante para la ordenación y clasificación de las muestras:

- **Análisis de Correlación Canónica (CCA)**: El objetivo de este tipo de técnica de ordenación es encontrar unos ejes que maximicen y pongan de manifiesto la posible estructura común en la distribución de dos tipos de datos, por ejemplo entre variables abióticas y abundancias de organismos, Gauch (1982). Este análisis trata de buscar combinaciones lineales de cada uno de los conjuntos de variables observadas, de manera que el primer par de combinaciones lineales -o variables canónicas- extraído, sea el de las variables cuyo coeficiente de correlación entre ellas sea máximo y los otros pares sucesivos sean también los de mayor correlación, con la condición de que sean ortogonales a todas las combinaciones lineales derivadas anteriormente.

En nuestro caso (capítulo VI.1), este análisis se realizó para comparar densidades poblacionales de zooplancton y fitoplancton, previamente transformadas como ln(x+1). El programa utilizado fue el 6M incluído en el paquete estadístico BMDP (Dixon *et al.*, 1983).

- **Análisis de Componentes Principales (PCA)**: Goodall, en 1954, fue el primero en aplicar este método a datos ecológicos, aunque el método había sido previamente desarrollado por Pearson en 1901. Esta técnica de ordenación multivariante trabaja con la estructura interna de las matrices. Con ella se particiona una matriz de correlación en un grupo de ejes ortogonales llamados componentes, cada uno de los cuales corresponde a un *eigenvalue* de la matriz (el *eigenvalue* es la varianza que explica cada eje). Los *eigenvalues* se extraen en orden descendiente de magnitud, por lo están ordenados según

la cantidad de varianza que explican. Como resultado se obtiene un reducido sistema de coordenadas que proporciona información acerca de las semejanzas entre las distintas muestras y sobre cuales son las variables más importantes en la ordenación de las muestras. En realidad; reduce la dimensionalidad de un conjunto de datos a unas proporciones manejables preservando tanto como sea posible la estructura original de los datos. Está considerada como una técnica de ordenación bastante objetiva, sin embargo presenta algunos problemas pues se requiere por ejemplo, que las variables sean independientes y que los datos estén normalmente distribuidos,es por ello que se han utilizado transformaciones como ln(x+1) para las densidades de las especies y para la mayoría de datos abióticos.

Ha sido utilizada en los capítulos IV.5 y IV.7, su aplicación se realizó mediante el programa 4M del paquete estadístico BMDP (Dixon *et al.*, 1983), y del programa SPSS para WINDOWS versión 6.1.3.

- **Twinspan (Two-Way Indicator Species Analysis)**: Es un programa en Fortran diseñado para la clasificación de datos multivariados presentados en una tabla de doble entrada (Hill, 1979). En nuestro caso ha sido utilizado para la clasificación de las diferentes lagunas en base, únicamente, a las diferencias y similitudes que presentaron sus comunidades zooplanctónicas. Este programa realiza un proceso dicotómico que se alcanza en dos fases: en primer lugar, ordena los datos mediante "reciprocal averaging" y divide esta ordenación en dos mitades, posteriormente perfila esta división identificando un cierto número de especies preferenciales; aquellas que el programa determina como las más preferenciales son llamadas especies indicadoras. En este análisis las especies indicadoras son aquellas que se dan en al menos un tercio de una parte de la división y muy raramente en la otra división. Este programa se aplicó al estudio de las muestras de primavera del capítulo IV.7.

III.- ÁREA DE ESTUDIO

III.- AREA DE ESTUDIO

III.1.- SISTEMAS CÁRSTICOS

La región del *Karst* situada al Norte del Adriático en la península de Istria (actualmente Eslovenia), fue la primera en la que se realizaron investigaciones científicas sobre la circulación del agua en rocas calizas siendo la que da nombre a este tipo de sistemas. El vocablo *Karst* significa "campo de piedras calizas" en yugoslavo, equivale también al *Carso* italiano y a la *Causse* en Francia. Como se ha comentado en la introducción, en España los lagos de origen cárstico tienen gran importancia cuantitativa debida a la escasez general de lagos. Aunque la carstificación es un fenómeno universal, que se da sobre cualquier masa de rocas solubles en la que se produzca una circulación más o menos abundante de agua, la intensidad de la misma depende de una serie de factores como son: (1) solubilidad y composición de la roca; (2) agresividad del agua; (3) estructura geológica de la zona y (4) clima.

Los sistemas cársticos son aquellos que deben su evolución al desarrollo de los fenómenos cársticos, es decir, el conjunto de transformaciones que se producen en una región como consecuencia de la circulación del agua y disolución de las rocas. Las formaciones rocosas en las que el fenómeno cárstico alcanza su máximo desarrollo, son aquellas constituidas principalmente por calizas y dolomías. Los fenómenos cársticos se deben al equilibrio que se establece entre el agua y los carbonatos. Cuando por circunstancias geológicas o climáticas la circulación del agua se detiene, el fenómeno cárstico se detiene a su vez, reanudándose si se reanuda la circulación del agua. Por tanto el clima y principalmente la pluviosidad determinarán la actividad de estos fenómenos. En nuestro caso, climas mediterráneos con precipitaciones entre 500-600 mm anuales, este tipo de fenómenos cársticos presentan una actividad intermitente, no muy intensa y con importantes oscilaciones en el caudal de agua, aunque en el pasado pudo tener una mayor importancia.

En la España peninsular existen unos 100000 Km^2 de dominio calizo de los que aproximadamente la mitad corresponden al Sistema Ibérico. Con el nombre de caliza designamos en realidad a un conjunto de rocas de composición a veces muy heterogénea, aunque en ellas domina como componente el CO_3Ca, en el caso de contener también CO_3Mg se denominan calizas dolomíticas o dolomías, según la proporción de magnesio. Los fenómenos cársticos también se pueden producir sobre otro tipo de rocas que presenten gran solubilidad en agua como son yesos y sales. En nuestro caso hemos estudiados lagunas cársticas formadas sobre dolomías y también

sobre margas yesosas, con las consiguientes implicaciones que esto tiene sobre la composición del agua, con una mayor cantidad de sulfatos en las aguas de las lagunas formadas sobre yesos.

Existe un conjunto de equilibrios químicos que determinan la disolución de las calizas y dolomías. Ésta fundamentalmente depende de la concentración de anhídrido carbónico que se disuelve en agua y forma ácido carbónico, este agua en contacto con la roca carbonatada disuelve los carbonatos formando bicarbonatos que son muy solubles en el agua. Hay varios factores que afectan a estos equilibrios, la cantidad de CO_2 disuelto en agua es muy variable y depende de varios factores como: la presión parcial en la atmósfera, la temperatura, la actividad de los organismos, etc...

La erosión producida por la disolución de las rocas da lugar a cubetas de forma circular, o muy próxima a la circular, este tipo de cubetas se conocen como dolinas que localmente se denominan torcas. Cuando dos o más dolinas se fusionan, se origina una formación denominada uvala. La mayoría de lagunas estudiadas en este trabajo están formadas por dolinas singulares e isótropas (es decir con relación de diámetros próxima a 1:1), existiendo un número reducido de lagunas formadas por la fusión de dos o más dolinas, pero que conservan una estructura de cubetas bien diferenciadas y separadas por una zona de aguas someras. Este tipo de erosión determina una serie de características morfométricas particulares de este tipo de lagunas como son: la forma circular (o de ∞ cuando son dos las dolinas), la gran profundidad relativa y lo abrupto de sus pendientes.

En la provincia de Cuenca encontramos sistemas cársticos desarrollados sobre dos tipos principales de sustratos; (1) sobre sustrato calizo o dolomítico como son las torcas (dolinas) de Cañada del Hoyo y el lago del Tobar, y (2) sobre margas yesosas como son los humedales de Arcas-Ballesteros y de la zona de Fuentes. En la figura III.1 se muestra la situación de las distintas zonas donde se localizan las lagunas, así como la ubicación de cada una de las lagunas en sus respectivas zonas.

Las lagunas estudiadas se encuentran en la parte noroccidental de la provincia de Cuenca. En su mayor parte están situadas en las primeras estribaciones de la serranía, a una altura cercana a los 1000 m pero inmersas en relieves suaves; por contra la laguna del Tobar esta situada cerca del límite con Guadalajara al norte de la provincia, en un enclave montañoso y a una altura próxima a los 1300 m.

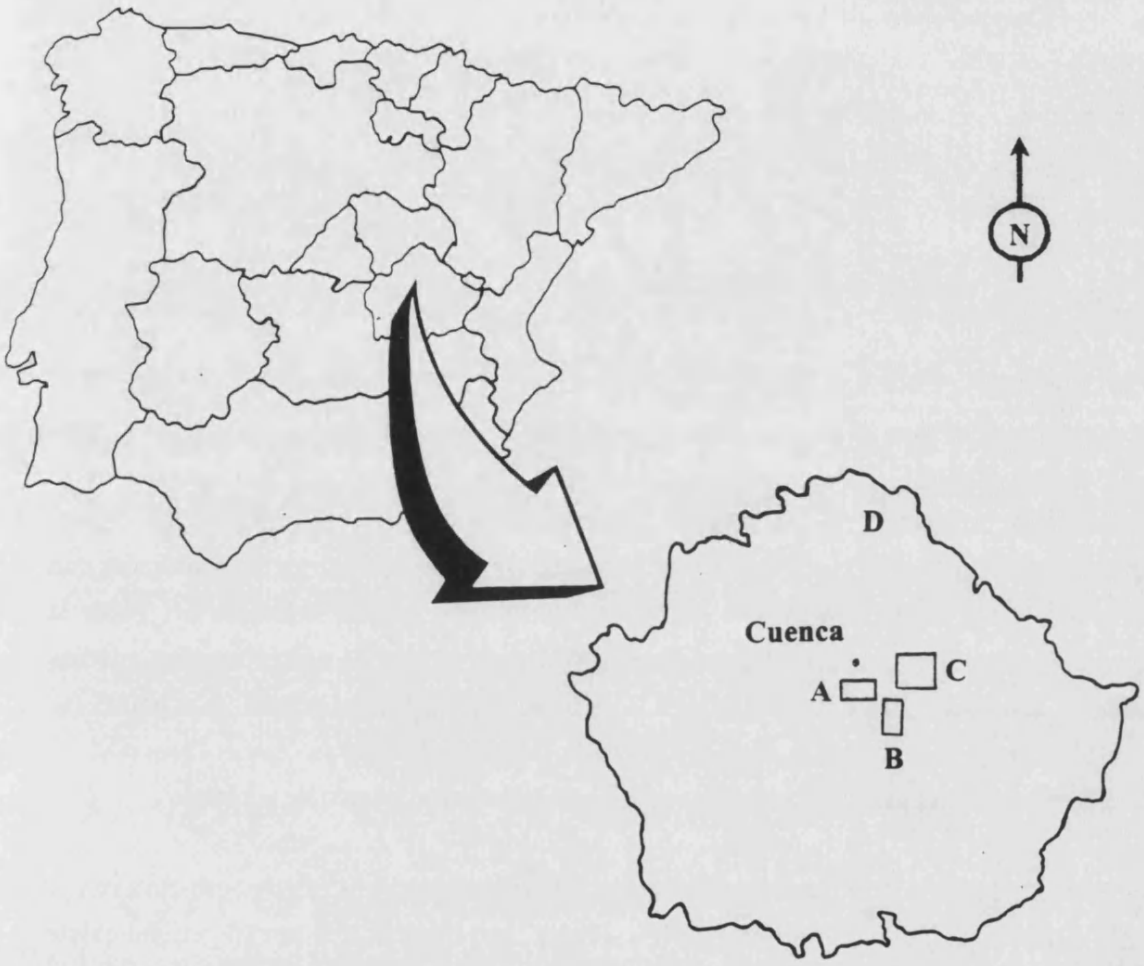
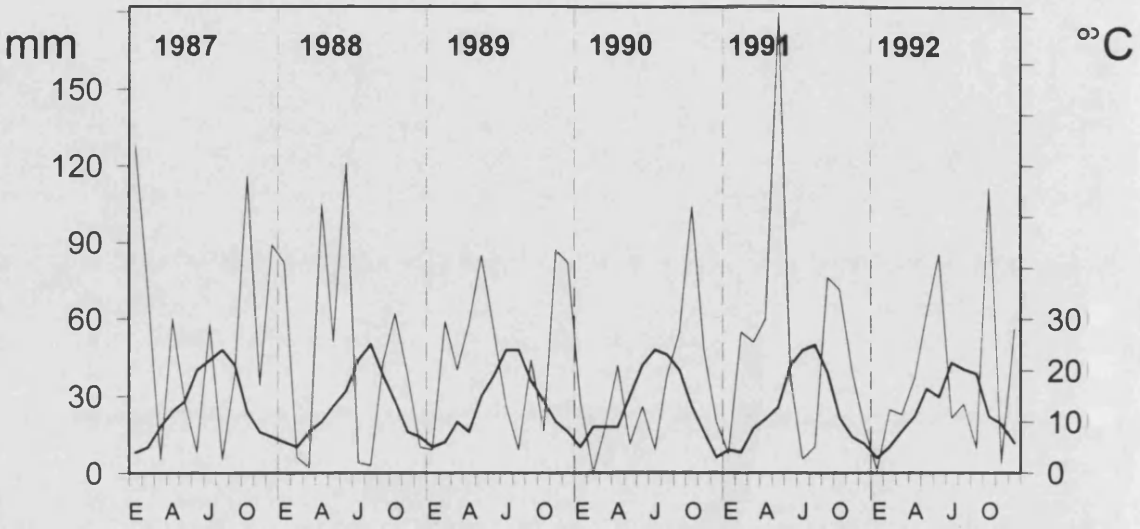


Figura III.1: Ubicación de las tres zonas con complejos lagunares estudiadas (A,B y C), así como del lago del Tobar (D) en la provincia de Cuenca.

A: Zona de Arcas-Ballesteros
B: Zona de Fuentes
C: Zona de Cañada del Hoyo
D: Lago del Tobar

Los datos meteorológicos que presentamos en la figura III.2 son los de lla Estación Meteorológica de la ciudad de Cuenca, pues a excepción de la laguna deel Tobar las otras lagunas solamente distan entre 9 y 24 Km de esta ciudad, estandlo inmersas en un relieve semejante al de los alrededores de la ciudad. En una amplia zonaa,



que incluye tanto a las lagunas como a la ciudad de Cuenca, el clima es semejante con precipitaciones anuales en torno a los 500-600 mm. Es de nuevo la laguna del Tobar lla que se encuentra en una zona ligeramente diferente en la que las precipitaciones mediias anuales sobrepasan los 650 mm anuales y las temperaturas son en general más bajas.

Figura III.2: Diagrama ombrotérmico de la estación meteorológica de Cuenca.

En el diagrama ombrotérmico (Figura III.2) se observa que por lo general existte una estación seca bien marcada, que corresponde al verano, y otro periodo secundario dle sequía poco marcado durante algunos de los inviernos.

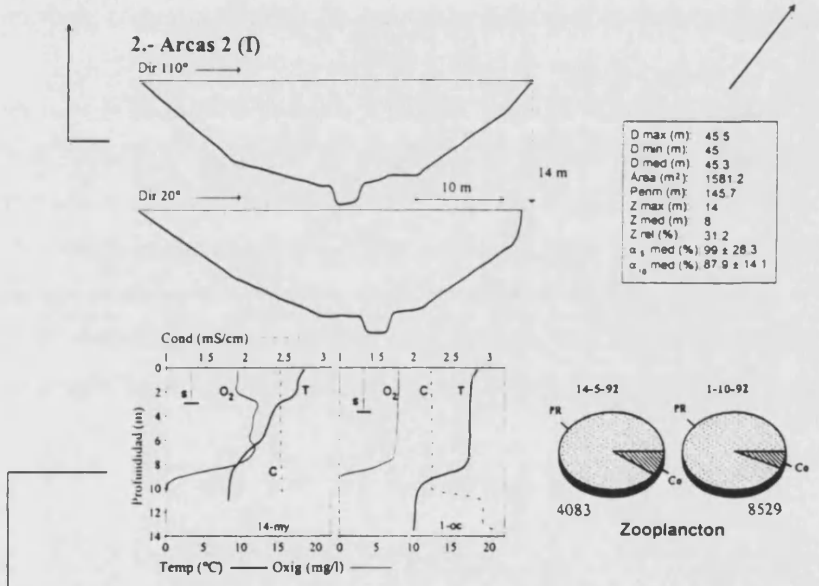
III.2.- CUADROS RESUMEN DE LAS PRINCIPALES CARACTERÍSTICAS DE LAS LAGUNAS ESTUDIADAS EN ESTE TRABAJO

A continuación se presentan una serie de fichas (cuadros) donde se resumen algunas características de las lagunas estudiadas. En primer lugar se presenta de manera breve la zona estudiada y posteriormente las fichas correspondientes a las lagunas de esa zona.

El siguiente esquema explica cómo están organizadas estas fichas:

Sección de dos perfiles batimétricos: el superior corresponde generalmente con el diámetro máximo y el inferior con el perpendicular a éste. La dirección de ambas secciones se indica en grados. El segmento indica la escala aproximada, que es la misma en sentido vertical y horizontal.

Principales características batimétricas y morfométricas .
D max-min-med= Diámetro máximo -mínimo-medio. Z max-med-rel = Profundidad máxima -media-relativa. α (5,10) med = Pendiente media en los 5 y 10 m de profundidad.



Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	13.3 ± 4	17.3 ± 1.2	Fosfato (µM):	0	0
Cond (mS/cm):	2.47 ± 0.01	2.24 ± 0.01	Silicato (µM):	169.1 ± 24.4	258.1 ± 25.9
Oxig (mg/l):	8.7 ± 5.1	6.4 ± 2.6	Sulfato (meq/l):	33.6 ± 1.6	38.7
Oxig (%sat):	82.5 ± 57.9	72 ± 30.4	Cloruro (meq/l):	0.23	0.26 ± 0.02
Secchi (m):	3.1	3.8	Alcalin (meq/l):	4.07 ± 0.16	4.07
pH:	8.1 ± 0.2	8 ± 0.1	Ca (mM):	16.95 ± 0.1	- -
Clor. a (mg /m):	4.54 ± 1.78	5.1 ± 0.3	Mg (mM):	2.95 ± 0.06	- -
Nitrito (µM):	0.05 ± 0.04	0.01 ± 0.02	Na (mM):	0.18 ± 0.01	- -
Nitrato (µM):	24.25 ± 5.06	12.6 ± 0.8	K (mM):	0.05	- -
Amonio (µM):	73.55 ± 39.2	21.3 ± 6.5	nº muestras (n):	4	3

Tabla en la que se muestran promediadas las principales características físico-químicas en las dos fechas de muestreo

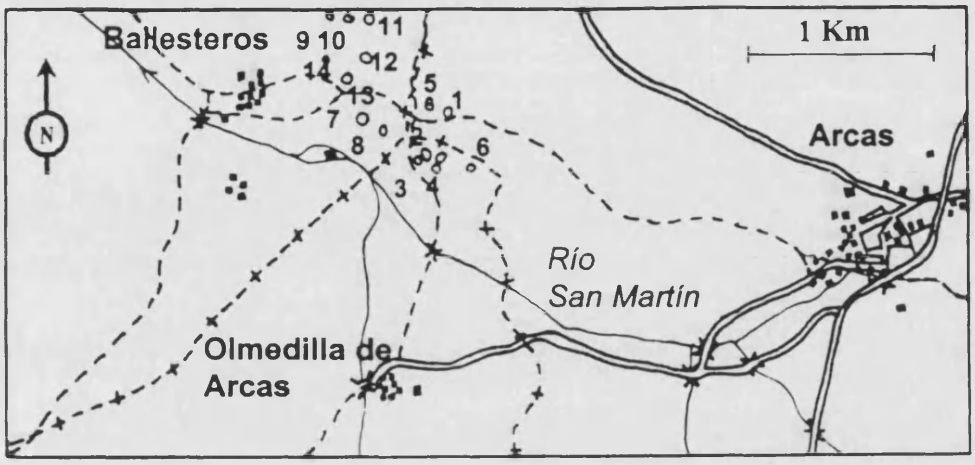
Perfiles verticales de algunos parámetros físico-químicos medidos *in situ*, indicando la fecha del muestreo. En los muestreos correspondientes al mes de octubre en los que se registró una apreciable disminución de la profundidad, el nuevo nivel del fondo se indica en la gráfica.

Gráfica de sectores que refleja la proporción de los grandes grupos del zooplancton en los diferentes muestreos. PR = rotíferos planctónicos, LR = rotíferos litorales, Co = copépodos, Cl = Cladóceros y Ot = otros grupos

a) Zona de Arcas-Ballesteros. Está formada por un conjunto de lagunas que se distribuyen por los términos municipales de Villar de Olalla, Arcas del Villar y Vardetórtola (UTM 30 SWK 732276), y dista aproximadamente 9 Km en línea recta de la ciudad de Cuenca. Las lagunas están situadas en la zona conocida como las Majadillas, en la margen derecha del río San Martín, donde se localizan al menos 35 dolinas, muchas con aguas permanentes, algunas con aguas temporales y otras sin agua. En su mayoría tienen forma casi circular y cuando presentan otras formas se debe generalmente a que están constituidas por yuxtaposición de dos o más dolinas. Las aguas de estas lagunas poseen conductividades entre 2 y 11 mS/cm y sus profundidades oscilaron en el momento de nuestro estudio entre 1.5 y 14.3 m. Desde un punto de vista físico-químico, el conjunto de estas lagunas fueron caracterizadas en 1986 (Rodrigo, 1997) y por Santos Cirujano en lo referente a la vegetación acuática. En este trabajo se han estudiado un total de 15 de estas dolinas con aguas permanentes, tres de ellas presentaban muy poca profundidad y, bajo condiciones de estiaje intenso, podrían reducir mucho su superficie (ver figuras III.1 y III.3).

Entre ellas destaca la denominada Arcas-2 formada por dos dolinas la mayor de las cuales presenta una marcada estratificación de sus aguas en el periodo estival. Sobre la laguna de Arcas-2 existen varios trabajos: una primera caracterización efectuada por Vicente *et al.* (1991), un estudio de la diversidad y distribución de las poblaciones de protozoos ciliados (Finlay *et al.*, 1991, Esteban *et al.*, 1993) y un estudio de la distribución de las poblaciones bacterianas (Camacho, 1997). En los capítulos IV.1, IV.4 y IV.5, se estudia el ciclo anual y la marcada estratificación de las poblaciones zooplanctónicas.

A.- Zona de Arcas-Ballesteros

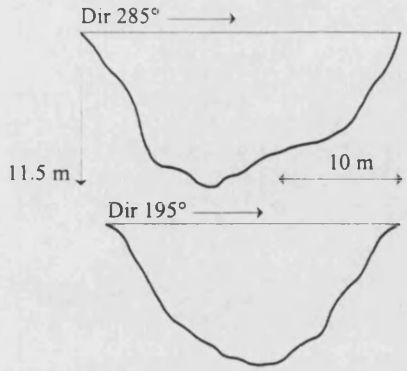


A.- Zona de Arcas-Ballesteros

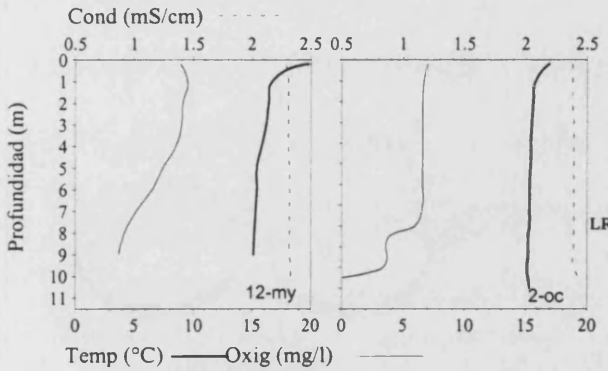
Lagunas de:

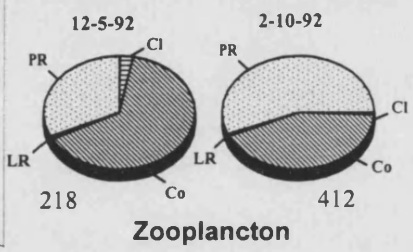
1.- Arcas 1
2.- Arcas 2 (I)
3.- Arcas 2 (II)
4.- Arcas 3 (II)
5.- Arcas 4
6.- Rincón
7.- Barraganes 1
8.- Barraganes 2
9.- Ballesteros 1
10.- Ballesteros 2
11.- Ballesteros 3
12.- Ballesteros 4
13.- Ballesteros 5
14.- Ballesteros 6

1.- Arcas 1



D max (m):	24
D min (m):	22
D med (m):	23
Área (m^2):	389.2
Perim (m):	74
Z max (m):	11.5
Z med (m):	6.9
Z rel (%):	51.7
α med (%):	149.0 ± 18.3
α^{5}_{10} med (%):	111.4 ± 14.2

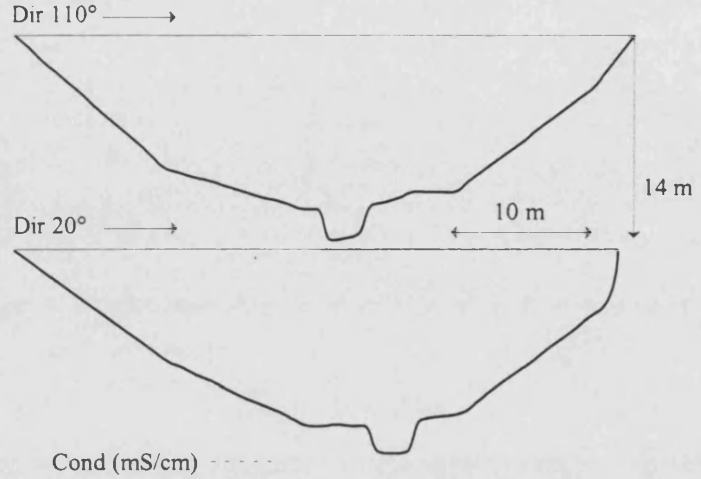




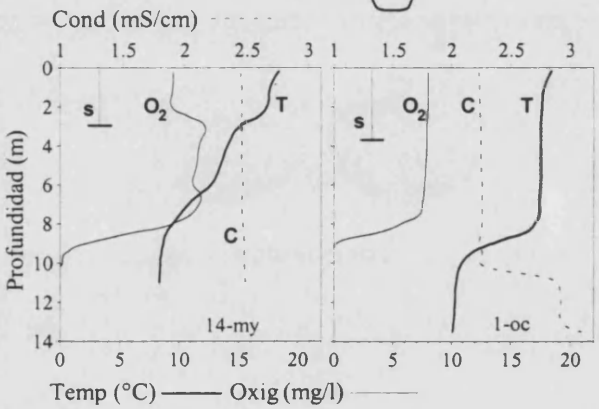
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	15.7 ± 0.9	15.4 ± 0.4	Fosfato (µM):	0.04 ± 0.06	0
Cond (mS/cm):	2.32 ± 0.01	2.39 ± 0.02	Silicato (µM):	134.8 ± 13.2	135.7 ± 3.1
Oxig (mg/l):	6.9 ± 2.9	5.1 ± 2.3	Sulfato (meq/l):	26.7 ± 0.4	31.7 ± 1.6
Oxig (%sat):	43.5 ± 34.9	60.7 ± 20.5	Cloruro (meq/l):	0.17 ± 0.01	0.20 ± 0.01
Secchi (m):	4.7	6.5	Alcalin (meq/l):	4.84 ± 0.05	4.80 ± 0.03
pH:	7.3 ± 0.2	7.3 ± 0.1	Ca (mM):	16.13 ± 0.23	- -
Clor. a (mg /m):	4.30 ± 1.80	3.70 ± 1.33	Mg (mM):	1.86 ± 0.01	- -
Nitrito (µM):	0.09 ± 0.02	0.44 ± 0.31	Na (mM):	0.1	- -
Nitrato (µM):	128.9 ± 4.5	99.9 ± 10.7	K (mM):	0.03	- -
Amonio (µM):	37.9 ± 17.8	9.0 ± 3.4	nº muestras (n):	3	3

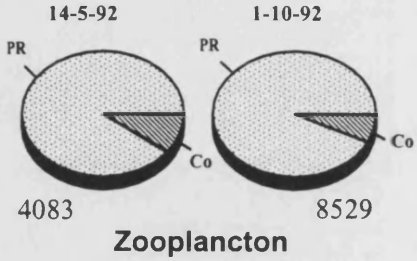
Cuadro 1

2.- Arcas 2 (I)



D max (m):	45.5
D min (m):	45
D med (m):	45.3
Área (m^2):	1581.2
Perim (m):	145.7
Z max (m):	14
Z med (m):	8
Z rel (%):	31.2
α_5 med (%):	99 ± 28.3
α_{10} med (%):	87.9 ± 14.1

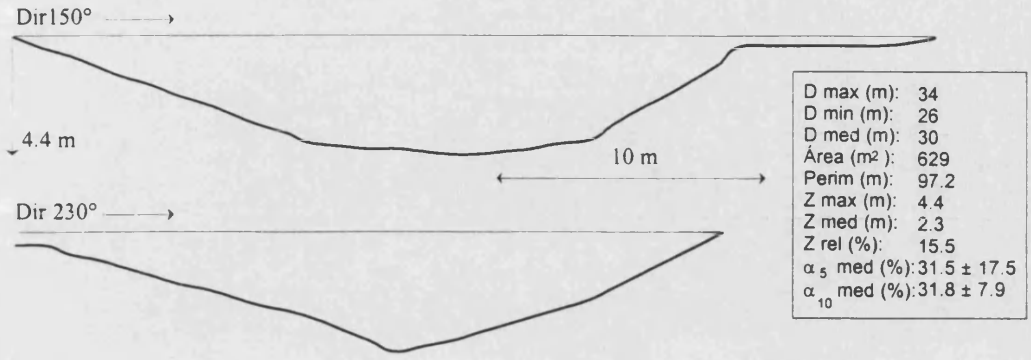




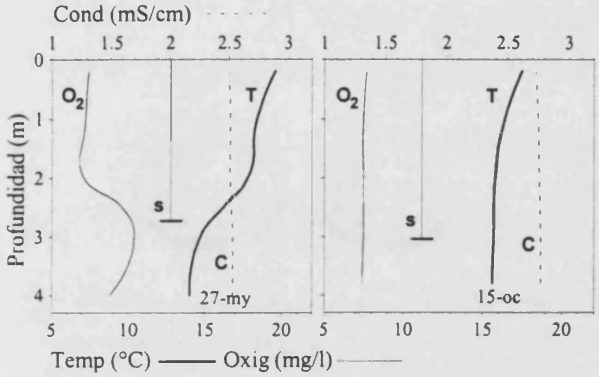
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	13.3 ± 4	17.3 ± 1.2	Fosfato (µM):	0	0
Cond (mS/cm):	2.47 ± 0.01	2.24 ± 0.01	Silicato (µM):	169.1 ± 24.4	258.1 ± 25.9
Oxig (mg/l):	8.7 ± 5.1	6.4 ± 2.6	Sulfato (meq/l):	33.6 ± 1.6	38.7
Oxig (%sat):	62.5 ± 57.9	72 ± 30.4	Cloruro (meq/l):	0.23	0.26 ± 0.02
Secchi (m):	3.1	3.8	Alcalin (meq/l):	4.07 ± 0.16	4.07
pH:	8.1 ± 0.2	8 ± 0.1	Ca (mM):	16.95 ± 0.1	- -
Clor. a (mg /m):	4.54 ± 1.78	5.1 ± 0.3	Mg (mM):	2.95 ± 0.06	- -
Nitrito (µM):	0.05 ± 0.04	0.01 ± 0.02	Na (mM):	0.18 ± 0.01	- -
Nitrato (µM):	24.25 ± 5.06	12.6 ± 0.8	K (mM):	0.05	- -
Amonio (µM):	73.55 ± 39.2	21.3 ± 6.5	nº muestras (n):	4	3

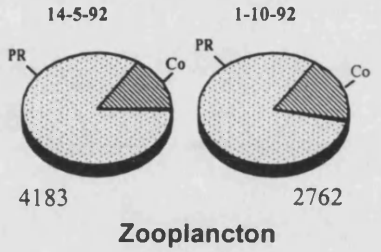
Cuadro 2

3.- Arcas 2 (II)



D max (m):	34
D min (m):	26
D med (m):	30
Área (m^2):	629
Perim (m):	97.2
Z max (m):	4.4
Z med (m):	2.3
Z rel (%):	15.5
α_5 med (%):	31.5 ± 17.5
α_{10} med (%):	31.8 ± 7.9

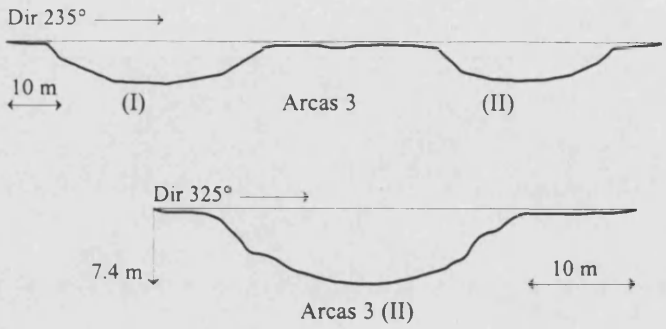




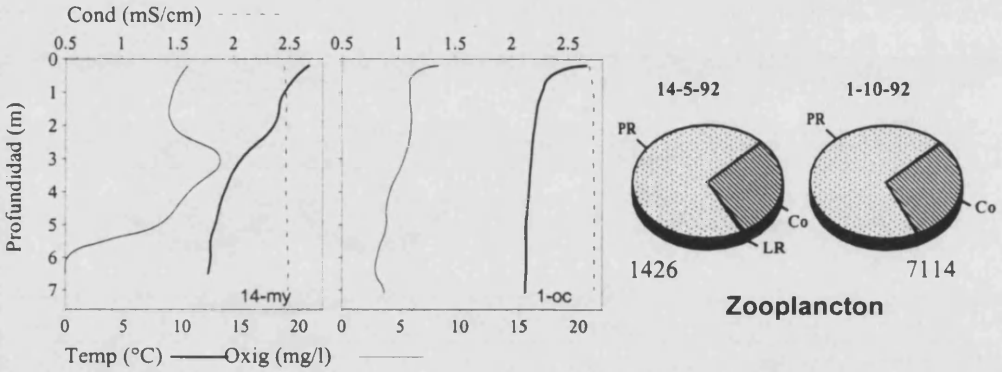
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	16.2	15.8	Fosfato (µM):	0	0
Cond (mS/cm):	2.52	2.77	Silicato (µM):	159.6	365.2
Oxig (mg/l):	9.6	7.5	Sulfato (meq/l):	30.8	40.6
Oxig (%sat):	106	81	Cloruro (meq/l):	0.23	0.24
Secchi (m):	2.7	3.1	Alcalin (meq/l):	4.02	3.81
pH:	7.9	7.9	Ca (mM):	17.4	- -
Clor. a (mg /m):	3.78	3.34	Mg (mM):	3.2	- -
Nitrito (µM):	0.1	0.04	Na (mM):	0.18	- -
Nitrato (µM):	14.4	6.9	K (mM):	0.05	- -
Amonio (µM):	81.1	21.5	nº muestras (n):	1	1

Cuadro 3

4.- Arcas 3 (II)



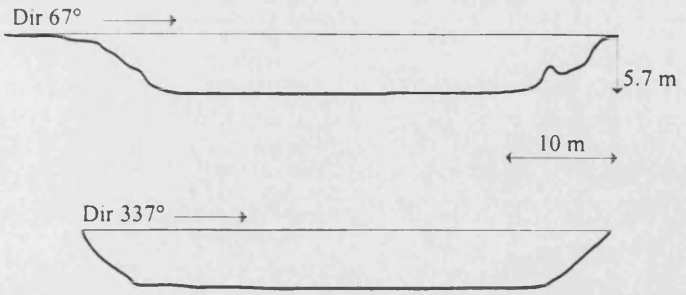
D max (m):	45
D min (m):	45
D med (m):	45
Área (m^2):	1590.4
Perim (m):	148.6
Z max (m):	7.4
Z med (m):	3.3
Z rel (%):	16.4
α_{med} (%):	35.5 ± 49.7
α^{5}_{10} med (%):	35.5 ± 28.1



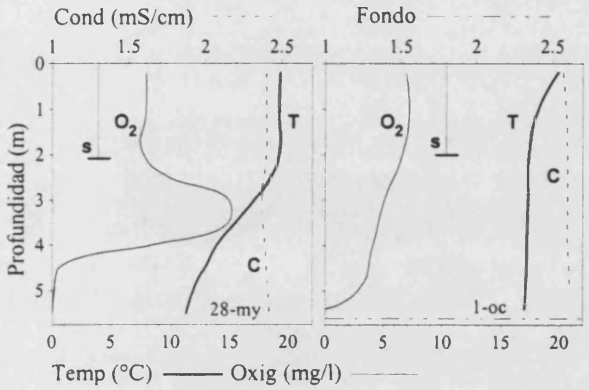
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	15.4 ± 3.2	16.1 ± 0.7	Fosfato (µM):	0	0
Cond (mS/cm):	2.47 ± 0.01	2.73 ± 0.01	Silicato (µM):	60.5 ± 8.2	300.5 ± 5.8
Oxig (mg/l):	8.6 ± 4.9	4.3 ± 1.5	Sulfato (meq/l):	31.4 ± 1.1	39.9
Oxig (%sat):	95 ± 55.3	47.7 ± 17.2	Cloruro (meq/l):	0.21 ± 0.01	0.29 ± 0.04
Secchi (m):	3	3.9	Alcalin (meq/l):	2.63 ± 0.23	2.88 ± 0.12
pH:	8.1 ± 0.2	7.6 ± 0.1	Ca (mM):	- -	- -
Clor. a (mg /m):	5.97 ± 1.80	5.46 ± 2.64	Mg (mM):	- -	- -
Nitrito (µM):	0.003 ± 0.01	0.02 ± 0.02	Na (mM):	- -	- -
Nitrato (µM):	0.08 ± 0.13	0.29 ± 0.07	K (mM):	- -	- -
Amonio (µM):	50.9 ± 37.7	30.4 ± 0.4	nº muestras (n):	3	3

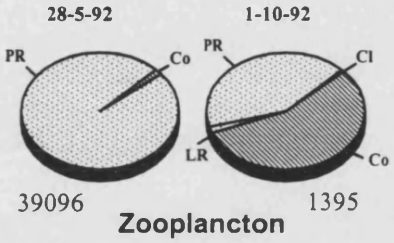
Cuadro 4

6.- Rincón



D max (m):	54.5
D min (m):	47
D med (m):	50.8
Área (m^2):	1427.8
Perim (m):	140
Z max (m):	5.7
Z med (m):	4.5
Z rel (%):	13.4
α_5 med (%):	72.8 ± 47.5
α_{10} med (%):	38.5 ± 20.5

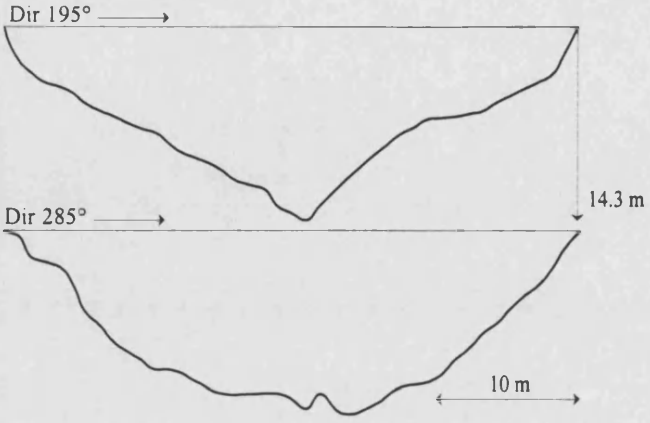




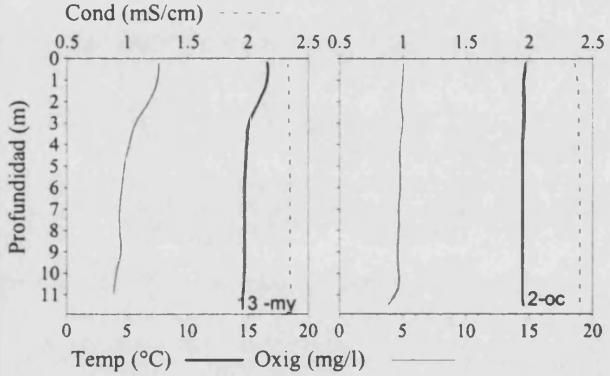
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	16.4 ± 3.2	17.6 ± 0.6	Fosfato (µM):	0.02 ± 0.04	0.01
Cond (mS/cm):	2.39 ± 0.02	2.60 ± 0.01	Silicato (µM):	37.7 ± 2.3	40.4 ± 0.1
Oxig (mg/l):	7.8 ± 7.2	5.0 ± 2.2	Sulfato (meq/l):	35.0 ± 0.6	36.7 ± 0.8
Oxig (%sat):	89 ± 81.1	57.3 ± 25.0	Cloruro (meq/l):	0.24 ± 0.03	0.26 ± 0.02
Secchi (m):	2.1	2.0	Alcalin (meq/l):	3.48 ± 0.07	3.28 ± 0.30
pH:	7.8 ± 0.1	7.6 ± 0.1	Ca (mM):	16.63 ± 0.25	- -
Clor. a (mg /m):	7.56 ± 1.55	20.03 ± 2.65	Mg (mM):	2.93 ± 0.06	- -
Nitrito (µM):	0.48 ± 0.18	0.02 ± 0.02	Na (mM):	0.17 ± 0.01	- -
Nitrato (µM):	0.62 ± 0.59	1.18 ± 0.21	K (mM):	0.1 ± 0.01	- -
Amonio (µM):	32.3 ± 27.8	25.6 ± 9.1	nº muestras (n):	3	3

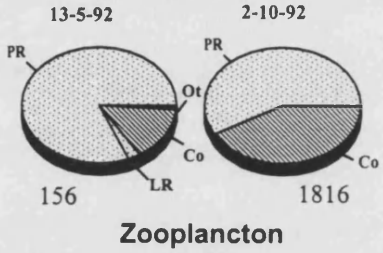
Cuadro 5

7.- Barraganes 1



D max (m):	42
D min (m):	42
D med (m):	42
Área (m^2):	1612.7
Perim (m):	147
Z max (m):	14.3
Z med (m):	8.1
Z rel (%):	31.6
α_5 med (%):	108.8 ± 14.2
α_{10} med (%):	93.8 ± 24.7



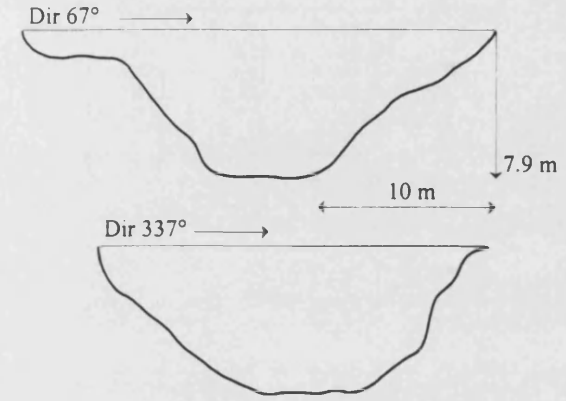


Zooplancton

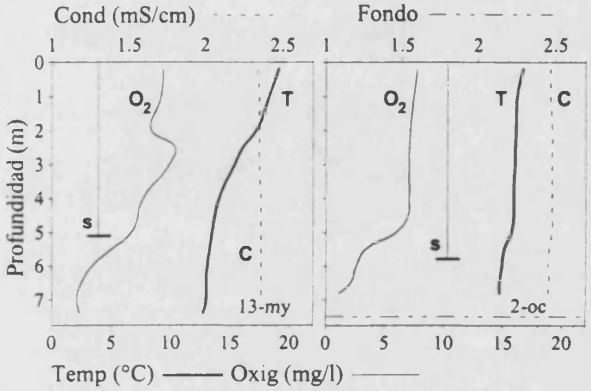
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	15.3 ± 4.5	14.5 ± 0.1	Fosfato (µM):	0.07 ± 0.06	0
Cond (mS/cm):	2.36 ± 0.02	2.39 ± 0.01	Silicato (µM):	155.1 ± 10.7	152.8 ± 4.2
Oxig (mg/l):	5.5 ± 1.8	4.8 ± 0.2	Sulfato (meq/l):	28.1 ± 0.5	31.0 ± 0.6
Oxig (%sat):	59.7 ± 20.6	51.3 ± 1.5	Cloruro (meq/l):	0.21 ± 0.03	0.26 ± 0.03
Secchi (m):	2.1	1.6	Alcalin (meq/l):	4.88 ± 0.07	4.88 ± 0.07
pH:	7.3 ± 0.1	7.2	Ca (mM):	15.27 ± 0.25	- -
Clor. a (mg /m):	7.92 ± 1.55	5.09 ± 1.96	Mg (mM):	2.23 ± 0.01	- -
Nitrito (µM):	0.07	0.08 ± 0.03	Na (mM):	0.13 ± 0.01	- -
Nitrato (µM):	161.5 ± 10.1	174.9 ± 9.2	K (mM):	0.04 ± 0.01	- -
Amonio (µM):	59.1 ± 13.8	17.5 ± 5.3	nº muestras (n):	3	3

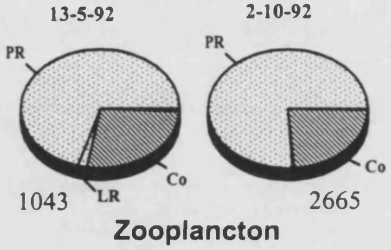
Cuadro 6

8.- Barraganes 2



D max (m):	24.8
D min (m):	20.5
D med (m):	22.7
Área (m^2):	283.5
Perim (m):	62.5
Z max (m):	7.9
Z med (m):	4.9
Z rel (%):	41.6
α_5 med (%):	86.0 ± 45.1
α_{10} med (%):	83.0 ± 19.1



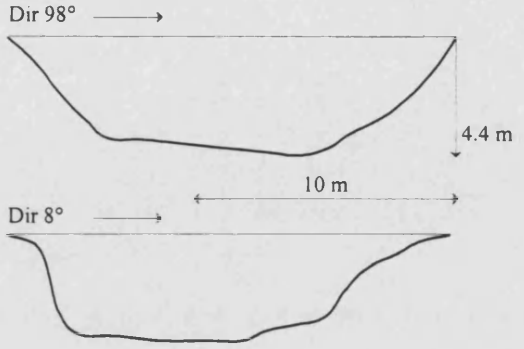


Zooplancton

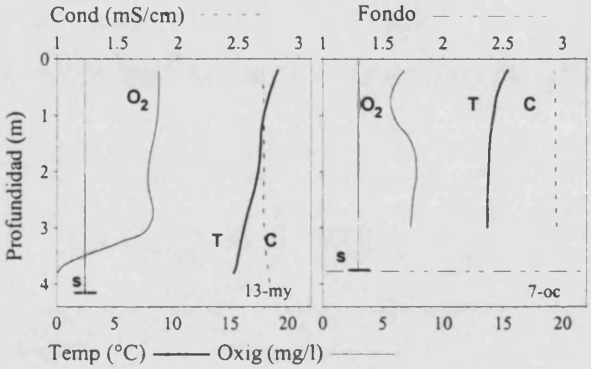
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	15.1 ± 2.8	15.8 ± 0.6	Fosfato (µM):	0.03 ± 0.05	0
Cond (mS/cm):	2.36 ± 0.01	2.47 ± 0.01	Silicato (µM):	80.1 ± 35.0	215.0 ± 7.1
Oxig (mg/l):	6.5 ± 3.5	6 ± 2.3	Sulfato (meq/l):	28.8 ± 0.6	33.5 ± 0.6
Oxig (%sat):	71.0 ± 40.6	66 ± 25.2	Cloruro (meq/l):	0.22 ± 0.01	0.24 ± 0.01
Secchi (m):	5.1	5.8	Alcalin (meq/l):	4.48 ± 0.05	4.48 ± 0.05
pH:	7.6 ± 0.2	7.5 ± 0.1	Ca (mM):	16.47 ±1.24	2.67-
Clor. a (mg /m):	3.23 ± 0.44	3.20 ± 0.19	Mg (mM):	± 0.15	- -
Nitrito (µM):	0.13 ± 0.05	0.19 ± 0.1	Na (mM):	0.20 ± 0.09	- -
Nitrato (µM):	51.13 ± 21.18	50.87 ± 8.06	K (mM):	0.04	- -
Amonio (µM):	99.9 ± 23.8	215.0 ± 7.1	nº muestras (n):	3	3

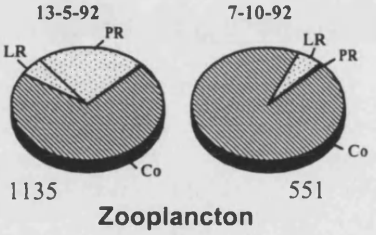
Cuadro 7

9.- Ballesteros 1



D max (m):	17
D min (m):	16.5
D med (m):	16.8
Área (m^2):	141.3
Perim (m):	43.7
Z max (m):	4.4
Z med (m):	2.9
Z rel (%):	32.8
α_5 med (%):	98.8 ± 35.8
α_{10} med (%):	66.8 ± 20.9

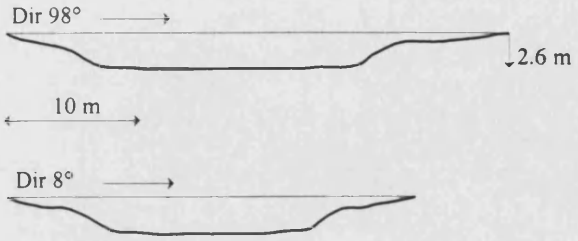




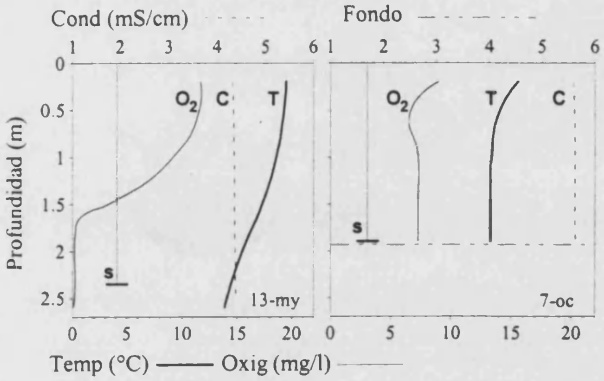
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	16.8 ± 1.6	14.3 ± 0.6	Fosfato (µM):	0.07 ± 0.09	0.17 ± 0.03
Cond (mS/cm):	2.72 ± 0.01	2.94 ± 0.01	Silicato (µM):	200.8 ± 5.7	328.5 ± 19.1
Oxig (mg/l):	5.5 ± 4.5	6.9 ± 1.3	Sulfato (meq/l):	38.5 ± 1.1	44.6 ± 0.9
Oxig (%sat):	62.5 ± 53	73 ± 12.7	Cloruro (meq/l):	0.24	0.46 ± 0.01
Secchi (m):	4.2 (f)	3.8 (f)	Alcalin (meq/l):	3.59 ± 0.16	4.75 ± 0.03
pH:	7.7	7.4	Ca (mM):	17.4	- -
Clor. a (mg /m):	3.45 ± 3.57	3.80 ± 0.16	Mg (mM):	4.35 ± 0.07	- -
Nitrito (µM):	0.15 ± 0.05	0.05 ± 0.01	Na (mM):	0.41 ± 0.01	- -
Nitrato (µM):	0.03 ± 0.04	0.26 ± 0.07	K (mM):	0.18 ± 0.14	- -
Amonio (µM):	86.8 ± 1.1	13.8 ± 8.5	nº muestras (n):	2	2

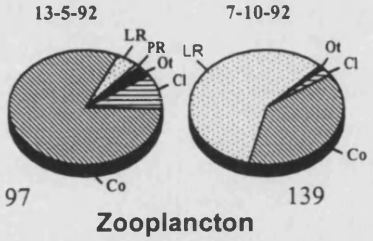
Cuadro 8

10.- Ballesteros 2



D max (m):	36.5
D min (m):	30
D med (m):	33.3
Área (m^2):	509.1
Perim (m):	84.6
Z max (m):	2.6
Z med (m):	1.7
Z rel (%):	10.2
α_5 med (%):	21.3 ± 7.4
α_{10} med (%):	27.6 ± 8.8



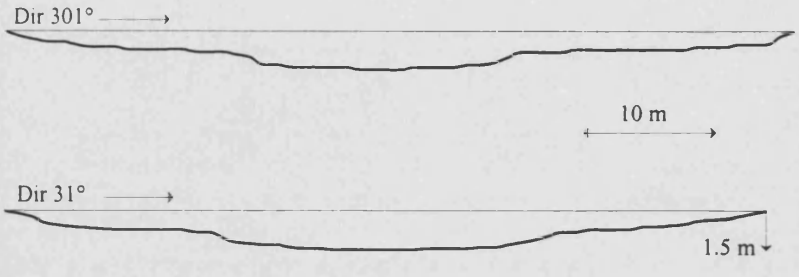


Zooplancton

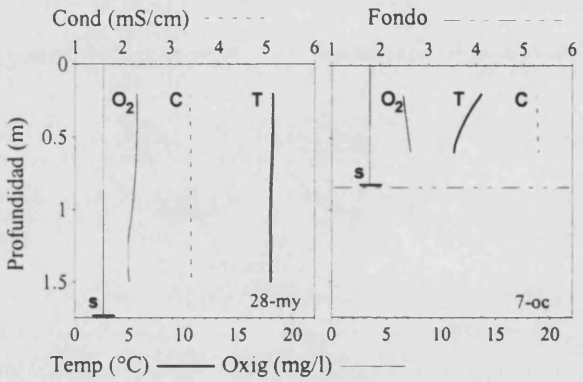
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	18.3 ± 1.4	13.7 ± 0.6	Fosfato (µM):	0.01 ± 0.02	0.15 ± 0.03
Cond (mS/cm):	4.34 ± 0.01	5.62 ± 0.01	Silicato (µM):	178.9 ± 6.4	610.5 ± 10.6
Oxig (mg/l):	7.5 ± 5.9	7 ± 0.4	Sulfato (meq/l):	78.9 ± 3.6	105.1 ± 2.7
Oxig (%sat):	85.5 ± 68.6	74 ± 4.2	Cloruro (meq/l):	1.99 ± 0.04	2.4
Secchi (m):	2.4	1.9 (f)	Alcalin (meq/l):	3.30 ± 0.06	4.12 ± 0.12
pH:	8.1 ± 0.1	8	Ca (mM):	14.93 ± 0.6	- -
Clor. a (mg /m):	1.28 ± 0.76	2.68 ± 0.31	Mg (mM):	28.80 ± 0.57	- -
Nitrito (µM):	0.12 ± 0.01	0.17 ± 0.01	Na (mM):	2.22 ± 0.03	- -
Nitrato (µM):	0.16 ± 0.07	0.02 ± 0.02	K (mM):	0.55	- -
Amonio (µM):	123 ± 29	29.1 ± 14.8	n° muestras (n):	2	2

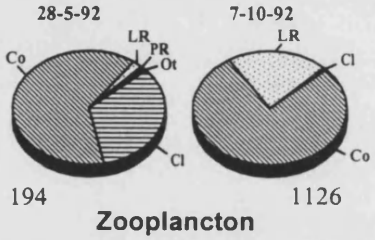
Cuadro 9

11.- Ballesteros 3



D max (m):	58
D min (m):	56
D med (m):	57
Área (m^2):	1592.4
Perim (m):	147.6
Z max (m):	1.5
Z med (m):	0.9
Z rel (%):	3.3
α med (%):	17.8 ± 5.3
α_{10}^{5} med (%):	14.5 ± 0.6



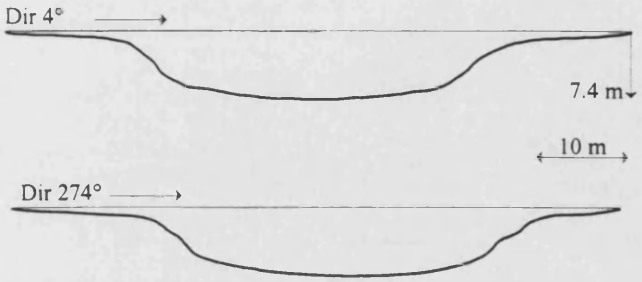


Zooplancton

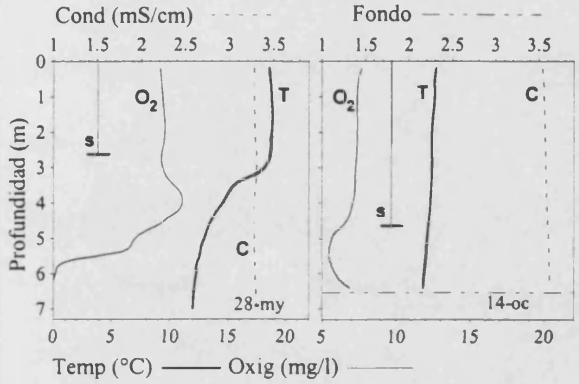
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	18.1 ± 0.1	11.5	Fosfato (µM):	0.07 ± 0.1	0.38
Cond (mS/cm):	3.43 ± 0.01	5.3	Silicato (µM):	238.3 ± 6.9	706
Oxig (mg/l):	5.35 ± 0.5	9	Sulfato (meq/l):	64 ± 0.1	79.7
Oxig (%sat):	62.0 ± 5.7	71	Cloruro (meq/l):	0.98 ± 0.01	1.97
Secchi (m):	1.75 (f)	0.8 (f)	Alcalin (meq/l):	2.96 ± 1.29	5.04
pH:	7.4 ± 0.1	7.8	Ca (mM):	14.6 ± 0.1	- -
Clor. a (mg /m):	0.86 ± 0.39	120.2	Mg (mM):	17.55 ± 0.07	- -
Nitrito (µM):	0.06 ± 0.02	0.29	Na (mM):	1.36 ± 0.04	- -
Nitrato (µM):	0	0	K (mM):	0.41 ± 0.01	- -
Amonio (µM):	25.4 ± 8.6	18.7	nº muestras (n):	2	1

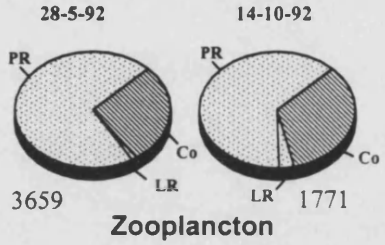
Cuadro 10

12.- Ballesteros 4



D max (m):	68
D min (m):	66
D med (m):	67
Área (m²):	3351.4
Perim (m):	214.5
Z max (m):	7.4
Z med (m):	3.8
Z rel (%):	11.3
α_{med} (%):	10.8 ± 2.3
α^{5}_{10} med (%):	10 ± 5.3



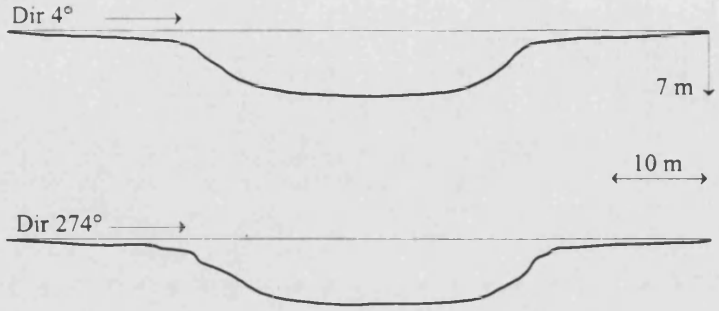


Zooplancton

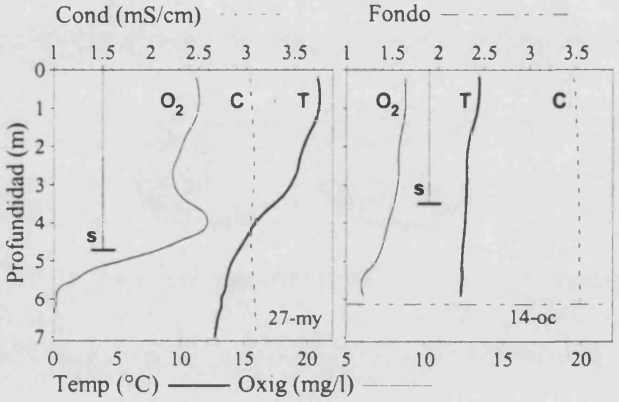
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	15.8 ± 3	12.2 ± 0.4	Fosfato (µM):	0	0.13 ± 0.04
Cond (mS/cm):	3.29 ± 0.01	3.60 ± 0.03	Silicato (µM):	7.8 ± 3.3	14.4 ± 0.4
Oxig (mg/l):	8.1 ± 3.7	6.7 ± 0.8	Sulfato (meq/l):	59.1 ± 1.8	66.2 ± 1.3
Oxig (%sat):	86.7 ± 41.3	67.7 ± 8.5	Cloruro (meq/l):	0.57 ± 0.01	0.72 ± 0.03
Secchi (m):	2.7	4.8	Alcalin (meq/l):	2.11 ± 0.10	1.21 ± 0.05
pH:	8.1 ± 0.2	7.9 ± 0.2	Ca (mM):	19.2 ± 0.3	- -
Clor. a (mg /m):	6.3 ± 1.5	4.7 ± 0.4	Mg (mM):	10.97 ± 0.32	- -
Nitrito (µM):	0.05 ± 0.03	0.2 ± 0.05	Na (mM):	0.78 ± 0.01	- -
Nitrato (µM):	1.94 ± 2.77	0.97 ± 0.2	K (mM):	0.19 ± 0.01	- -
Amonio (µM):	18.9 ± 9.4	34.3 ± 4.1	nº muestras (n):	3	3

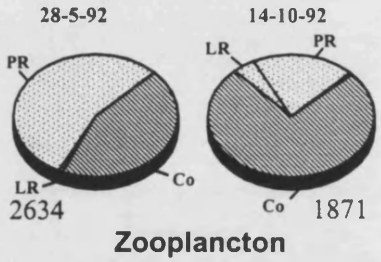
Cuadro 11

13.- Ballesteros 5



D max (m):	73
D min (m):	73
D med (m):	73
Área (m^2):	3381.9
Perim (m):	213.5
Z max (m):	7
Z med (m):	3.1
Z rel (%):	10.7
α_5 med (%):	8.5 ± 1.9
α_{10} med (%):	6

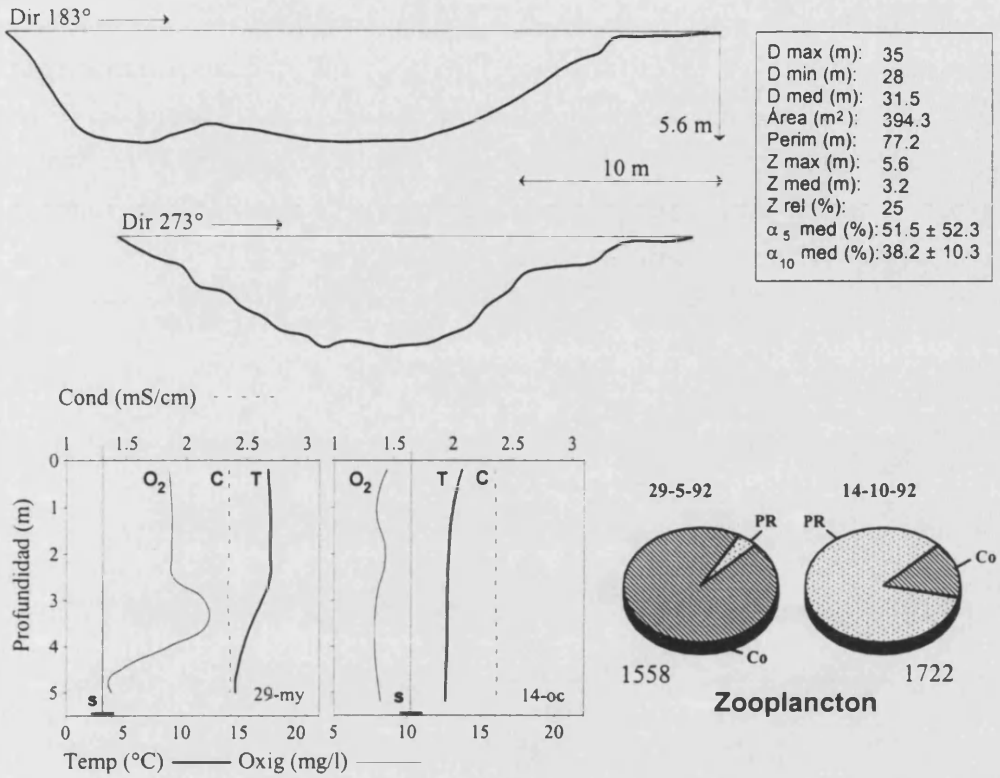




Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	16.3 ± 3.3	12.8 ± 0.5	Fosfato (µM):	0.02 ± 0.03	0.06 ± 0.03
Cond (mS/cm):	3.07 ± 0.02	3.53 ± 0.02	Silicato (µM):	28.7 ± 16.2	35.9 ± 0.3
Oxig (mg/l):	7.5 ± 6.4	7.5 ± 1.4	Sulfato (meq/l):	53.9 ± 1.5	63.2 ± 0.1
Oxig (%sat):	85.7 ± 72.8	76.7 ± 15.5	Cloruro (meq/l):	13.25 ± 22.3	0.49 ± 0.01
Secchi (m):	4.9	3.5	Alcalin (meq/l):	1.54 ± 0.68	0.9
pH:	8.4 ± 0.6	8.1 ± 0.1	Ca (mM):	19.2 ± 0.3	- -
Clor. a (mg /m):	4.4 ± 2.6	10.28 ± 1.46	Mg (mM):	10.97 ± 0.32	- -
Nitrito (µM):	0.03	0.14 ± 0.04	Na (mM):	0.78 ± 0.01	- -
Nitrato (µM):	0.02 ± 0.03	0.33 ± 0.14	K (mM):	0.19 ± 0.01	- -
Amonio (µM):	4 ± 6.9	26.4 ± 7.1	nº muestras (n):	3	3

Cuadro 12

14.- Ballesteros 6

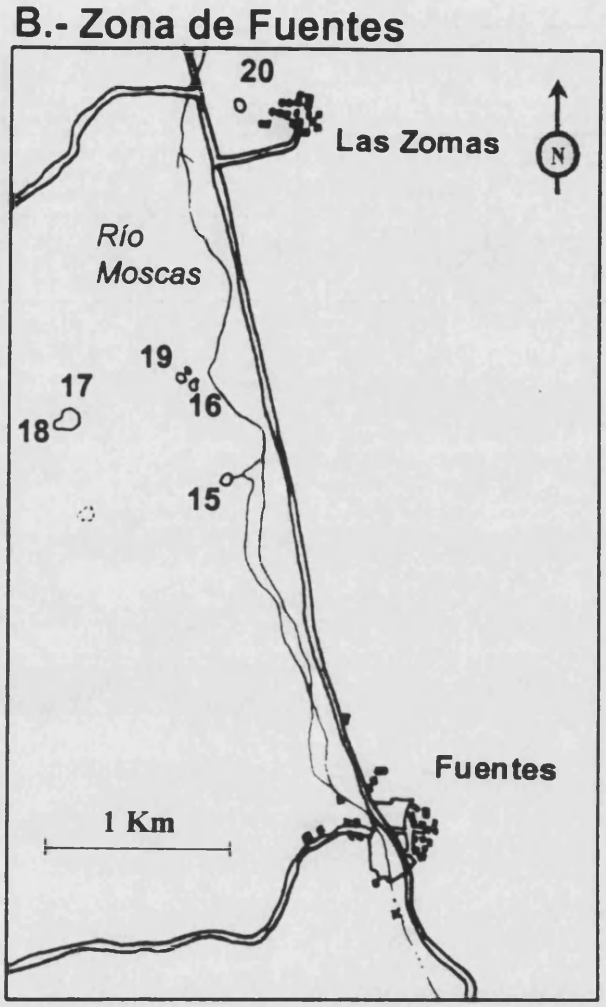


D max (m):	35
D min (m):	28
D med (m):	31.5
Área (m^2):	394.3
Perim (m):	77.2
Z max (m):	5.6
Z med (m):	3.2
Z rel (%):	25
α_5 med (%):	51.5 ± 52.3
α_{10} med (%):	38.2 ± 10.3

Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	16.5 ± 1.6	12.8 ± 0.3	Fosfato (µM):	0.01 ± 0.01	0.19 ± 0.05
Cond (mS/cm):	2.35 ± 0.01	2.36	Silicato (µM):	129.5 ± 15.5	37.2 ± 0.2
Oxig (mg/l):	8.3 ± 4.2	8 ± 0.1	Sulfato (meq/l):	30.4 ± 0.6	29.0 ± 0.5
Oxig (%sat):	93 ± 48.1	81.7 ± 0.6	Cloruro (meq/l):	0.16 ± 0.02	0.20 ± 0.02
Secchi (m):	5.5 (fondo)	5.5 (fondo)	Alcalin (meq/l):	4.85 ± 0.13	4.13 ± 0.09
pH:	7.5 ± 0.2	7.6	Ca (mM):	18.87 ± 0.59	- -
Clor. a (mg /m):	2.73 ± 1.21	2 ± 0.65	Mg (mM):	8.87 ± 0.61	- -
Nitrito (µM):	0.03	0.23 ± 0.01	Na (mM):	0.53 ± 0.02	- -
Nitrato (µM):	111.7 ± 24.5	63.1 ± 1.3	K (mM):	0.14 ± 0.03	- -
Amonio (µM):	14.1 ± 2.9	40.9 ± 5.8	nº muestras (n):	3	3

Cuadro 13

b) Zona de Fuentes. En esta zona que dista unos 14 Km en línea recta desde la ciudad de Cuenca, se han estudiado un grupo de seis lagunas/cubetas permanentes que se sitúan entre los términos municipales de Fuentes y las Zomas, cinco de ellas en la margen izquierda del río Moscas y la última en la margen derecha. Sus conductividades durante la época de estudio oscilaron entre 2 y 2,5 mS/cm y sus profundidades variaban entre los 2.3 y 15.1 m. Igual que en el caso de las lagunas de Arcas y Cañada del Hoyo fueron muestreadas en las campañas extensivas de primavera y otoño de 1992. Santos Cirujano (1995) realizó un estudio de la vegetación acuática de estas lagunas. También existen datos previos sobre la físico-química de las mismas (Rodrigo, 1997).

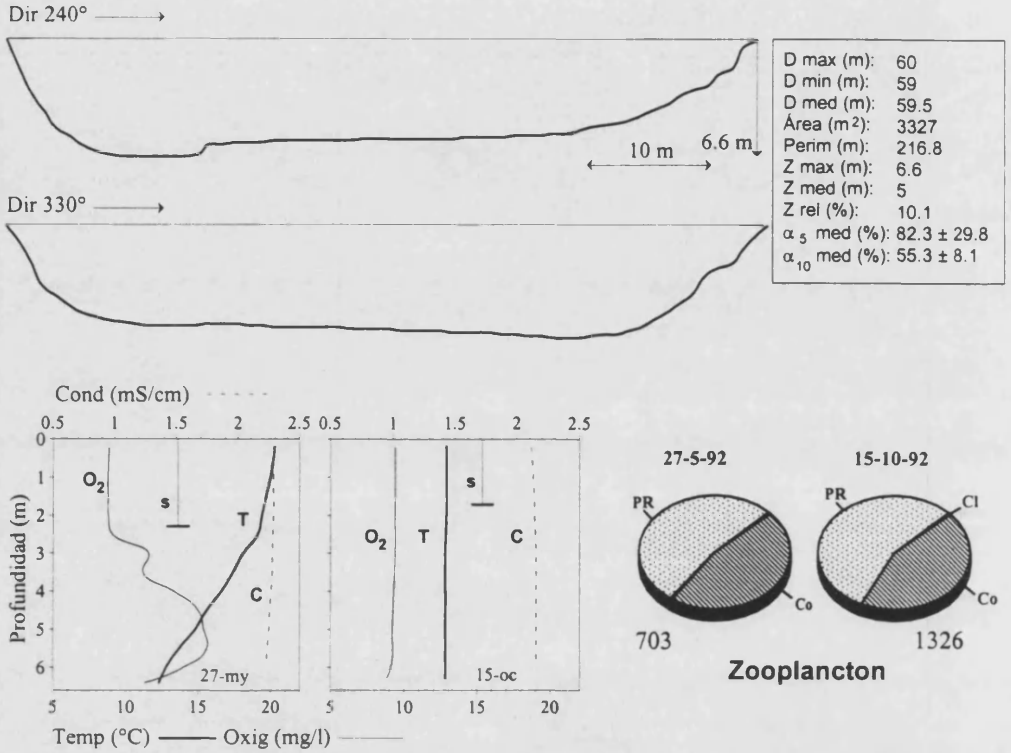


B.- Zona de Fuentes

Lagunas de:

15.- Fuentes 1
16.- Fuentes 2
17.- Fuentes 3 (I)
18.- Fuentes 3 (II)
19.- Fuentes 4
20.- Las Zomas

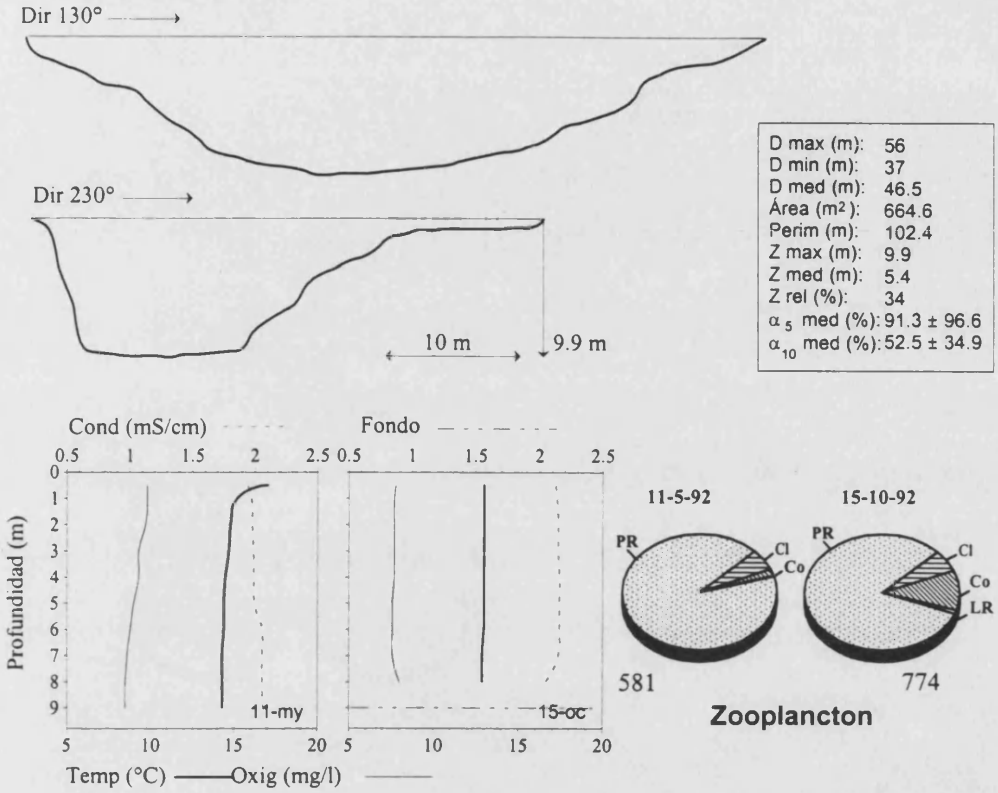
15.- Fuentes 1



Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	16.7 ± 3.7	12.8 ± 0.1	Fosfato (µM):	0	0.11 ± 0.02
Cond (mS/cm):	2.27 ± 0.03	2.14 ± 0.01	Silicato (µM):	36.3 ± 10.9	18.6 ± 0.3
Oxig (mg/l):	11.3 ± 2.6	9.3 ± 0.2	Sulfato (meq/l):	26.6 ± 0.5	24.9 ± 1.4
Oxig (%sat):	127.3 ± 19.6	97 ± 1.7	Cloruro (meq/l):	0.16 ± 0.01	0.21 ± 0.02
Secchi (m):	2.3	1.7	Alcalin (meq/l):	3.77 ± 0.14	3.7 ± 0.4
pH:	7.7 ± 0.1	7.9	Ca (mM):	15 ± 0.82	- -
Clor. a (mg /m):	4.81 ± 1.78	5.18 ± 0.25	Mg (mM):	1.63 ± 0.04	- -
Nitrito (µM):	0.02 ± 0.02	0.5 ± 0.05	Na (mM):	0.11 ± 0.02	- -
Nitrato (µM):	103.5 ± 11.6	73.3 ± 2.4	K (mM):	0.03	- -
Amonio (µM):	17.5 ± 3.1	25.7 ± 2.1	nº muestras (n):	3	3

Cuadro 14

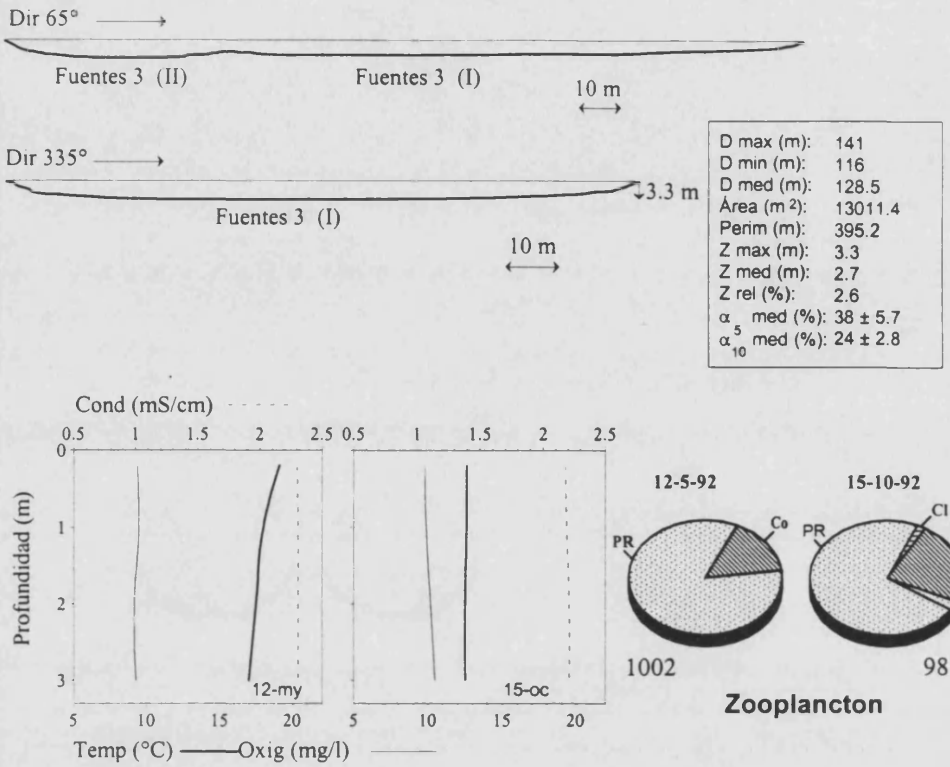
16.- Fuentes 2 (II)



Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	14.6 ± 0.5	13.0 ± 0.1	Fosfato (µM):	0.06 ± 0.06	0.13 ± 0.03
Cond (mS/cm):	2.01 ± 0.05	2.15 ± 0.01	Silicato (µM):	95.3 ± 9.2	22.6 ± 0.3
Oxig (mg/l):	9.1 ± 0.7	7.7 ± 0.1	Sulfato (meq/l):	21.7 ± 1.2	23.1 ± 0.1
Oxig (%sat):	97.3 ± 8.1	80 ± 1	Cloruro (meq/l):	0.16 ± 0.01	0.2 ± 0.01
Secchi (m):	2.9	2.8	Alcalin (meq/l):	5.53 ± 0.06	4.86 ± 0.04
pH:	7.3 ± 0.1	7.4	Ca (mM):	14.50 ± 0.52	- -
Clor. a (mg /m):	0.50 ± 0.25	2.28 ± 0.65	Mg (mM):	1.17 ± 0.06	- -
Nitrito (µM):	0.04 ± 0.04	0.12 ± 0.04	Na (mM):	0.12 ± 0.06	- -
Nitrato (µM):	171.5 ± 9.8	140.6 ± 6.2	K (mM):	0.02	- -
Amonio (µM):	67.5 ± 21.6	22.2 ± 5.8	nº muestras (n):	3	3

Cuadro 15

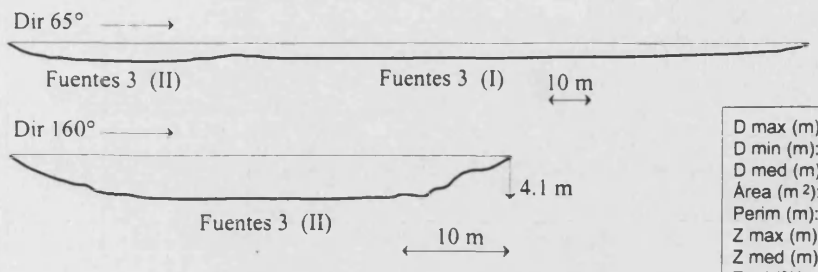
17.- Fuentes 3 (I)



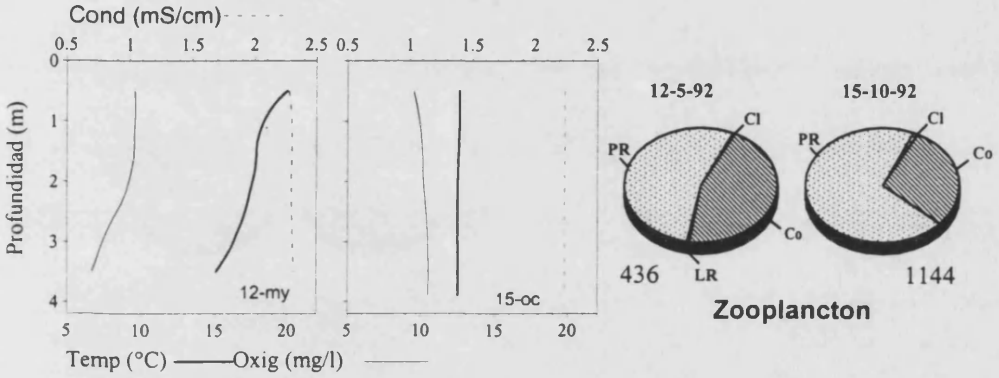
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	17.6 ± 0.6	12.6	Fosfato (µM):	0.02 ± 0.03	0.25
Cond (mS/cm):	2.31	2.20	Silicato (µM):	134.5 ± 1.2	28.1
Oxig (mg/l):	9.3 ± 0.3	10.1	Sulfato (meq/l):	26.3 ± 1.1	27.7
Oxig (%sat):	106.0 ± 4.2	105	Cloruro (meq/l):	0.23 ± 0.01	0.24
Secchi (m):	2.5	3.3 (f)	Alcalin (meq/l):	5.06 ± 0.02	4.42
pH:	7.7 ± 0.1	7.7	Ca (mM):	15.90 ± 0.57	- -
Clor. a (mg /m):	1.55 ± 0.42	0.54	Mg (mM):	2.15 ± 0.06	- -
Nitrito (µM):	0	0	Na (mM):	0.12	- -
Nitrato (µM):	181.2 ± 2.1	144.9	K (mM):	0.03	- -
Amonio (µM):	98.3 ± 7.5	25.8	nº muestras (n):	2	1

Cuadro 16

18.- Fuentes 3 (II)



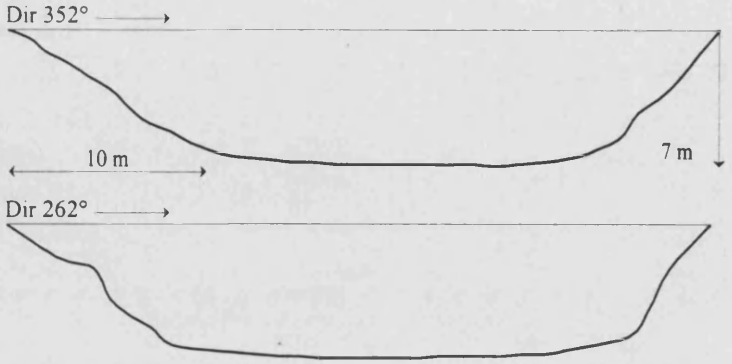
D max (m):	55
D min (m):	46
D med (m):	50.5
Área (m 2):	1700
Perim (m):	159
Z max (m):	4.1
Z med (m):	3.2
Z rel (%):	6.3
α_{5} med (%):	44 ± 5.7
α^{5}_{10} med (%):	35.5 ± 0.7



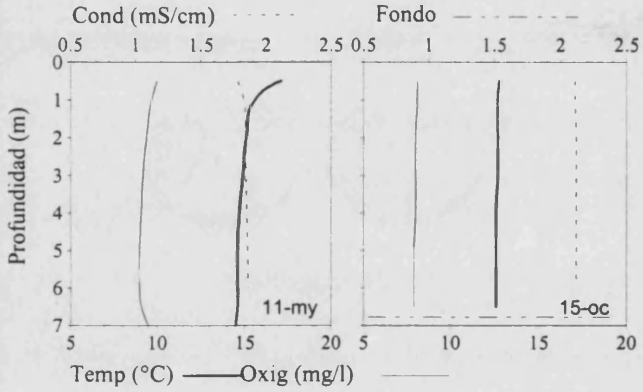
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	17.4 ± 1.5	12.6 ± 0.1	Fosfato (µM):	0.04 ± 0.06	0.09 ± 0.03
Cond (mS/cm):	2.31 ± 0.01	2.24	Silicato (µM):	135.3 ± 1.6	28.7 ± 0.4
Oxig (mg/l):	8.5 ± 1.6	10.2 ± 0.4	Sulfato (meq/l):	28.3 ± 0.1	27.0
Oxig (%sat):	96.5 ± 20.5	105.0 ± 4.2	Cloruro (meq/l):	0.22	0.22 ± 0.01
Secchi (m):	- -	- -	Alcalin (meq/l):	5.03 ± 0.01	4.14 ± 0.16
pH:	7.5 ± 0.1	7.7 ± 0.1	Ca (mM):	15.35 ± 0.49	- -
Clor. a (mg /m):	1.85	0.77 ± 0.11	Mg (mM):	2.2	- -
Nitrito (µM):	0.08 ± 0.07	0.76 ± 0.06	Na (mM):	0.12	- -
Nitrato (µM):	188.1 ± 2.5	152.0 ± 0.4	K (mM):	0.03	- -
Amonio (µM):	107.7 ± 77.4	33.8 ± 5.2	nº muestras (n):	2	2

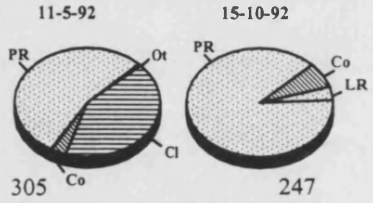
Cuadro 17

19.- Fuentes 4



D max (m):	35
D min (m):	34
D med (m):	34.5
Área (m^2):	667.6
Perim (m):	95.2
Z max (m):	7
Z med (m):	5.2
Z rel (%):	23.8
α_5 med (%):	94.5 ± 28.5
α_{10} med (%):	75.8 ± 13.1



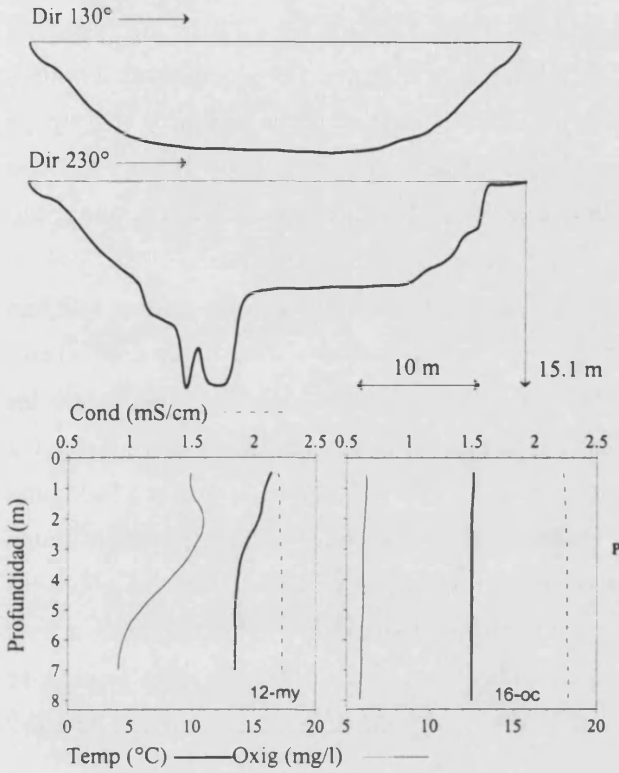


Zooplancton

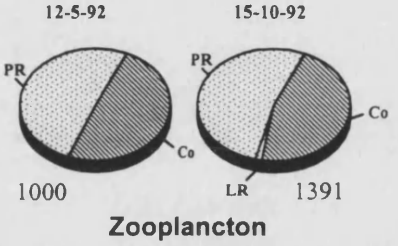
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	15.0 ± 0.5	12.7 ± 0.1	Fosfato (µM):	0.08	0.12 ± 0.01
Cond (mS/cm):	1.85 ± 0.02	2.12 ± 0.01	Silicato (µM):	80.9	22.3 ± 0.4
Oxig (mg/l):	9.3 ± 0.3	8.0 ± 0.1	Sulfato (meq/l):	20.5 ± 2.5	- -
Oxig (%sat):	101.3 ± 5.9	83 ± 1	Cloruro (meq/l):	0.16 ± 0.01	0.19 ± 0.01
Secchi (m):	2.4	2.7	Alcalin (meq/l):	5.20 ± 0.25	4.86 ± 0.05
pH:	7.5	7.4 ± 0.1	Ca (mM):	13.90 ± 0.85	- -
Clor. a (mg /m):	0.79 ± 0.24	1.06 ± 0.30	Mg (mM):	1.14 ± 0.01	- -
Nitrito (µM):	0.04	0.19 ± 0.02	Na (mM):	0.10 ± 0.01	- -
Nitrato (µM):	164.4	132.0 ± 3.1	K (mM):	0.02	- -
Amonio (µM):	67.5 ± 21.6	22.6 ± 8.3	nº muestras (n):	3	3

Cuadro 18

20.- Las Zomas



D max (m):	39
D min (m):	39
D med (m):	39
Área (m^2):	960.3
Perim (m):	113.9
Z max (m):	15.1
Z med (m):	6.7
Z rel (%):	17.4
α med (%):	89.8 ± 7.8
α^{5}_{10} med (%):	79.8 ± 12.3



Zooplancton

Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	14.2 ± 1.0	12.5 ± 0.1	Fosfato (µM):	0	0.14 ± 0.01
Cond (mS/cm):	2.22 ± 0.01	2.26 ± 0.02	Silicato (µM):	130.0 ± 15.7	35.3 ± 0.7
Oxig (mg/l):	7.7 ± 3.4	6.0 ± 0.2	Sulfato (meq/l):	26.4 ± 0.6	77.7 ± 4.7
Oxig (%sat):	82.3 ± 37.6	63.0 ± 2.0	Cloruro (meq/l):	0.24 ± 0.01	0.25 ± 0.01
Secchi (m):	2.5	1	Alcalin (meq/l):	5.45	4.92 ± 0.05
pH:	7.4 ± 0.3	7.4	Ca (mM):	16.20 ± 0.56	- -
Clor. a (mg /m):	6.56 ± 2.88	6.63 ± 0.88	Mg (mM):	1.63 ± 0.06	- -
Nitrito (µM):	0.21 ± 0.11	2.15 ± 0.06	Na (mM):	0.16 ± 0.05	- -
Nitrato (µM):	204.1 ± 21.6	158.1 ± 2.5	K (mM):	0.06	- -
Amonio (µM):	77.7 ± 4.7	32.5 ± 2.7	nº muestras (n):	3	3

Cuadro 19

c) Zona de Cañada del Hoyo. Estas torcas se encuentran en el paraje cárstico denominado Los Oteros (UTM 30 SWK 962272), en el término de Cañada del Hoyo situado en la parte sur de la serranía de Cuenca (Sistema Ibérico), a una altitud que oscila entre los 960-1000 m y a una distancia aproximada de 24 Km de la ciudad de Cuenca. El complejo esta formado por 34 dolinas distribuidas en dos conjuntos a ambos lados del río Guadazaón, 12 de ellas están situadas en la margen izquierda y el resto en la margen derecha del río. Entre estas últimas destaca un conjunto de 10 dolinas con agua, 7 de las cuales poseen agua de manera permanente y tres solo de manera temporal. Durante, el periodo 1987-1997 estas últimas tuvieron agua únicamente en 1988, 1991 y 1997 en las épocas de lluvias. Las dolinas de aguas permanentes son las únicas que han sido tratadas en este trabajo, en orden decreciente de tamaño son: laguna del Tejo, laguna de la Cruz, laguna de la Parra, laguna Llana, lagunillo del Tejo, laguna de las Cardenillas y lagunillo de las Cardenillas. Sus conductividades oscilaron entre 0.4 y 1.2 mS/cm y sus profundidades oscilaron entre los 4.3 y 32 m. Entre ellas destaca la laguna de la Cruz por su caracter meromíctico, es decir una parte de las aguas del fondo nunca se mezcla con las de arriba, con la consiguiente repercusión de este fenómeno sobre las poblaciones de zooplancton, varios capítulos están dedicados exclusivamente a esta laguna. Además de los muestreos de primavera y otoño de 1992, en esta laguna se realizaron muestreos durante el ciclo anual 1987-1988 y también en septiembre de 1989 para la realización de un ciclo diario.

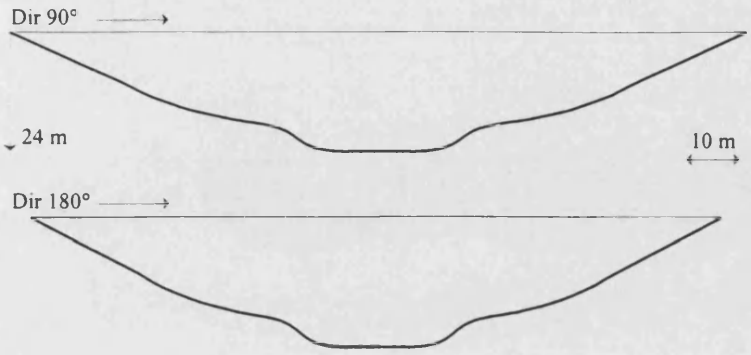
Rodrigo (1997) ha estudiado las características físico-químicas de estas lagunas en años previos y Santos Cirujano ha estudiado la vegetación acuática, en Rojo y Miracle (1987) se encuentra un estudio introductorio del fitoplancton y el lagunillo del tejo fue descrito por Vicente y Miracle (1988). La laguna de la Cruz ha sido la más estudiada Dasí y Miracle (1991) y Dasí *et al.*, (en prensa) estudiaron diversos aspectos del fitoplancton, también Esparcia (1993) ha realizado trabajos sobre los rotíferos de la oxiclina, Rodrigo *et al.* (1993) estudiaron aspectos sobre la precipitación de cristales y finalmente Julià *et al.* (en prensa), estudiaron su sedimento.

C.- Zona de Cañada del Hoyo

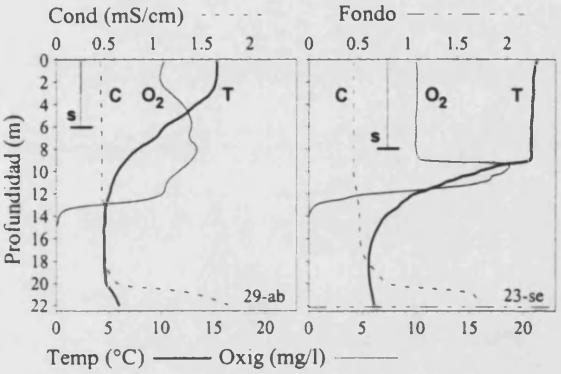
C.- Zona de Cañada del Hoyo

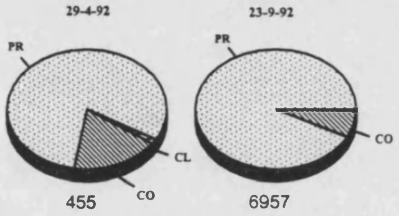
21.- Laguna de La Cruz
22.- Laguna del Tejo
23.- Lagunillo del Tejo
24.- Laguna de la Parra
25.- Laguna Llana
26.- Laguna de las Cardenillas
27.- Lagunillo de las Cardenillas

21.- La Cruz



D max (m):	136
D min (m):	128
D med (m):	132
Área (m^2):	11816.3
Perim (m):	399.2
Z max (m):	24
Z med (m):	13.2
Z rel (%):	19.9
α med (%):	77.9 ± 14.5
α^{5}_{10} med (%):	75.3 ± 3.9





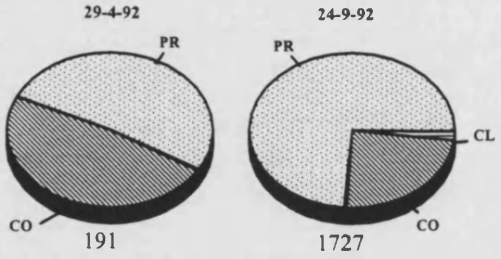
Zooplancton

Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	9.5 ± 5.1	15.3 ± 5.1	Fosfato (µM):	0.22 ± 0.05	0.27 ± 0.02
Cond (mS/cm):	0.475 ± 0.011	0.469 ± 0.024	Silicato (µM):	- -	- -
Oxig (mg/l):	8.8 ± 5.4	9.1 ± 6.4	Sulfato (meq/l):	0.04 ± 0.01	0.05 ± 0.01
Oxig (%sat):	87.0 ± 53.3	104.2 ± 73.2	Cloruro (meq/l):	0.26 ± 0.02	0.28 ± 0.01
Secchi (m):	6	8	Alcalin (meq/l):	6.85 ± 0.55	6.25 ± 0.32
pH:	8.9 ± 0.3	8.8 ± 0.3	Ca (mM):	0.51 ± 0.01	- -
Clor. a (mg /m):	7.73 ± 6.18	13.3 ± 17.0	Mg (mM):	2.66 ± 0.05	- -
Nitrito (µM):	0.11 ± 0.05	0.07 ± 0.08	Na (mM):	0.20 ± 0.05	- -
Nitrato (µM):	4.93 ± 2.69	1.55 ± 1.14	K (mM):	0.06 ± 0.01	- -
Amonio (µM):	74.3 ± 13.6	26.8 ± 3.4	nº muestras (n):	4	5

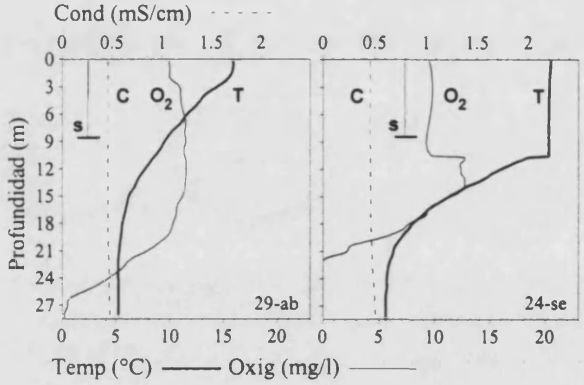
Cuadro 20

22.- Laguna del Tejo

D max (m):	- -
D min (m):	- -
D med (m):	145
Área (m^2):	16245.9
Perim (m):	469.2
Z max (m):	32
Z med (m):	- -
Z rel (%):	22.1
α_{10}^{5} med (%):	- -



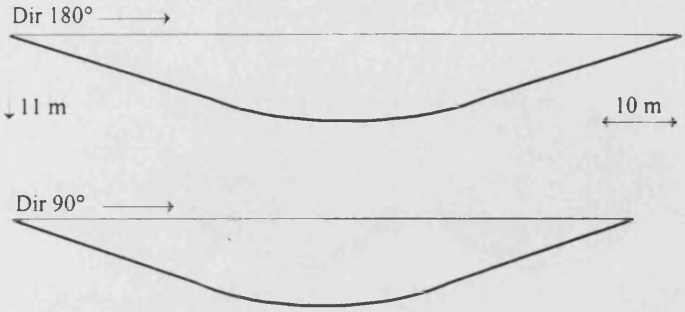
Zooplancton



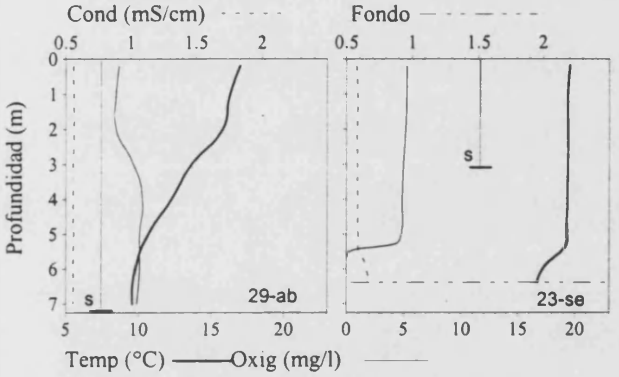
Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	8.5 ± 4.6	12.8 ± 6.2	Fosfato (µM):	0.15 ± 0.01	0.47 ± 0.03
Cond (mS/cm):	0.462 ± 0.007	0.462 ± 0.008	Silicato (µM):	1.53 ± 1.34	0.94 ± 1.03
Oxig (mg/l):	8.1 ± 4.4	8.5 ± 4.7	Sulfato (meq/l):	0.09	0.12 ± 0.03
Oxig (%sat):	77.2 ± 44.1	92.0 ± 53.5	Cloruro (meq/l):	0.23 ± 0.01	0.44 ± 0.37
Secchi (m):	8.5	8.5	Alcalin (meq/l):	6.61 ± 0.88	6.18 ± 0.09
pH:	8.8 ± 0.2	8.7 ± 0.2	Ca (mM):	0.36 ± 0.01	- -
Clor. a (mg /m):	4.69 ± 2.20	2.48 ± 1.07	Mg (mM):	2.76 ± 0.05	- -
Nitrito (µM):	0.08 ± 0.02	0.07 ± 0.03	Na (mM):	0.19 ± 0.03	- -
Nitrato (µM):	1.47 ± 0.19	1.40 ± 0.76	K (mM):	0.05	- -
Amonio (µM):	51.7 ± 9.6	22.1 ± 3.3	nº muestras (n):	5	5

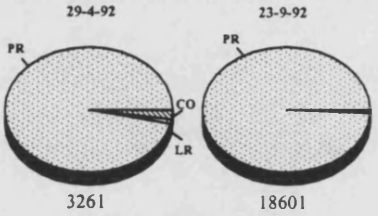
Cuadro 21

23.- Lagunillo del Tejo



D max (m):	86
D min (m):	80
D med (m):	83
Área (m^2):	5253.7
Perim (m):	266.1
Z max (m):	11
Z med (m):	6.1
Z rel (%):	13.3
α med (%):	42.2 ± 4.5
α^{5}_{10} med (%):	35.5 ± 3.1





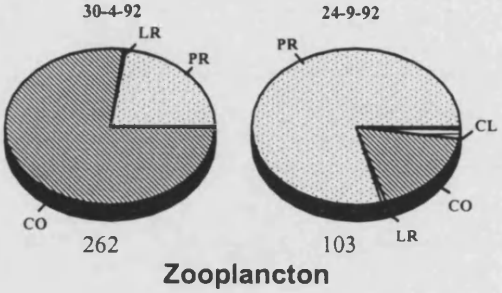
Zooplancton

Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	12.8 ± 3.3	19.4 ± 0.1	Fosfato (µM):	0.15 ± 0.02	0.32 ± 0.01
Cond (mS/cm):	0.561 ± 0.001	0.589 ± 0.005	Silicato (µM):	39.0 ± 10.2	12.68 ± 0.28
Oxig (mg/l):	9.7 ± 0.9	4.9 ± 0.4	Sulfato (meq/l):	0.44 ± 0.01	0.54 ± 0.02
Oxig (%sat):	100.0 ± 3.5	59.3 ± 4.0	Cloruro (meq/l):	0.20 ± 0.13	0.36 ± 0.02
Secchi (m):	7.25 (f)	3.1	Alcalin (meq/l):	7.78 ± 0.11	8.5 ± 0.01
pH:	9.4 ± 0.1	9.3	Ca (mM):	0.29 ± 0.01	- -
Clor. a (mg /m):	2.72 ± 0.38	2.79 ± 0.57	Mg (mM):	3.97 ± 0.04	- -
Nitrito (µM):	0.13 ± 0.02	0.08 ± 0.04	Na (mM):	0.19 ± 0.01	- -
Nitrato (µM):	0	0	K (mM):	0.05	- -
Amonio (µM):	40.5 ± 8.6	26.2 ± 1.5	nº muestras (n):	3	3

Cuadro 22

24.- Laguna de la Parra

D max (m):	- -
D min (m):	- -
D med (m):	105
Área (m^2):	8987.2
Perim (m):	351.8
Z max (m):	16
Z med (m):	- -
Z rel (%):	15.2
α med (%):	- -
α^{5}_{10} med (%):	- -



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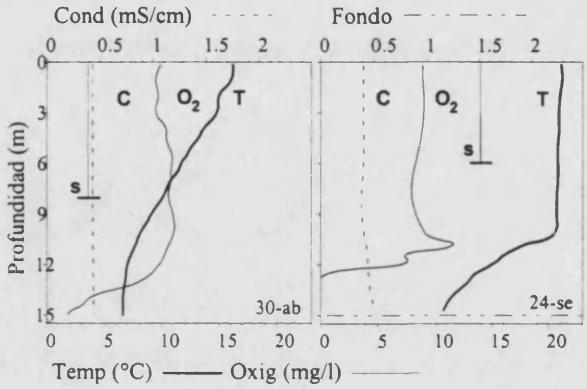
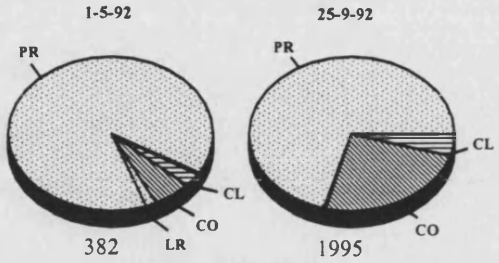


Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	10.9 ± 4.8	18.5 ± 3.0	Fosfato (µM):	0.19 ± 0.06	0.0.42 ± 0.03
Cond (mS/cm):	0.435 ± 0.006	0.43 ± 0.02	Silicato (µM):	69.37 ± 17.82	7.3 ± 10.0
Oxig (mg/l):	7.9 ± 3.7	8.9 ± 1.6	Sulfato (meq/l):	0.09 ± 0.02	0.14 ± 0.02
Oxig (%sat):	80.0 ± 40.7	104.5 ± 21.4	Cloruro (meq/l):	0.15 ± 0.10	0.22 ± 0.01
Secchi (m):	7.9	6	Alcalin (meq/l):	5.69 ± 0.07	5.43 ± 0.25
pH:	8.7 ± 0.2	8.4 ± 0.2	Ca (mM):	0.86 ± 0.01	- -
Clor. a (mg /m):	2.90 ± 2.08	2.60 ± 2.16	Mg (mM):	1.87 ± 0.02	- -
Nitrito (µM):	0.02 ± 0.03	0.07 ± 0.05	Na (mM):	0.11	- -
Nitrato (µM):	12.78 ± 2.96	6.26 ± 1.62	K (mM):	0.07 ± 0.01	- -
Amonio (µM):	88.17 ± 12.25	28.15 ± 6.28	nº muestras (n):	3	4

Cuadro 23

25.- Laguna Llana

D max (m):	- -
D min (m):	- -
D med (m):	100
Área (m^2):	8603.1
Perim (m):	343.5
Z max (m):	6.6
Z med (m):	- -
Z rel (%):	6.6
α med (%):	- -
α^{5}_{10} med (%):	- -



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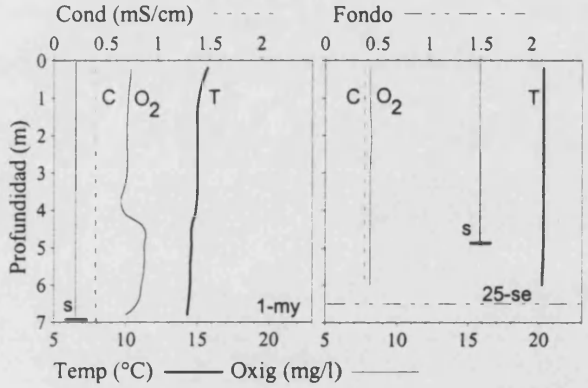
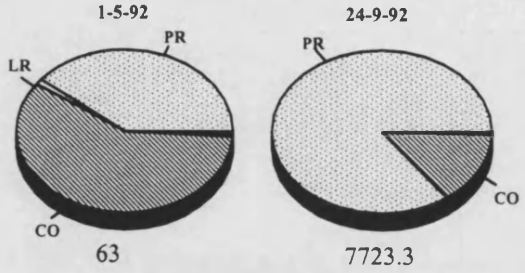


Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	14.7 ± 0.4	20.3 ± 0.1	Fosfato (µM):	0.12 ± 0.02	0.22 ± 0.06
Cond (mS/cm):	0.402 ± 0.002	0.375	Silicato (µM):	3.03 ± 2.32	7.9 ± 0.3
Oxig (mg/l):	10.8 ± 0.6	8.1	Sulfato (meq/l):	- -	0.11 ± 0.01
Oxig (%sat):	115.0 ± 5.6	98.7 ± 0.6	Cloruro (meq/l):	0.22 ± 0.02	0.21 ± 0.01
Secchi (m):	7 (f)	4.85	Alcalin (meq/l):	5.39 ± 0.05	4.55 ± 0.58
pH:	8.8	8.8	Ca (mM):	0.63 ± 0.01	- -
Clor. a (mg /m):	0.9 ± 0.1	2.06 ± 0.69	Mg (mM):	1.99 ± 0.01	- -
Nitrito (µM):	0.03 ± 0.02	0.03	Na (mM):	0.1	- -
Nitrato (µM):	0.26 ± 0.07	0.43 ± 0.15	K (mM):	0.04	- -
Amonio (µM):	74.0 ± 11.1	24.6 ± 7.7	nº muestras (n):	3	3

Cuadro 24

26.- Laguna de las Cardenillas

D max (m):	- -
D min (m):	- -
D med (m):	90
Área (m^2):	6921.3
Perim (m):	315
Z max (m):	12
Z med (m):	- -
Z rel (%):	13.3
α med (%):	- -
α^5_{10} med (%):	- -



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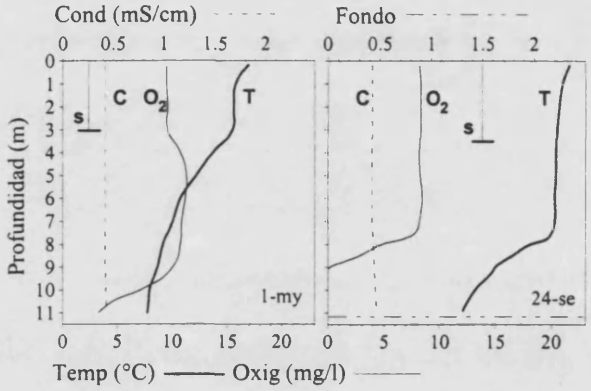
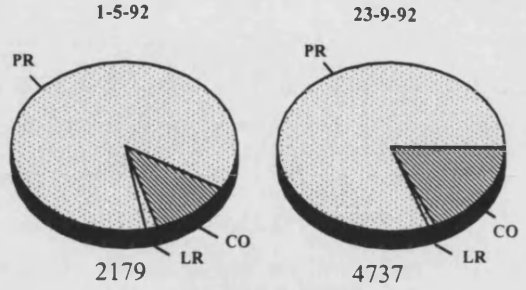


Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	13.2 ± 4.1	19.3 ± 2.4	Fosfato (µM):	0.12 ± 0.02	0.52 ± 0.02
Cond (mS/cm):	0.425 ± 0.007	0.431 ± 0.008	Silicato (µM):	4.43 ± 1.81	0.66 ± 0.33
Oxig (mg/l):	8.4 ± 3.5	6.4 ± 3.2	Sulfato (meq/l):	0.09	0.15 ± 0.01
Oxig (%sat):	89.0 ± 38.9	77.3 ± 40.1	Cloruro (meq/l):	0.22 ± 0.01	0.21 ± 0.04
Secchi (m):	3	3.5	Alcalin (meq/l):	5.61 ± 0.05	5.40 ± 0.14
pH:	8.8 ± 0.2	8.7 ± 0.2	Ca (mM):	0.66 ± 0.01	- -
Clor. a (mg /m):	3.63 ± 1.72	1.40 ± 0.74	Mg (mM):	2.06 ± 0.07	- -
Nitrito (µM):	0.11 ± 0.09	0.05 ± 0.01	Na (mM):	0.12 ± 0.01	- -
Nitrato (µM):	0.79 ± 0.75	0.18 ± 0.13	K (mM):	0.06	- -
Amonio (µM):	25.5 ± 11.4	20.2 ± 1.5	nº muestras (n):	3	3

Cuadro 25

27.- Lagunillo de las Cardenillas

D max (m):	- -
D min (m):	- -
D med (m):	65
Área (m^2):	2363.7
Perim (m):	185.6
Z max (m):	6
Z med (m):	- -
Z rel (%):	9.2
α med (%):	- -
α^{5}_{10} med (%):	- -



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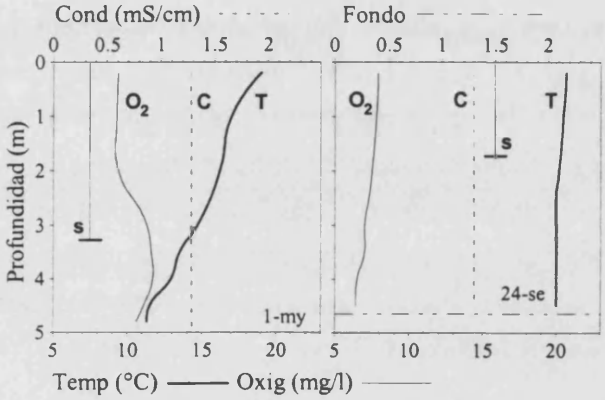

Parámetro	primavera	otoño	Parámetro	primavera	otoño
Temp (°C):	12.5 ± 1.4	20.2 ± 0.3	Fosfato (µM):	0.18 ± 0.07	0.11 ± 0.06
Cond (mS/cm):	1.286 ± 0.001	1.303 ± 0.004	Silicato (µM):	131.5 ± 7.3	31.1 ± 0.3
Oxig (mg/l):	11.4 ± 0.4	7.2 ± 0.7	Sulfato (meq/l):	0.39 ± 0.01	0.42 ± 0.03
Oxig (%sat):	118.0 ± 7.1	87.3 ± 9.0	Cloruro (meq/l):	0.74 ± 0.03	0.88 ± 0.10
Secchi (m):	3.3	1.75	Alcalin (meq/l):	21.38 ± 0.23	22.93 ± 0.17
pH:	9	8.8 ± 0.1	Ca (mM):	0.46	- -
Clor. a (mg /m):	10.06 ± 6.32	11.36 ± 1.90	Mg (mM):	6.80 ± 0.09	- -
Nitrito (µM):	0.13 ± 0.02	0.05 ± 0.03	Na (mM):	0.66 ± 0.07	- -
Nitrato (µM):	0	0	K (mM):	0.31 ± 0.02	- -
Amonio (µM):	89.5 ± 3.7	18.9 ± 6.2	nº muestras (n):	2	3

Cuadro 26

d) Lago del Tobar. Dista en línea recta unos 53 Km de la ciudad de Cuenca y está situado en la parte norte de la serranía de Cuenca, casi en el límite con la provincia de Guadalajara, a una altitud de 1250 m (UTM 30 TWK 806888). El lago se asienta en un terreno de rocas calizas y en él se distinguen dos cubetas principales. La más grande es una cubeta holomíctica, con una profundidad máxima de 12.8 m, y que se presenta alargada en la dirección este-oeste; existen unos manantiales en la orilla este y tiene una salida, regulada por una compuerta, en la orilla oeste. La cubeta pequeña, se sitúa al norte de la cubeta grande y es un limnocreno de forma aproximadamente circular, formada por disolución de caliza como el resto de la laguna, pero presenta un hundimiento adicional debido a la disolución de rocas salinas (estratos del *Keuper*) que se sitúan por debajo de la caliza. Esta cubeta es pues más profunda con un máximo de 19.5 m y sus orillas están rodeadas de abruptas paredes que alcanzan en su parte norte los 60 m de altura y la protejen del efecto del viento. Esta cubeta tiene carácter meromíctico debido a la capa de agua salada profunda (la conductividad media del monimolimnion está entre 150-200 mS/cm), y presenta una estratificación térmica marcada debido a la protección frente al viento que ofrecen las paredes. Este lago está descrito en cuanto a su morfometría y características físico-químicas en Vicente *et al.*, 1993 y su vegetación acuática también se describe en Santos Cirujano, 1995. También se han realizado estudios sobre la migración vertical y estructura poblacional de poblaciones de cladóceros (King y Miracle, 1995; King *et al.*, 1995).

D.- Lago del Tobar

Datos de Vicente *et al.*, 1993

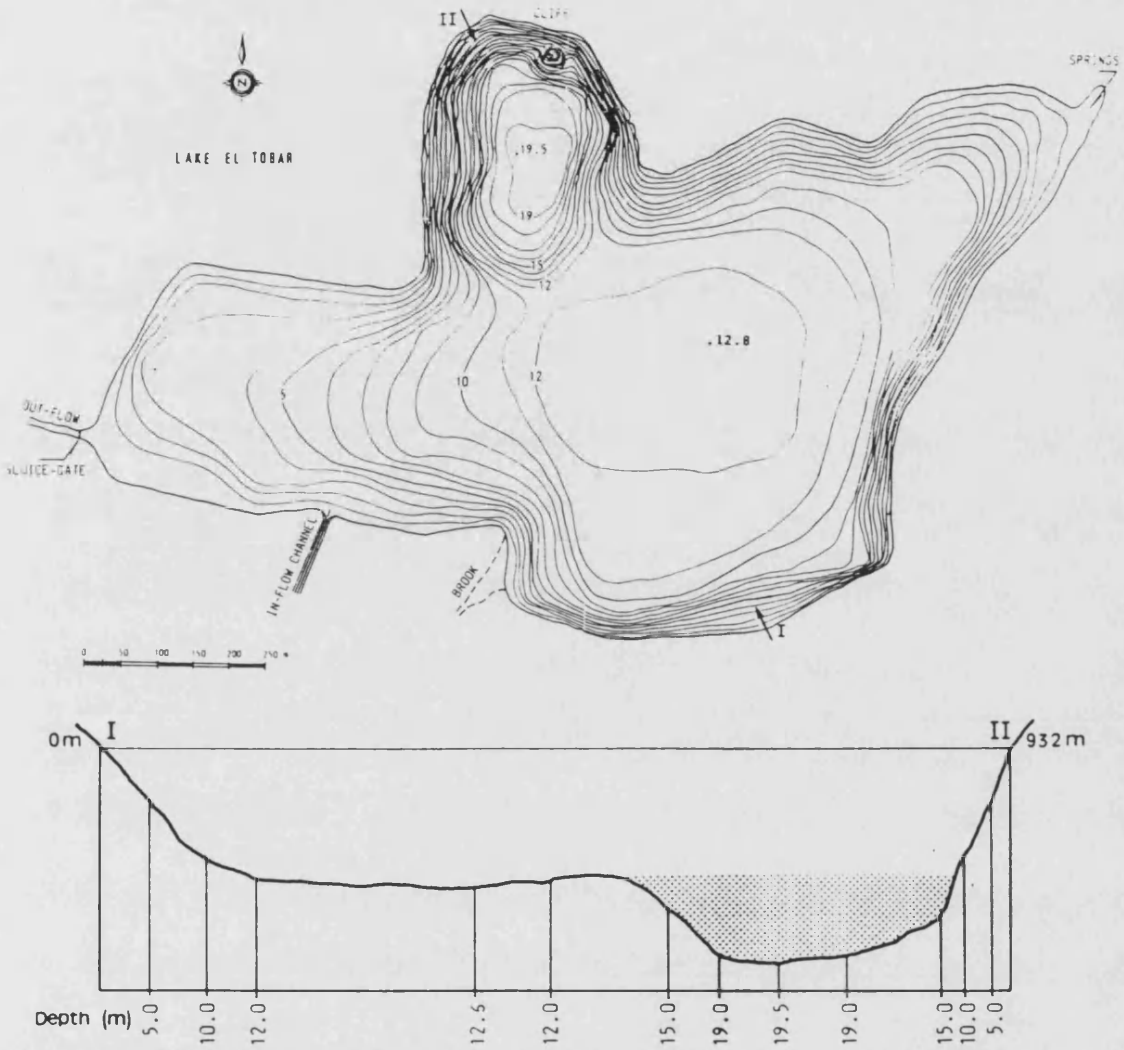

Fig. 2. Bathymetric map of Lake El Tobar. The meromictic basin (19.5 m deep) is located sideways north of the main basin (12.8 m of depth). The lake profile of transect I – II is also plotted. Monimolimnion of the meromictic basin has been shaded.

IV.- ARTÍCULOS

IV.- ARTÍCULOS PUBLICADOS (REPRINTS)

IV.1 - Vertical distribution of *Anuraeopsis* species as related to oxygen depletion in two stratified lakes.

IV.2 - Vertical distribution of planktonic rotifers in a karstic meromictic lake.

IV.3 - Extreme meromixis determines strong differential planktonic vertical distributions.

IV.4 - Population dynamics of oxyclinal species in lake Arcas-2 (Spain).

[IV.1]

VERTICAL DISTRIBUTION OF *Anuraeopsis* SPECIES AS RELATED TO OXYGEN DEPLETION IN TWO STRATIFIED LAKES.

A. Esparcia, **J. Armengol**, E. Vicente and M.R. Miracle

Departament de Microbiologia i Ecologia, Universitat de València, 46100 Burjassot, (Valencia, Spain)

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Vertical distribution of *Anuraeopsis* species as related to oxygen depletion in two stratified lakes

Angeles Esparcia, Javier Armengol, Eduardo Vicente and Maria Rosa Miracle

Introduction

The global distribution of the rotifer genus *Anuraeopsis* (from which only 7 – 8 species have been recognized) is pantropical (Dumont 1983) and only the cosmopolitan species, *Anuraeopsis fissa*, is frequent in Europe where it has been considered a southern and a summer or warm water species. However, when more complete vertical profiles were undertaken this species was found in great numbers in a thin layer of water in contact with the bottom in Scandinavian lakes (Pejler 1961) even under the ice and always in poor oxygen conditions (Pejler 1957). Studies on rotifer distributions of large areas in northern latitudes characterize *A. fissa* as a eutrophic species (Maemets 1983) or indicate that it can colonize the environments where the lowest oxygen concentrations were measured (Běrzinš & Pejler 1989). It has been reported also from the oxycline of a hypereutrophic tarn in England (Stewart & George 1987). *A. fissa* in Spain is a typical species of the oxycline of meromictic or well stratified karstic lakes in summer (Miracle 1976, 1977, Miracle & Vicente 1983) and it is also abundant in Lake Cisó which, provided with a relatively large anoxic hypolimnion, becomes anaerobic up to the surface in winter overturn (Alfonso & Miracle 1987). Sometimes this species has been classified as heleoplanktonic or semiplanktonic (Pourriot 1965).

In this paper we propose that the reason for this distribution relies in the particular niche of *Anuraeopsis*: a planktonic zone where decomposition predominates over production, very rich in organic material, and in many cases just above the oxidative-reductive interface. Tolerance to low oxygen conditions is an advantage for those species which are detritophagous or microphagous filter feeders. *Anuraeopsis* has classically been recognized as triptophagous in the literature (Pourriot 1977, Pejler 1983).

Furthermore, we will show, from data of two small karstic lakes, that there exists a new species of *Anuraeopsis*, *A. miraclei* which is more highly associated to those extreme microaerobic environments than *A. fissa*. Mass developments of this new species can be found when the oxic-anoxic boundary in properly sampled.

Methods

Lakes La Cruz (UTM 30SWK 962272) and Arcas-2 (UTM 30SWK 732276) are located in an important karstic area near the town of Cuenca. They are both water bodies occupying doline basins, with subterranean feeding. Lake La Cruz is a circular depression with a mean diameter of 121 m and maximum depth of 25 m (Vicente & Miracle 1988). Arcas-2 is formed by a doble doline but of smaller area and with a maximum depth of 14.5 m (Vicente et al. in press).

Water samples of 2 to 4 litres were collected with a peristaltic pump connected to a thin layer inlet sampler (Vicente et al. 1991) at different depths (10 cm intervals in the oxyclinal zone) at the dates indicated in Table 1. Zooplankton was concentrated in situ, by filtering, these samples through a 30 μm mesh nytal and preserved in 5 % formaldehyde. All organisms were counted under an inverted microscope at 100 or 200 × magnification. Living samples from microaerobic layers were also studied to confirm their active life.

Temperature and oxygen were measured in situ with a WTW thermocouple and silver-gold electrode, respectively. Several Winkler's oxygen analyses were also made for verification.

Estimations of gravity centers of the *Anuraeopsis* distributions, reported in Table 1 and Figs. 1 and 2, were calculated as $\epsilon x_i d_i / \epsilon x_i$ for mean depth and $\epsilon x_i y_i / \epsilon x_i$ for mean oxygen; where d_i is the depth of the i^{th} sample and x_i and y_i are, respectively, the number of individuals and oxygen concentration at depth d_i.

Results and discussion

The trends of the annual cycle in each lake are shown by some representative temperature and oxygen isopleths (Fig. 1). Lake Arcas-2 has a long stratified period with an anoxic hypolimnion rich in sulphide (Vicente et al. in press). It has a complete winter overturn and an outflow of water maintains its level. Temperature records at sampling dates were never below 6.5 °C. Lake La Cruz is a closed meromictic water body, it is more

Table 1. Density of population of the two *Anuraeopsis* species, for each sampling date and lake, with reference to a water column of 1 m^2 divided in two sections: the upper section from the surface to the indicated oxycline depth (the depth of the upper sample taken at the top of the oxygen depletion gradient) and the lower section from this depth to the bottom. The oxygen concentration at the oxycline depth (ODO) is also indicated. Mean oxygen is the oxygen concentration around which *Anuraeopsis* species are distributed (see Methods). Arcas-2 has a holomictic period in which the water column is not divided (Nov. and Feb.).

Day	20	17	27	25	27	20	14	4
Month	June	July	August	September	November	February	April	June
Year	1987					1988		
Lake la Cruz								
Oxycline depth (m)	14	13.2	13	13.5	16.5	17.0	14.75	11.75
ODO ($mg \cdot l^{-1}$)	2.4	4.6	4.3	6.7	5.9	5.6	4.75	5.85
Anuraeopsis fissa (x 10^3 ind $\cdot m^{-2}$)								
Upper	160.2	290.6	0	1231.0	0	226.5	25.4	8555.9
Lower	9.4	60.5	0	48.0	0	11.7	0.1	3547.8
Mean oxygen ($mg \cdot l^{-1}$)	6.4	4.8	–	8.4	–	5.7	5.7	4.1
Anuraeopsis miraclei sp. nov. (x 10^3 ind $\cdot m^{-2}$)								
Upper	0	0	1.5	309.6	257.1	942.7	86.3	185.9
Lower	8.4	6.9	556.8	16139.6	141.6	941.3	135.2	287.5
Mean oxygen ($mg \cdot l^{-1}$)	0.3	0.6	1.2	1.7	3.5	3.0	2.6	1.0
Lake Arcas-2								
Oxycline depth (m)	9.0	7.4	6.0	7.2	14.5*	14.5*	9.3	
ODO ($mg \cdot l^{-1}$)	0.2	4.0	5.4	6.1	8.9	6.5	4.8	
Anuraeopsis fissa (x 10^3 ind $\cdot m^{-2}$)								
Upper	65.7	537.6	24.6	7956.2	2012.2	12.4	151.8	
Lower	0	819.9	8.8	1040.5			2.0	
Mean oxygen ($mg \cdot l^{-1}$)	9.6	2.3	3.6	4.2	8.8	9.6	9.1	

* Lake bottom.

stable and deeper, with a permanent anoxic monimolimnion (Vicente & Miracle 1988). Its waters are less conductive, rich in bicarbonates but not sulphate. Temperature gets colder in winter and under the thermocline. A slight temperature inversion is always present in bottom layers due to the ground water temperature (6.5 °C are constantly found at maximum depth).

Two species of *Anuraeopsis* (Fig. 2) have been distinguished in those lakes, *A. fissa* and a new species, *Anuraeopsis miraclei* sp. nov. (Koste 1991). The vertical distributions of these species are shown in Figs. 3 A, B.

Anuraeopsis miraclei sp. nov. has a striking distribution highly associated with the oxycline (marked oxygen gradient leading to its depletion) of Lake La Cruz, where it develops a permanent population; only very few individuals are found in the mixolimnetic section of the water column, with the exception of the mixing periods (Fig. 3 A, Table 1). At the time of pronounced thermal stratification a neat plate of this species is formed with mass developments up to 28,000 ind $\cdot l^{-1}$ at the end of summer. These high densities in the microaerobic zone correspond to an active reproducing population. In September, at the depths around the maximum of 28,000 ind $\cdot l^{-1}$, at oxygen concentrations below 1 ppm, the ratio egg/female was $\approx$ 50 %. At other dates, at the depths around the profile maxima, this ratio was 25–30 % except in June–July when the highest values of the egg/female ratio (100 %) were found. At other depths, the values were usually much smaller.

The bulk of the population was usually localized within a 1 m thick layer, with a very small dispersion around the weighted mean depth (Fig. 1), at the end of the oxycline, following the 1 ppm oxygen isopleth. Vertical migrations have not been studied here, but Stewart & George (1987) have reported that diel vertical movements of *A. fissa* were not pronounced and associated with variations in the depth of the oxycline. *Anu-*

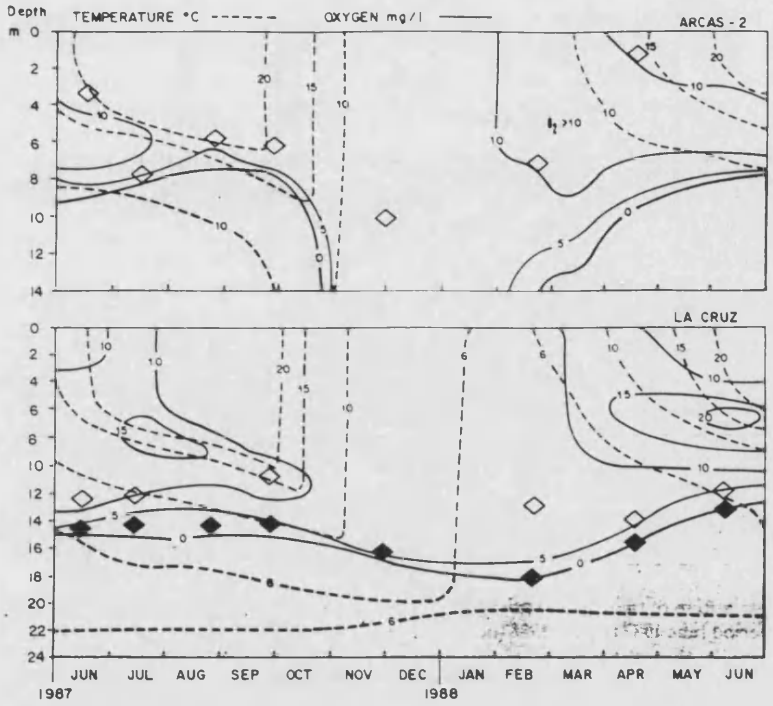

Fig. 1. Isopleths representing depth and temporal distributions of temperature and oxygen during the sampling period in lakes Arcas-2 and La Cruz. The diamonds indicate the mean depths (see Methods) of *Anuraeopsis miraclei* sp. nov. (closed symbols) and *Anuraeopsis fissa* (open symbols) at each sampling date.

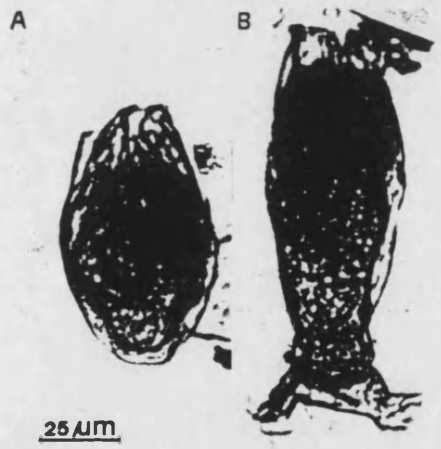

Fig. 2. Micrographs of the *Anuraeopsis* species found: (A) *Anuraeopsis fissa* and (B) *A. miraclei*.

raeopsis miraclei sp. nov. seems to be even more permanently restricted to the oxycline zone than *A. fissa*, and especially during thermal stratification, when both temperature and density barriers prevent its vertical displacement. This species has seldomly been found over 10 °C (Fig. 4). Cold stenotherms are less likely to be sensitive to low oxygen. *Anuraeopsis miraclei* sp. nov. is highly adapted to oxygen depletion as it is evident from the very low weighted mean oxygen concentrations, shown in Table 1, around which this species is distributed in the vertical profiles. Thus, when both low oxygen and not very high temperature conditions go together, as in this lake, it is advantageous for the species to be adapted to low values of these parameters. In this way, it would be able to stand more extreme oxygen depletion values, although it will lose ubiquity, having a more restricted distribution. Fig. 4 shows the limited range of temperature-oxygen values in which the species has been found. *Anuraeopsis miraclei* sp. nov. does not develop populations in Lake Arcas-2, which is much warmer; only sporadically rare occurrences were detected, in February and June, 1988.

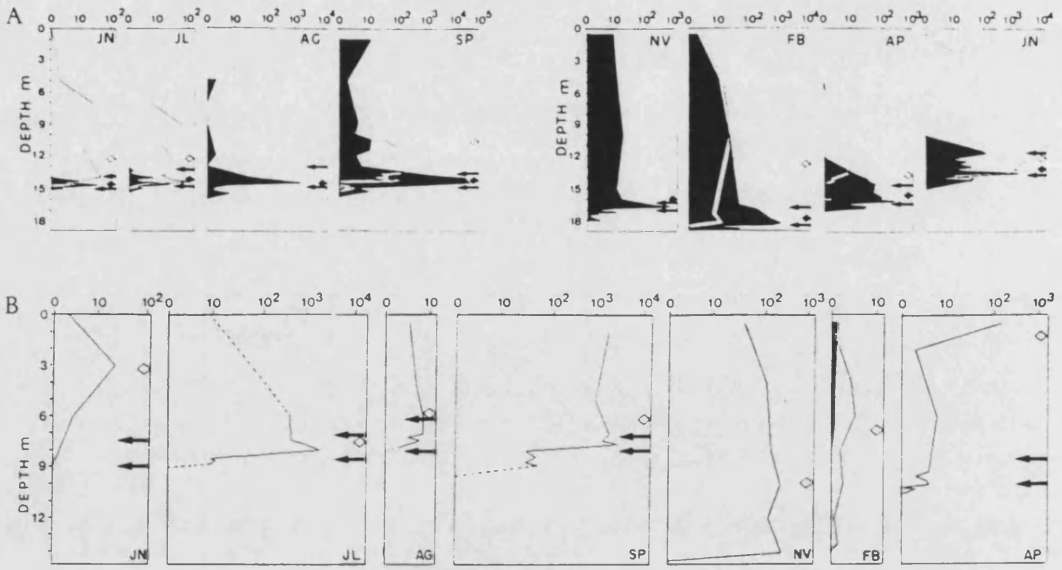

Fig. 3. Vertical distribution of two *Anuraeopsis* species. *A. fissa* (white area) and *A. miraclei* (black area), at different dates during the period June 1987 to June 1988 (months in right corners, the same dates as in Table 1). Number of individuals per litre on the abscissa and depth (m) on the ordinate. The arrows show the oxycline position. Diamonds show the mean depths or gravity centers of the *Anuraeopsis* species profiles.
A. Lake La Cruz; B. Lake Arcas-2.

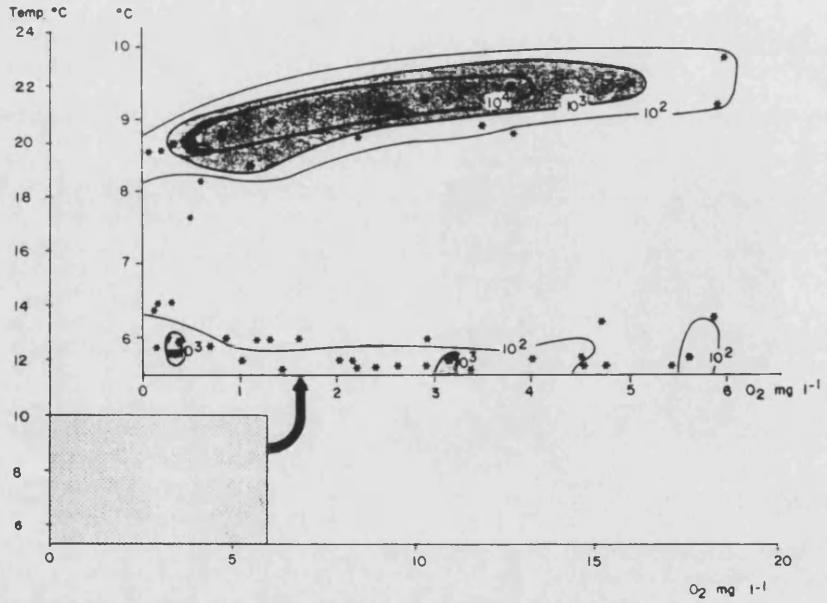

Fig. 4. *Anuraeopsis miraclei* distribution (isopleths in numbers of individuals per liter) with respect to temperature and oxygen. Points indicate the occurrence of more than 10 ind · l^{-1}. Shaded area, amplified above, indicates the position of the *Anuraeopsis* sp. nov. population within the whole range of environmental values found.

Anuraeopsis miraclei sp. nov. has a high maximum at the end of summer when it can profit from the energy, which has been accumulating during the productive season, in the density gradient at the top of the monimolimnion, where the oxidative-reductive zone is stablished. Although almost no experimental work exist on the genus *Anuraeopsis*, the literature (references mentioned in the Introduction) attributes a detritivorous role to it. We have found that a strain of *Anuraeopsis fissa* grew better in cultures fed with frozen-thawed algae than with living algae, but it did not grow well in soil extract. HILLBRICHT (1961) found that when macrophytes were added in experimental aquaria where they decomposed, a gross development of *A. fissa* subsequently occurred. *Anuraeopsis* species are then adapted to profit the energy pathway in the decomposition zone.

Anuraeopsis fissa in the studied lakes showed a more dispersed distribution and a much higher niche amplitude. However, our results demonstrate that when it coexists with *Anuraeopsis miraclei* sp. nov. its realized niche is reduced. In Arcas-2 where *A. fissa* is the only important representative of the genus, it shows an important deeper occurrence at oxycline portion of the water column (Fig. 3 B, Table 1) and annual maximum in September. However, in Lake La Cruz, where it coexists with *Anuraeopsis miraclei*, it is almost confined to the mixolimnetic section of the water column and has the annual maximum displaced to June, under an incipient thermocline.

Congeneric species of rotifers are usually found when environmental heterogeneity is present. The genus *Anuraeopsis* has differenciated in species to match the gradients in the decomposition zones, but their seggregation is only apparent where abrupt discontinuities are produced in the environmental range of conditions and the created heterogeneity is sufficiently large in the space and durable in time. Thus, in Lake La Cruz where these conditions may be encountered, two species of *Anuraeopsis* can coexist.

Acknowledgements

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Authors' address:

Ecology and Microbiology Fac. C. Biologicas, Universitat de Valencia, E-46100 Burjassot (Valencia), Spain.

[IV.2]

VERTICAL DISTRIBUTION OF PLANKTONIC ROTIFERS IN A KARSTIC MEROMICTIC LAKE

J. Armengol, A. Esparcia, E. Vicente and M.R. Miracle

Departament de Microbiologia i Ecologia, Universitat de València, 46100 Burjassot, (Valencia, Spain)

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Vertical distribution of planktonic rotifers in a karstic meromictic lake

Javier Armengol-Díaz, Angeles Esparcia, Eduardo Vicente & Maria Rosa Miracle
Area of Ecology, Universitat de Valencia, 46100-Burjassot, (Valencia) Spain

Key words: rotifers, meromixis, vertical distribution, oxycline, karstic lake

Abstract

Vertical distribution of planktonic rotifers is described in relation to temperature and oxygen in Lake La Cruz, a single-doline, closed karstic lake (121 m diameter and 25 m maximum depth) which shows iron meromixis. Samples were taken by peristaltic pumping at 10 cm depth intervals in the oxycline zone from June 1987 to September 1988. A model of rotifer vertical structure in stratified lakes is proposed. Rotifers concentrate their populations at the depths with intense gradients. As stratification develops some rotifer populations show a downward migration following the thermocline and some others show an upward migration following the oxycline. The production-respiration balance in the lake, and so the position of the oxycline with respect to the thermocline and the layer of maximum production, depends on meteorological conditions. A shift in the dominance of congeneric or related species can occur in consecutive years. In Lake La Cruz, mixing conditions and subterranean inflow in spring were much more intense in 1988 than 1987, and the distance between production and decomposition depths was smaller in 1988. *Anuraeopsis miraclei*, an oxycline-bound species with high abundance in 1987, was displaced by *A. fissa* in 1988. *A. fissa*, which was a metalimnetic species during early summer, reached peak densities (3×10^4 ind l^{-1}) at the oxycline, equaling the abundance of *A. miraclei* the preceeding year.

Introduction

The planktonic rotifer community in highly stratified lakes shows a distinct vertical structure, which is very much related to the thermal and oxygen concentration gradients (Larsson, 1971; Ruttner-Kolisko, 1980; Hofmann, 1987; Miracle & Vicente, 1983; Mikschi, 1989). In this paper we compare the vertical distribution of rotifers in a meromictic, karstic lake in two consecutive but meterologically different years. We discuss how the different mixing conditions in spring overturn and the differences in subterranean inflow from year to year can affect the rotifer populations of this highly stratified lake. The observed shift of dominance in these years between congeneric species, occurring in the oxic/anoxic boundary, indicates the importance of interannual metereological variations to planktonic rotifer assemblages.

The lake

Lake La Cruz (UTM 30 SWK 962272) is a small dissolution lake, located at 1000 m altitude, in an important limestone karstic area near the town of Cuenca (Spain). It is a closed lake sunk in a circular depression with a mean diameter of 121 m and a maximum depth in the center of 24.5–25.5 m, depending on the season. The lake level and flow of water into the lake depends

on the water table. The lake is believed tó have a long water renewal time, which favors stratification.

Its morphometry, i.e. small surface/depth ratio, and its location inside a dissolution basin having steep vertical walls rising 20–30 m above the water surface, produces an important reduction of wind mixing. The stability of the water layers is also enhanced by density gradients due primarily to dissolved ferrous bicarbonate and other ions common to dissolution lakes. Iron meromixis has been described in this lake (Vicente & Miracle, 1988). A sharp redoxcline was established at 14 to 20 m, depending on the season, with a completely anoxic bottom layer of water.

Methods

Water samples were collected in the center of the lake with a peristaltic pump connected to a thin layer inlet sampler (Miracle & Vicente, 1985) at different depths, indicated in Fig. 2 by horizontal lines in the vertical profiles. The oxyclinal zone was sampled at 10 cm depth intervals. Zooplankton was concentrated by filtering *in situ* 2 to 4 liters of water through 30 μm nylon mesh and preserved in 4% formaldehyde. All the organisms in each sample were then counted with an inverted microscope at 200 × magnification. Water samples were also taken with 2.7 liters transparent Van Dorn bottles from the epilimnion to complete the data. No significant differences in rotifer densities were observed between these bottle samples and those collected by pumping. To confirm that rotifers were alive in microaerobial layers, fresh samples were also observed. Temperature and oxygen were measured *in situ*, at the same time of the sampling with a WTW thermocouple and silvergold oxygen electrode, respectively. Several Winkler oxygen analyses were made for verification.

Results

A total of 26 rotifer species was identified in the samples, among which 11 were predominant. Table 1 shows the integrated values per water column of these species at the different sampling dates. The water column was fractioned in two parts. During thermal stratification, the epi-metalimnion layers were separated from the hypolimnion-oxycline layers. The depth corresponding to the separation between the water column fractions was more or less coincident with the 12 °C isotherm (Figs 1 and 2). During late autumn and winter, the oxyclinal depths were separated from the mixolimnion above it. Rotifers, although showing high concentrations in the oxycline, do not occur below the oxygen extinction depth. So the integrated numbers of rotifers in the hypolimnion-oxycline zone correspond to a much smaller fraction of the water column (Table 1 bottom).

From the data in Table 1, two groups of species are easily discriminated: (1) species with a higher proportion of individuals in the hypolimnion and oxycline and (2) epi-metalimnetic species. The vertical profiles of these two groups of species are represented, respectively, in Figs 1 and 2 in relation to the oxygen isopleths. The above mentioned 12 °C isotherm has been included to indicate the lower part of the thermocline. Profiles correspond to samples taken during the afternoon (12–16 U.T.). Vertical migration experiments performed in this lake (unpublished data) suggest that the profiles for the group (1) of hypolimnetic-oxyclinal species have very slight diel changes. The maxima are maintained at the same depth, and movements seem to be restricted within a narrow zone around them. Similar results are reported from other lakes with an oxycline (Stewart & George, 1987; Boagert & Dumont, 1989). Diel profiles for the group (2) of epi-metalimnetic species may be more variable, with much higher relative densities at the surface during the night.

The two years under study were noticeably different: 1988 had a much warmer winter and a much more rainy spring than 1987 (Fig. 3). Since this lake is completely closed, its level rose because of the precipitations, and summer level in 1988 was 0.5 m higher than in 1987. The intense subterranean inflow in 1988 disturbed the strati-

Table 1. Seasonal changes in the numbers of individuals (10^3 ind m^{-2}) in two fractions of the water column: (E) water from the surface to the indicated metalimnetic depth, which corresponds to the bottom of the metalimnion during stratification and to the bottom of the mixolimnion during mixing and (H) from there to the indicated oxygen extinction depth. The annual mean percentage of the species population in these fractions is indicated at the right.

Rotifer species		1987				1988						Mean percentage	
		Stratified				Mixing			Stratified			Mixing	Stratified
		JN	JL	AG	SP	NV	FB	AB	JN	JL	SP		
Anuraeopsis fissa	E	75.5	261.9	0.0	1209.5	0.0	219.7	62.8	3214.7	12294.8	14172.0	96	36
	H	96.5	121.8	0.0	110.6	0.0	18.4	0.8	10051.3	16638.1	27939.3	5	64
Anuraeopsis miraclei	E	0.0	0.0	6.0	67.1	203.7	341.7	33.2	0.0	3.0	25.5	28	7
	H	9.5	6.9	557.3	16308.5	251.8	1155.6	185.4	545.2	282.1	30.7	72	93
Polyarthra dolichoptera	E	16.9	537.5	41.5	224.5	437.2	1315.3	718.1	11.5	142.8	1422.5	96	28
	H	671.9	378.2	71.1	464.1	27.2	21.9	44.9	182.3	362.7	2770.3	4	72
Keratella quadrata	E	263.5	85.9	7.9	6.1	1.7	14.2	619.5	51.9	22.0	46.9	99	39
	H	443.9	466.3	2.1	1.1	0.0	0.5	1.5	67.1	1282.6	443.5	1	84
Filinia hofmanni	E	0.6	28.0	0.0	5.8	0.0	1.0	1.8	1.5	210.0	9.8	20	50
	H	0.0	12.2	0.3	0.2	1.5	2.2	4.8	23.1	400.2	12.2	80	50
Hexarthra mira	E	94.0	882.5	657.8	505.0	0.0	0.0	0.0	1015.5	379.0	692.5	0	97
	H	14.0	3.6	46.6	5.7	0.0	0.0	0.0	0.0	0.0	0.0	0	3
Trichocerca similis	E	411.2	243.0	94.8	228.3	38.2	0.0	29.8	196.1	260.0	212.0	0	96
	H	13.6	2.9	20.9	0.0	1.2	0.0	0.1	2.9	3.0	4.5	2	4
Synchaeta pectinata	E	87.2	29.0	315.5	87.4	1036.6	20.4	1.0	123.0	105.3	30.0	96	95
	H	2.9	1.5	41.0	0.3	17.2	0.0	0.1	4.6	11.2	0.0	4	5
Ascomorpha ecaudis	E	188.4	83.9	4.0	11.8	88.2	3.0	16.7	0.0	0.0	0.0	99	79
	H	100.0	38.4	0.0	2.6	0.1	0.0	0.0	0.0	0.0	0.0	1	21
Ascomorpha salans	E	65.4	0.0	22.5	35.1	0.0	0.0	0.0	0.0	0.0	18.1	0	96
	H	5.8	0.0	1.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0	4
Asplanchna girodi	E	0.0	0.0	0.0	7.6	0.0	0.0	0.0	158.7	2.5	0.0	0	100
	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0
Metalimnetic depth		10.0	10.5	11.5	13.0	16.0	16.0	13.5	9.0	10.0	11.0		
O_2 Extinction depth		15.0	15.0	14.9	14.9	16.9	18.7	16.6	13.9	12.7	14.1		

fication, resulting in a much higher primary production than in the preceding year – indicated by a higher metalimnetic oxygen maximum (Figs 1–3) – as well as by a lower depth of the oxycline (Table 1, Figs 1–3). The stratification of the phytoplankton populations was also reduced in 1988 (Dasi & Miracle, 1991).

The species which showed the most striking oxyclinal profiles is the recently described *Anuraeopsis miraclei* (Koste, 1991). It was described from that lake, but now it has also been found in the Alps (Austria), but in the same habitat: the late winter oxycline of the karstic lake Grosser Feichtauersee (Koste, personal communication). The growth of *A. miraclei* in Lake La Cruz (Fig. 1) is restricted to the lower end of the oxycline, with maxima at oxygen concentrations most frequently below 1 ppm. *A. miraclei* was perennial in this lake and always restricted to the oxycline, except during mixing, when it was somewhat dispersed

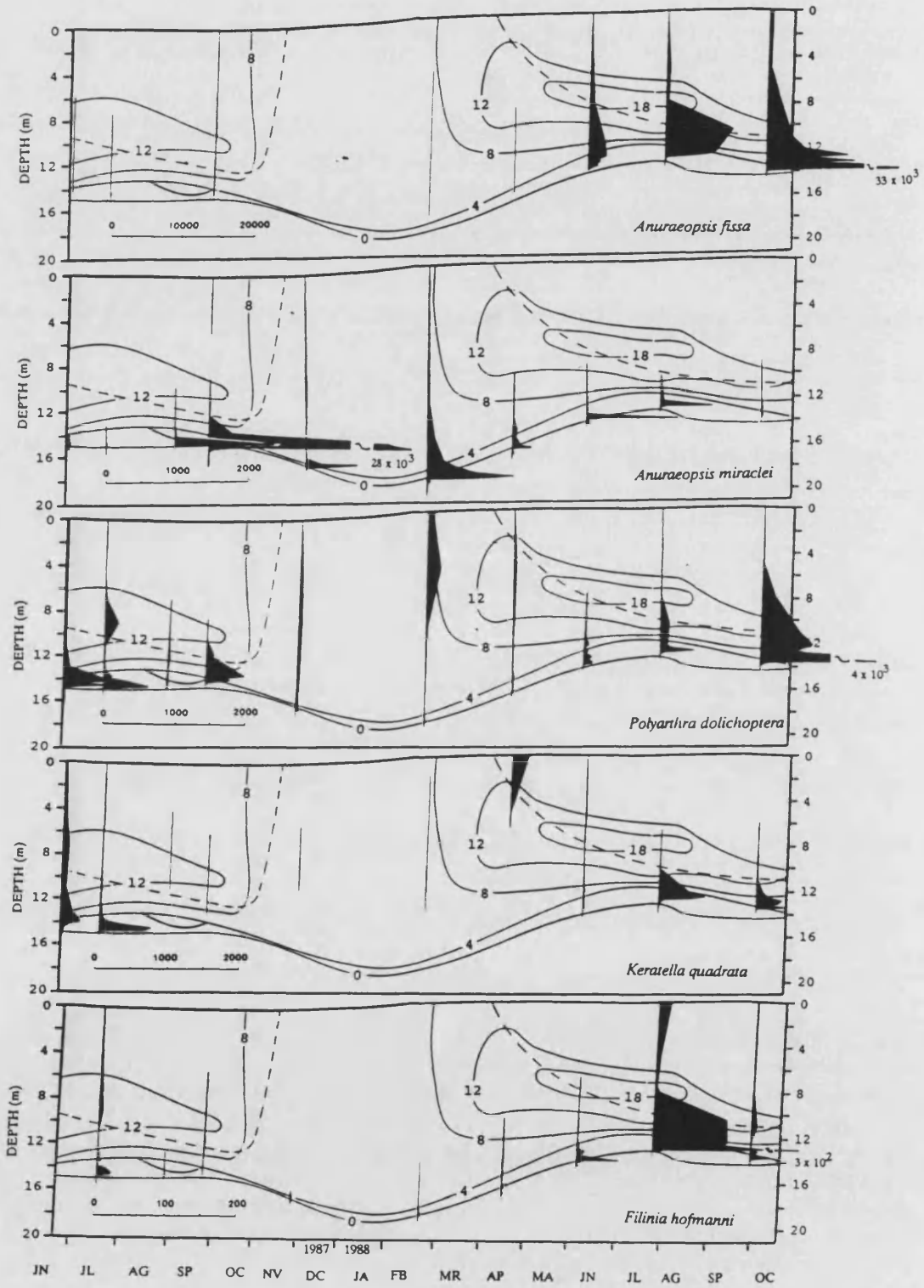

DEPTH (m)
Anuraeopsis fissa
33 x 10³
Anuraeopsis miraclei
28 x 10³
Polyarthra dolichoptera
4 x 10³
Keratella quadrata
Filinia hofmanni
3 x 10²
1987
1988
JN JL AG SP OC NV DC JA FB MR AP MA JN JL AG SP OC

Fig. 1.

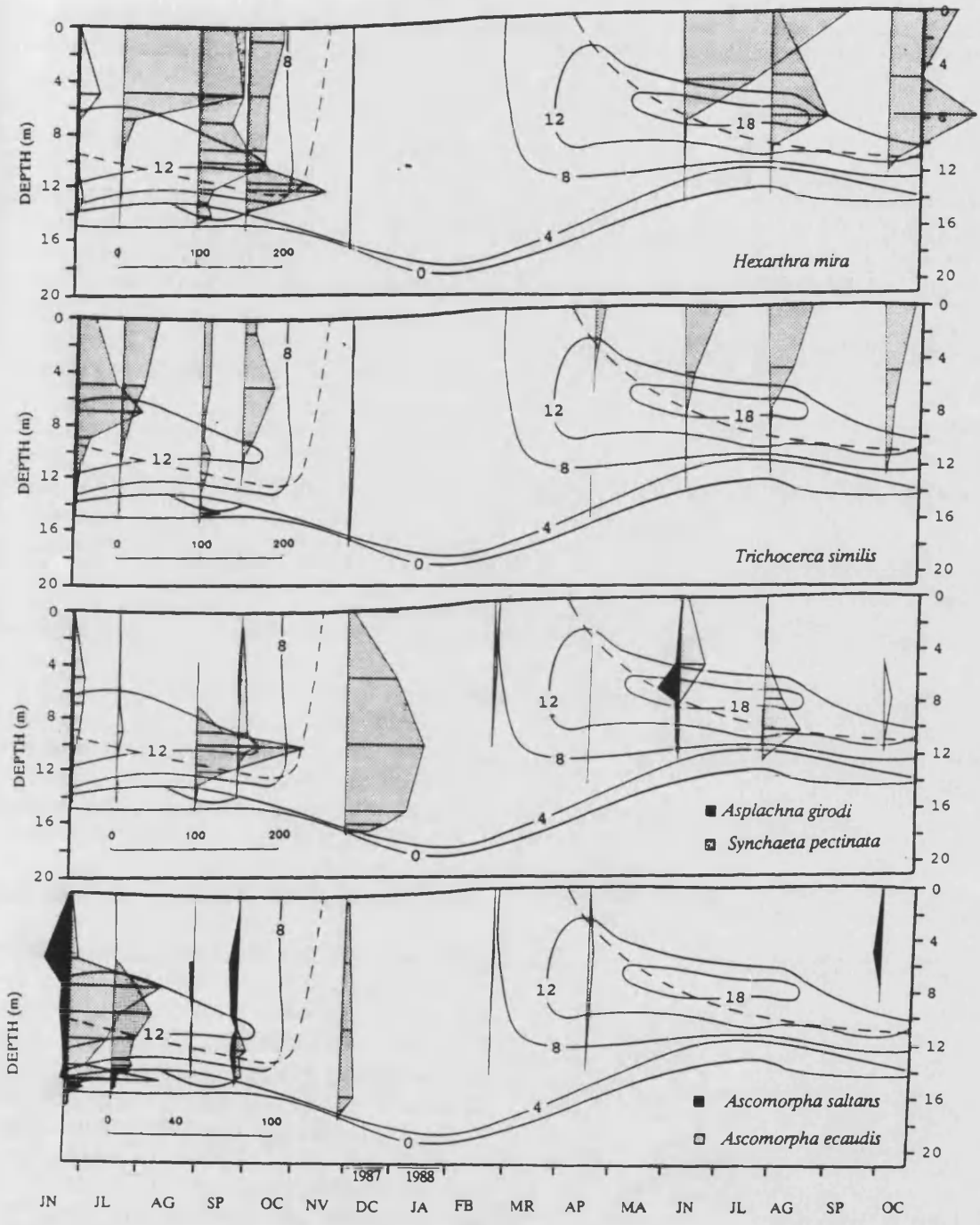
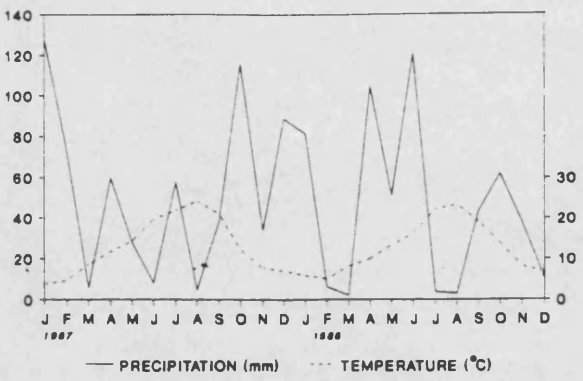
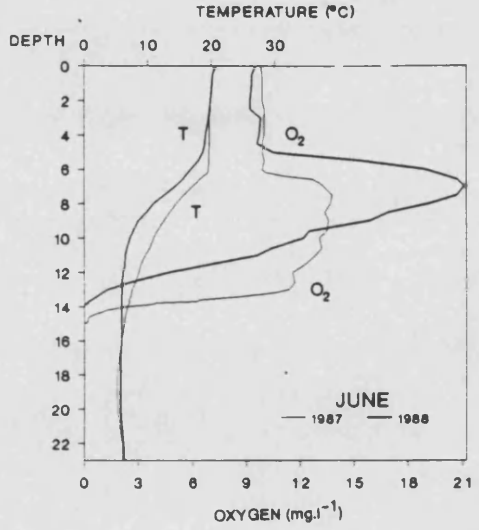


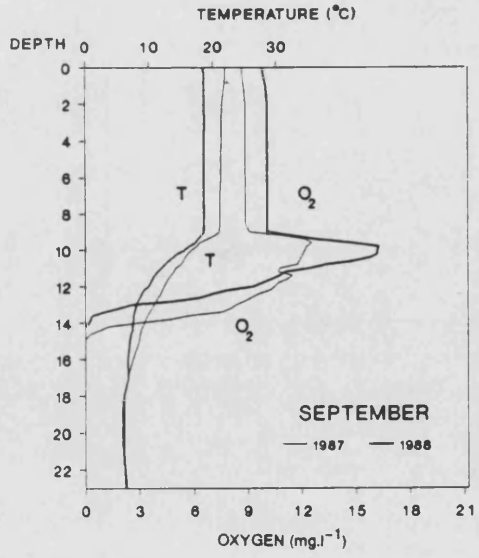
Fig. 2.

Fig. 1. Vertical profiles of epi and metalimnetic species, in individuals l^{-1}, at different dates from June 1987 to October 1988. Oxygen isopleths are indicated in solid lines. The 12 °C isotherm is indicated with a broken line.

Fig. 2. Vertical profiles of hypolimnetic and oxyclinal species, in individuals l^{-1}, at different dates from June 1987 to October 1988. Oxygen isopleths are indicated in solid lines. The 12 °C isotherm is indicated with a broken line.







throughout the whole water column, but then always maintaining oxyclinal densities one or two orders of magnitude higher than in the water above.

In a previous paper (Esparcia *et al.*, 1991) we reported: (1) the narrow and low range of temperature-oxygen values in which this species was found in Lake La Cruz, and (2) the vertical segregation between this species and *Anuraeopsis fissa* when they coexist. The additional data presented here show the alternation of these species in the temporal dimension. In 1987 *A. miraclei* grew exponentially in a thin layer (25–50 cm) of the deeper oxycline from a population in June with less than 10^2 ind l^{-1} to almost 3×10^4 ind l^{-1} in late September. On the other hand, in 1988, it was *A. fissa* which grew in this thin layer, replacing *A. miraclei* at the end of that summer by reaching the same final density: 3×10^4 ind l^{-1} (Fig. 1). However, *A. fissa* was not exclusively in this layer, as was *A. miraclei*, but also showed rather high densities above it: at the lower part of the metalimnion, where, in fact, it had its maximum at the beginning of summer.

Filinia hofmanni, together with *A. miraclei*, showed deep maxima usually at the same depth as those of the latter although more dispersed throughout the profile. However, *F. hofmanni* during the study period was scarce and never showed high densities at any depth.

The other two hypolimnetic species, *Polyarthra dolichoptera* and *Keratella quadrata*, had abundance peaks in the epilimnion during winter-spring, but they shifted downwards during summer, showing then an hypolimnetic distribution. The results from the small scale sampling at the oxycline showed a slight segregation between the late-summer peak densities of these species: *K. quadrata* had its peak 10–20 cm above that of *P. dolichoptera*, and the latter had its peak at about the same depth (occasionally 10 cm above) as that of *A. fissa* and 10–20 cm above that of

Fig. 3. Comparison between years 1987 and 1988. Climate diagram (top) and vertical profiles of oxygen and temperature on two selected dates at the beginning and end of the stratification period.

A. miraclei or *F. hoffmanni*. However, *P. dolichoptera* is capable of short diel migrations which could slightly change its distribution during the night. *P. dolichoptera* also showed on some occasions secondary peaks at the metalimnion. They could be due to other ecotypes, or even to some extent to related species such as *P. vulgaris*. Because of the difficulty in differentiating *Polyarthra* species during counting, individuals of this genus were counted together. However, specimens isolated later for identification from a large number of samples always belonged to *P. dolichoptera*.

The vertical profiles of species showing maximal developments in more superficial and well-oxygenated waters are represented in Fig. 2. Their population densities were much lower than those of the hypolimnetic species (Fig. 2). *Hexarthra mira* was a summer species which occupied the epilimnion in early summer but later in this season had its maximum density at the metalimnion, occasionally with a secondary surface peak. *Trichocerca similis* was also a summer species occurring preferentially in the epilimnion. *Synchaeta pectinata* occurred at all dates with its maximum development in November; in summer it was clearly metalimnetic. *S. tremula* appeared in low numbers (< 1 ind l^{-1}) only during February 1988. *Ascomorpha ecaudis*, *A. saltans* and *Asplanchna girodi* were more scarcely represented; *A. girodi* was exclusively epilimnetic, and *A. ecaudis* was frequent in summer 1987, occupying the metalimnion but also showing a deeper density peak.

Some other rotifers were found sporadically. *Trichocerca rattus* appeared with a maximum of 27 ind l^{-1} in July 1988. A few individuals of several littoral species belonging to the genera *Lecane* (5 spp.), *Machrochaetus* (2 spp.), *Heterolepadella*, *Colurella*, *Lepadella*, and *Cephalodella* were present in the samples.

Discussion

The seasonal cycle of rotifer vertical distribution reported here seems to be a rather regular event; similar patterns of distribution are recorded in different stratified lakes with an oxic-anoxic boundary (e.g. Larsson, 1971; Ruttner-Kolisko, 1975; Hofmann, 1975, 1987; Miracle, 1976; Mikschi, 1989; Miracle *et al.*, 1991; Bogaert & Dumont, 1989). From winter to summer, most species show a tendency to concentrate their populations at the zone of gradients or interphases. Considering only the summer hypolimnetic species, two trends of variation can be seen. (1) Species are more or less dispersed at low densities throughout the water column in winter and then have an important growth in spring at the incipient thermocline. As summer season advances, populations migrate downwards with the themocline, establishing metalimnetic maxima, and from there descend further and produce extremely dense concentrations near the oxic-anoxic boundary. (2) Species are bound to the oxycline, and always show deep maxima. When the summer season advances, they migrate upwards with the oxycline.

In Lake La Cruz the species showing the first trend are *P. dolichoptera*, *K. quadrata*, and *A. fissa*. Species showing the second trend are *A. miraclei* and *F. hofmanni*, although the latter was scarce during study period. These same trends were observed by Hoffmann (1987) in the Plußsee, where *F. hofmanni* and *Keratella hiemalis* were the species bound to the oxycline. Similar models can be deduced from other studies on rotifer distribution in lakes with oxic-anoxic boundaries – e.g. Blankvatn in Norway (Larsson, 1971) and Lunzer Obersee in Austria (Ruttner-Kolisko, 1975, Mikschi, 1989) – where the oxyclinal species were also *K. hiemalis* and *F. hofmanni* (the last species, due to its recent description, had other names in earlier papers).

At the end of summer, when the thermocline and the oxycline come more closely together, both types of species have to coexist in an increasingly narrower zone of the vertical profile. The dominance of a species over its congeneric partner, or over a closely related counterpart in the food web, depends on the situation of the thermocline and oxycline during the year. The oxic-anoxic boundary in Lake La Cruz is not located at the

chemocline 'sensu stricto' (mixo-monimolimnion interphase), but depends on the productivity-respiration balance in the lake that year, which in turn depends on turbulence and mixing.

Thus, the primary difference in rotifer distribution between the two years of study was the different distance in the vertical profile between production and decomposition. This distance in 1988 was shorter than in 1987; therefore at the end of summer 1988 the development of the true oxycline-bound species, i.e. *A. miraclei*, was restricted, while that of *A. fissa* was favored, thus the latter extended beyond the metalimnion and occupied the oxycline. In other meromictic lakes where the oxycline is always associated with the chemocline (Miracle & Alfonso, 1992), the stratification of congeneric species may be more constant throughout the years.

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[IV.3]

EXTREME MEROMIXIS DETERMINES STRONG DIFFERENTIAL PLANKTONIC VERTICAL DISTRIBUTION

M.R. Miracle, **J.. Armengol** and M.J. Dasí

Departament de Microbiologia i Ecologia, Universitat de València, 46100 Burjassot, (Valencia, Spain)

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Extreme meromixis determines strong differential planktonic vertical distributions

Maria R. Miracle, Javier Armengol-Díaz and M. José Dasí

Introduction

Meromictic lakes are characterized by a special deep zone at the bottom of the mixolimnion, where planktonic populations can reach densities much higher than in the zones above. Furthermore these populations are structured in fine stable zonations. The aim of this paper is to describe the vertical distribution of phytoplanktonic and zooplanktonic organisms and their temporal variation, in Lake El Tobar. This is a meromictic saline lake located in a karstic formation, North of the Cuenca Mountains (Spain), which shows a striking stratification;; conductivity changes from 0.6 mS · cm^{-1} in the mixolimnion to almost 200 mS · cm^{-1} at the bottom of the monimolimnion (Table 1).

The present study is a part of the introductory investigations undertaken in this lake. The other part consisting of the description of the peculiar morphometry and physicochemical characteristics of Lake El Tobar is reported in VICENTE et al. (1993).

Methods

Phytoplankton and zooplankton samples were taken at 1 m depth intervals in the water column, on several days, during mixing and stratification periods, in the centre of the meromictic basin of the karstic Lake El Tobar.

Water samples were taken with a 2.6 l Ruttner bottle. From it 250 ml were used for phytoplankton analysis and the rest for chemical tests. The phytoplankton was fixed in situ with Lugol's solution. Depending on the algal density of the samples, 50 or 100 ml were sedimented and counted, under inverted microscope at 400 and 1000 × magnification, according to the Utermöhl method.

Zooplankton was collected by filtering in situ through a 30 µm mesh, the water taken with a double Van Dorn bottle (5.4 l). To improve the evaluation of crustacean numbers additional samples were taken with a 25 l Patalas trap (100 µm mesh). Day and night profiles were made. Zooplankton was preserved in 4 % formaldehyde and counted under an inverted microscope at 100 and 200 × magnification.

Physico-chemical parameters such as temperature, light, conductivity, O_2, and chlorophyll *a*, were also measured simultaneously (VICENTE et al. 1993).

Table 1. Conductivity values (mS · cm^{-1}) in Lake El Tobar, at 1 m intervals in the zone of variation. Surface and bottom values are also indicated as a reference.

	1991			1992	
Depth (m)	11 Aug.	23 Sept.	19 Nov.	23 Apr.	18 Aug.
0	0.5	0.5	0.5	0.5	0.5
9	0.7	0.7	0.5	0.5	0.7
10	0.9	1.0	0.5	0.5	1.0
11	1.8	2.1	0.8	3.7	3.8
12	6.0	14.0	8.7	7.6	17.7
13	28.6	34.0	31.5	28.2	28.9
14	117.0	135.0	123.0	165.0	144.0
15	143.0	160.0	145.0	200.0	176.0
18.5	175.0	182.0	168.0	200.0	200.0

A canonical correlation analysis between phytoplankton and zooplankton population densities was performed, on previously ln (x + 1) transformed data, using the 6M program of BMDP.

Results and discussion

The extreme stratification of Lake El Tobar due to crenogenic meromixis is shown in VICENTE et al. (1993). The dense salt water bottom layer determines the uniqueness of the biotic characteristics of the lake. It provides special features for the planktonic organisms at the fresh-salt water boundary:

1) A year-round stable temperature at the bottom of about 13 °C (with a pronounced temperature inversion from autumn to spring), 2) special light conditions, 3) an interface with an exponential salinity gradient (Table 1) and 4) high concentrations of nutrients and detritus. Planktonic organisms are concentrated near this boundary, located around 12 m of depth. Just below it there is an anoxic brine where almost no organisms are found, with the exception of bacteria.

Phytoplankton

A sharp peak in both oxygen and chlorophyll *a* concentration is characteristic of the fresh-salt water interface at around 12 m in depth (VICENTE et al. 1993). These peaks are related to the growth of several organisms at that depth, mainly stratifying cyanobacteria. A large number of very small cells ($\sim 0.7 \times 1.2\,\mu m$), which show fluorescence under green light (546 nm), characteristic of cyanobacterial phycocyanin, was observed. They seem to correspond to the *Synechococcus* described by CRAIG (1987) from the chemocline of Little Round Lake. In addition, the cyanobacterium *Gloeocapsa* sp., with a strong orange colour, forms a thick layer just above the brine with its maximum coincident with the oxygen and chlorophyll *a* peaks (Fig. 1). There, *Gloeocapsa* has a permanent population of about 10^5 cells · ml^{-1}, with highest density at the end of summer (up to 3×10^5 cells · ml^{-1}). The cells are surrounded by a thick gelatine capsule that enlarges greatly at the end of summer and may form clumps or aggregates. Other exclusive species of this layer are *Chlamydomonas* sp. (one order of magnitude less abundant than *Gloeocapsa*, Fig. 1) which shows an important growth in November, and some species of *Astasia* in summer. A *Chlamydomonas* plate at the oxic-anoxic limit above photosynthetic bacteria was reported also by LINDHOLM & WEPPLING (1987) and CRAIG (1987) in temporally meromictic lakes due also to a salt bottom layer. A flagellate, *Scourfieldia caeca*, was also found associated with the chemocline in meromictic lakes with the saline monimolimnion in Tasmania (CROOME & TYLER 1985, MIRACLE et al. 1991).

Other algae increase their population density in the deep layers just above the *Gloeocapsa-Chlamydomonas* plate: *Cryptomonas erosa* and *Gymnodinium* sp. have their maxima at around 11 m of depth and *Rhodomonas minuta* and *Pedinomonas minor* show a secondary maximum (only in summer) at the same depth.

In the mixolimnion a seasonal succession takes place. Dominance of Chlorophytes, at the end of summer, mainly *P. minor* (several *Scenedesmus* and *Monoraphidium* species were also abundant) shifted to dominance of diatoms, mainly *Cyclotella ocellata*, in autumn, and to Cryptophytes in winter–early spring, when *R. minuta* clearly dominated over the rest (Fig. 2).

Zooplankton

Zooplankton populations show striking vertical distributions with two clear maxima; one near the surface (at the upper metalimnion, when present) and the other at the bottom, above the halocline, from 10 to 12 m of depth (Fig. 3).

Rotifers have higher population densities than Crustaceans, representing between 60 % of total zooplankters in summer and 90 % in spring. *Keratella quadrata* is the main species (Fig. 3), having a permanent population with a clear preference for surface (at the upper metalimnion, when present)

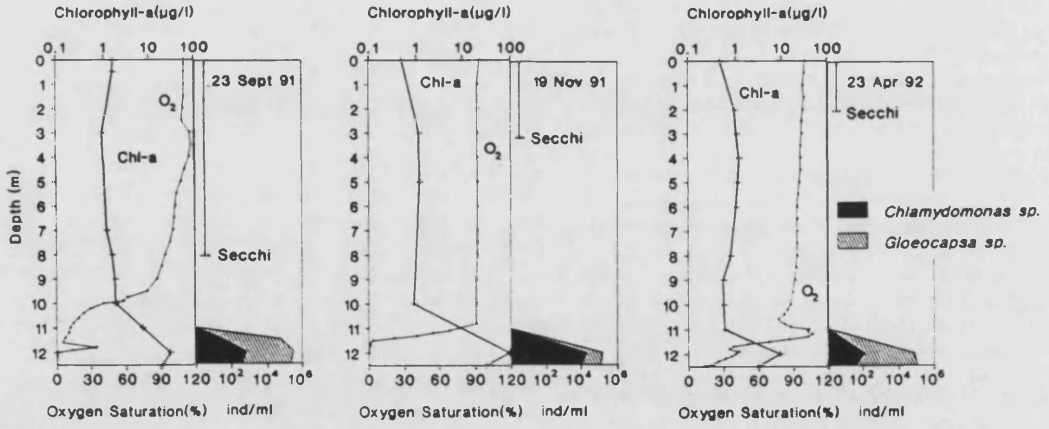

Fig. 1. Vertical profiles, for the indicated dates, of percent saturation of oxygen and chlorophyll *a* concentration, together with the corresponding profiles of the accumulated number of individuals of *Chlamydomonas* sp. and *Gloeocapsa* sp. (in logarithmic scale). Secchi disk depth is also indicated.

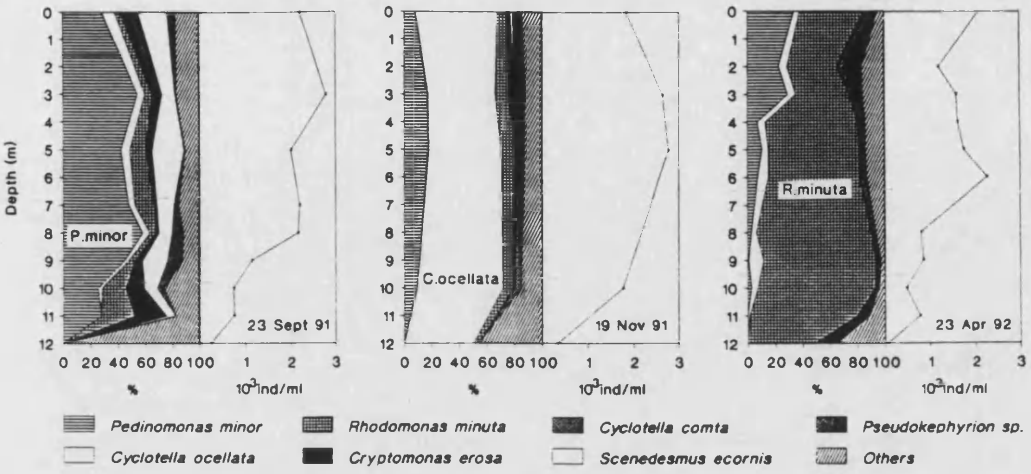

Fig. 2. Vertical profiles, for the indicated dates, of the proportions (%) of the main phytoplankton species excluding the halocline stratifying species: *Chlamydomonas* sp., *Gloeocapsa* sp. and *Synechococcus* sp. The total number of phytoplankton individuals considered for the proportions (i.e. without the mentioned species) is also plotted at the right.

and the layers near the halocline, with a year-round maximum at 11 m depth. Numbers of individuals of *K. quadrata* vary from about 10^2 ind · l^{-1} at the end of summer to about 10^3 ind · l^{-1} in spring.

Polyarthra spp. (*P. vulgaris*, *P. longiremis* and *P. dolichoptera*) are also abundant in summer and autumn, altogether with *Ascomorpha ovalis*, *Trichocerca similis* and *Testudinella patina*. Other species of *Trichocerca* were also observed, including *T. brachyurum*, *T. tenuior* and *T. porcellus*. It is also interesting to report the presence of *Testudinella incisa*. This is its first recorded observation in Spain. *Asplanchna girodi* was also abundant in summer–autumn in the bottom waters, with maxima at the same depth as *K. quadrata* (in fact loricas of *K. quadrata* were found inside *A. girodi*) *Anuraeopsis fissa* and *Collotheca* sp. were found almost exclusively in summer at the epilimnion.

In autumn, *Synchaeta* spp. (mainly *S. oblonga* and *S. pectinata*) start to increase their numbers, becoming dominant in winter–spring. In spring *S. tremula* was also observed. The group of species *S. tremula-oblonga* (counted together due to the difficulty of differentiating them in fixed samples) was completely dominant in spring in the upper waters. Its distribution was reversed to that of *K. quadrata* dominant in the bottom waters (Fig. 3).

Other rotifer species had very low abundances (less than 1 ind · l^{-1}) except for *Ascomorpha ecaudis* and *Polyarthra dolichoptera* which reached maximum densities in the vertical profile slightly over 5 ind · l^{-1}.

Cladocerans represented only 6 % in September of total zooplankton individuals and 1 % in April. Fig. 3 shows the proportion with respect to total crustaceans (35 % and 6 % in September and April respectively). In order of abundance we found: *Daphnia longispina*, *Bosmina longirostris* and *Ceriodaphnia quadrangula*. They were more or less localized in the epimetalimnion, except *Daphnia longispina* which in summer showed two maxima corresponding to a metalimnetic and to a deeper population. The segregation of genetically diverse populations in the vertical profile was made evident by isozyme electrophoretical studies (King & Miracle, in press). The genetic structure of *D. longispina* in September showed the existence of two main clones (composite electromorphs based on three enzymes), one more frequent in the top waters and the other located in the bottom waters (10–11 m). At the time of sampling the deep population of *D. longispina* was heavily parasitised by *Gurleya vavrai* (Green). During mixing *D. longispina* was concentrated in the upper 6 m of depth, the deep peak disappeared, as well as the deep clone, from which almost no individuals remained. Mazunder & Dickman (1989) found, also in a meromictic lake, a maximum population of pink *Daphnia* in the bottom waters which was

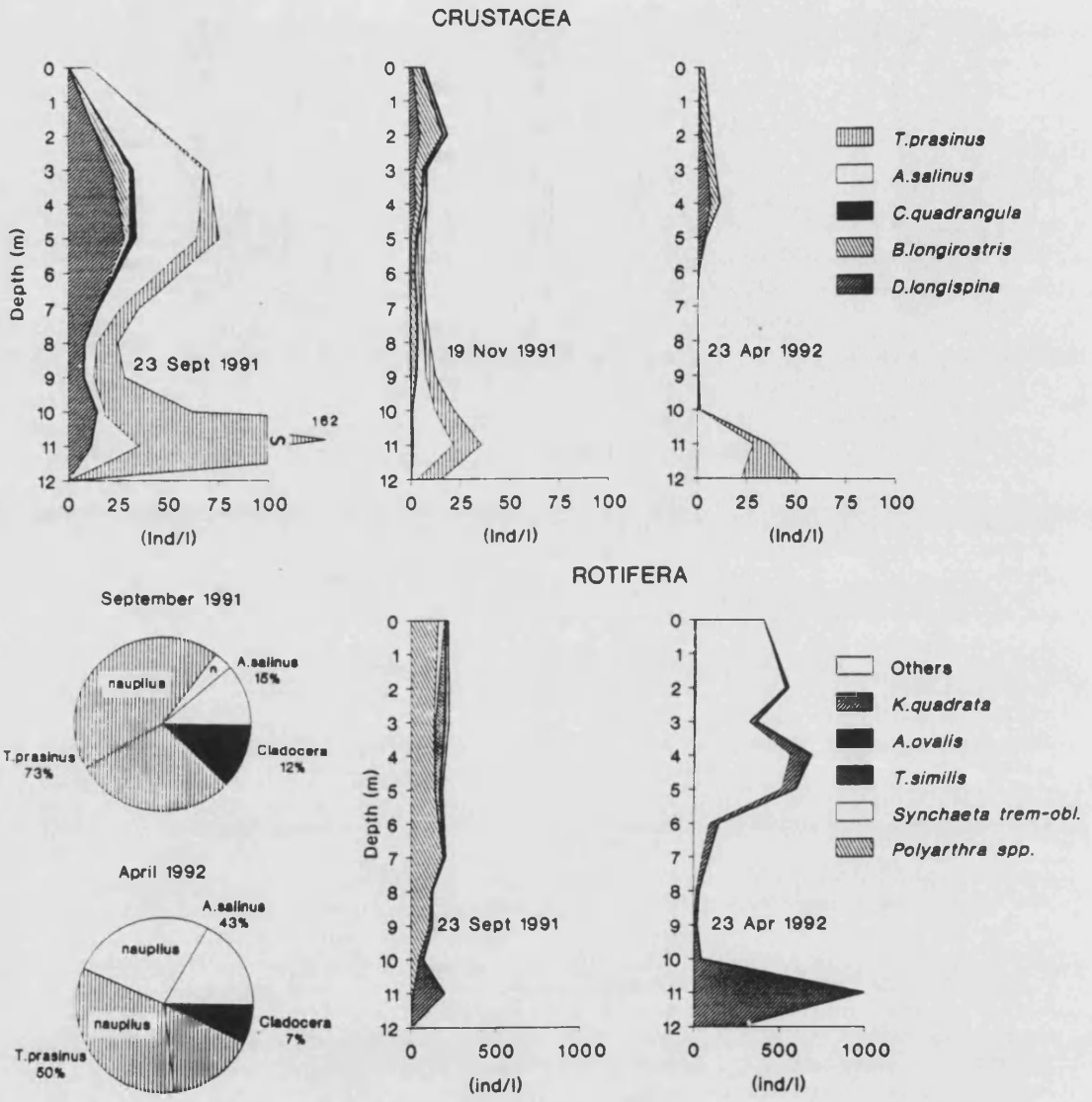

Fig. 3. Vertical profiles of the accumulated densities of the main zooplankton species (ind · l^{-1}) at the indicated dates. For copepods, densities correspond to copepodites + adults (nauplii are not included). At bottom left, the percentage of the main copepods, including nauplii, with respect to total crustaceans in the whole water column, is plotted for two sampling dates (*A. salinus* white, *T. prasinus* stripes, *cladocera* black).

easily differentiated from the *Daphnia* population in the waters above.

On the other hand, from autumn to spring copepods are localized in the deep layers (10 – 12 m) with very few individuals above. The main species were *Arctodiaptomus salinus*, *Tropocyclops prasinus* and *Cyclops abyssorum*, but the latter had very low densities. In summer they occur also in the upper layers, may be incited, in part, by the high presence of *Chaoborus* larvae in the deep waters.

In summer a bimodal distribution was observed in *A. salinus*, with a peak at the metalimnion and another at the deep layers, above the brine. *A. salinus* nauplius are localized also in these deep layers.

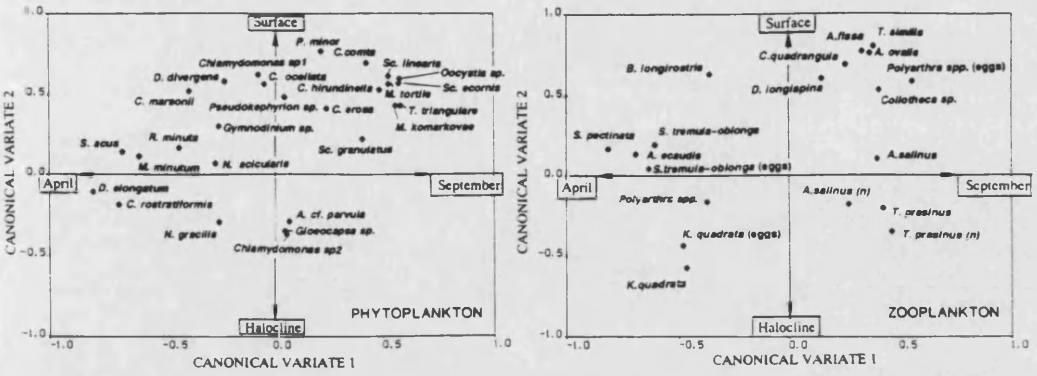

Fig. 4. Correlations between the phytoplankton (left) and zooplankton (right) taxa and the two derived canonical variates with the highest redundancy index (variates which explained the highest proportion of variance of each set of variables). The labels *surface-halocline* and *April – September* indicate the main directions in the species distributions. Complete names are in the text, except for *Cryptomonas marssoni*, *Dinobryon divergens*, *Nitzschia acicularis* and *Scenedesmus granulatus*.

Furthermore, at the time of higher reproductive activity, April and November, the whole population with a high frequency of egg-bearing females is concentrated at the fresh-salt water boundary. In November 1986, there was a double oxygen extinction (Vicente et al. 1993) and *A. salinus* and other copepods were trapped in between. A vertical distribution of copepods clearly skewed toward the chemocline or bimodal has been reported from other meromictic lakes (Culver & Brunskill 1969, Swift & Hammer 1979).

A. salinus is a circummediterranean species which extends to central Asia, with a tendency to show an east-west disjunction. In Spain it is mainly localized in the endorheic shallow saline waters of the steppic lands (Miracle 1981). Its presence in this karstic lake, which has a low mineralization, is puzzling. The conductivity of Lake El Tobar (Vicente et al. 1993) is 0.6 mS · cm^{-1} in the mixolimnion but up to 4 mS · cm^{-1} at the oxic-anoxic boundary where *A. salinus* concentrates.

The presence of *A. salinus* is more interesting if we consider that it is also one of the main species in the zooplankton of Banyoles Lake (Miracle 1976) another freshwater, but also karstic lake with a conductivity of around 1 mS · cm^{-1} in most of the lake (2 mS · cm^{-1} in the monimolimnion of a meromictic basin). *A. salinus* has been also reported from Lake Tiselit (Atlas Mountains, François 1949). *A salinus* in Lakes El Tobar and Banyoles have some features which differentiate it from saline lakes, mainly a smaller size and lower fecundity.

Canonical correlation analysis

The relationships between the phyto- and zooplankton were explored by means of a canonical correlation analysis with these two sets of variables. The canonical variate 2 accounted for 26 % of the variance of phytoplankton species densities and for 20 % of the variance of zooplankton species densities. The canonical variate 1 accounted respectively for 23 % of the phytoplankton variance and 18 % of that for zooplankton. Canonical variate 2 separated the species with a higher abundance at the surface from those with a clear tendency to concentrate in deep waters. Canonical variate 1 separated summer species from those which occur or are most frequent in spring. The position of each species in the canonical correlation variates (Fig. 4) visualises the distribution along the water column and through the year. *Gloeocapsa*, *Chlamydomonas*, and *Astasia* cf. *parvula* come as a compact group in the negative side of C.C.V. 2. High negative correlations with this variate are also shown by *K. quadrata* and copepods specially their nauplii. Nauplii are more abundant than the other stages, so they show a more compact occurrence in the deeper waters, near the halocline. *A. salinus* copepodites and adults have a low correlation, in the positive side, because of its metalimnetic occurrence in summer. Another group of species is that of *Ceratium hirundinella*, *Cyclotella comta*, *Tetrastrum triangulare*, several species of *Monoraphidium* (*M. komarkovae*, *M. tortile*) and *Scenedesmus* (*Sc. ecornis*, *Sc.*

linearis) which have summer superficial distribution and they are located at the positive side for both canonical variates. The same position is shown by the zooplankters *Ascomorpha ovalis*, *Anuraeopsis fissa* and *Trichocerca similis* which had also a summer surface distribution. On the negative side of CCV 1 we find the corresponding winter–spring species of phytoplankton, *R. minuta*, *Synedra acus*, *Monoraphidium minutum*, *Diatoma elongatum*, *Cryptomonas rostratiformis*, and of zooplankton, *Synchaeta* spp. (*S. pectinata* and *S. tremula-oblonga*) and *Ascomorpha eucaudis*.

Concluding comment

The salt-freshwater interface in this lake is the most metabolic active stratum in the water column, due to its enrichment by the settling and decomposition of the biomass produced above and quite constant temperature. As enough light, although with very low intensities, reaches it, coccoid cyanobacteria and small green algae develop exclusive dense populations there. Moreover, organisms of the phytoplankton and zooplankton which are widespread through the vertical profile, show important deep mixolimnetic peaks, just above or in the upper part of this interface. In some cases, the deep maxima of these species correspond to different populations or ecotypes adapted to the special conditions of the interface, such as low light and low oxygen tensions.

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Authors' address:

Area of Ecology, Faculty of Biological Sciences, Universitat de València, E-46100 Burjassot, Spain.

[IV.4]

POPULATION DYNAMICS OF OXYCLINAL SPECIES IN LAKE ARCAS-2 (SPAIN)

M.R. Miracle & **X. Armengol**

Departament de Microbiologia i Ecologia, Universitat de València, 46100 Burjassot, (Valencia, Spain)

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

Maria Rosa Miracle & Xavier Armengol-Díaz
Departament l'Ecologia i Microbiologia. Facultat de Biologia. Universitat de València. 46100 Burjassot (Valencia), Spain

Key words: Filinia hofmanni, Anuraeopsis fissa, population dynamics, reproductive patterns, mixis strategies, oxicline, solution lakes

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.

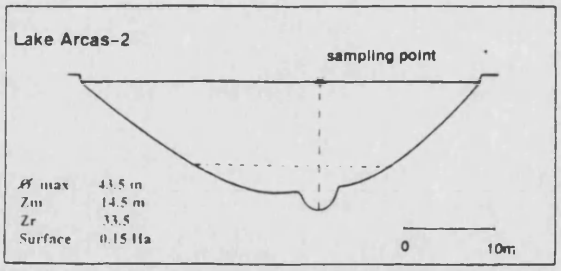

Fig. 1. Vertical cross-section of lake Arcas-2 largest basin, showing the position of the sampling site and the oxygen extinction depth in summer (dashed line). The scale is the same for vertical and horizontal dimensions. Some morphometric parameters to show the high depth/diameter ratio are also indicated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

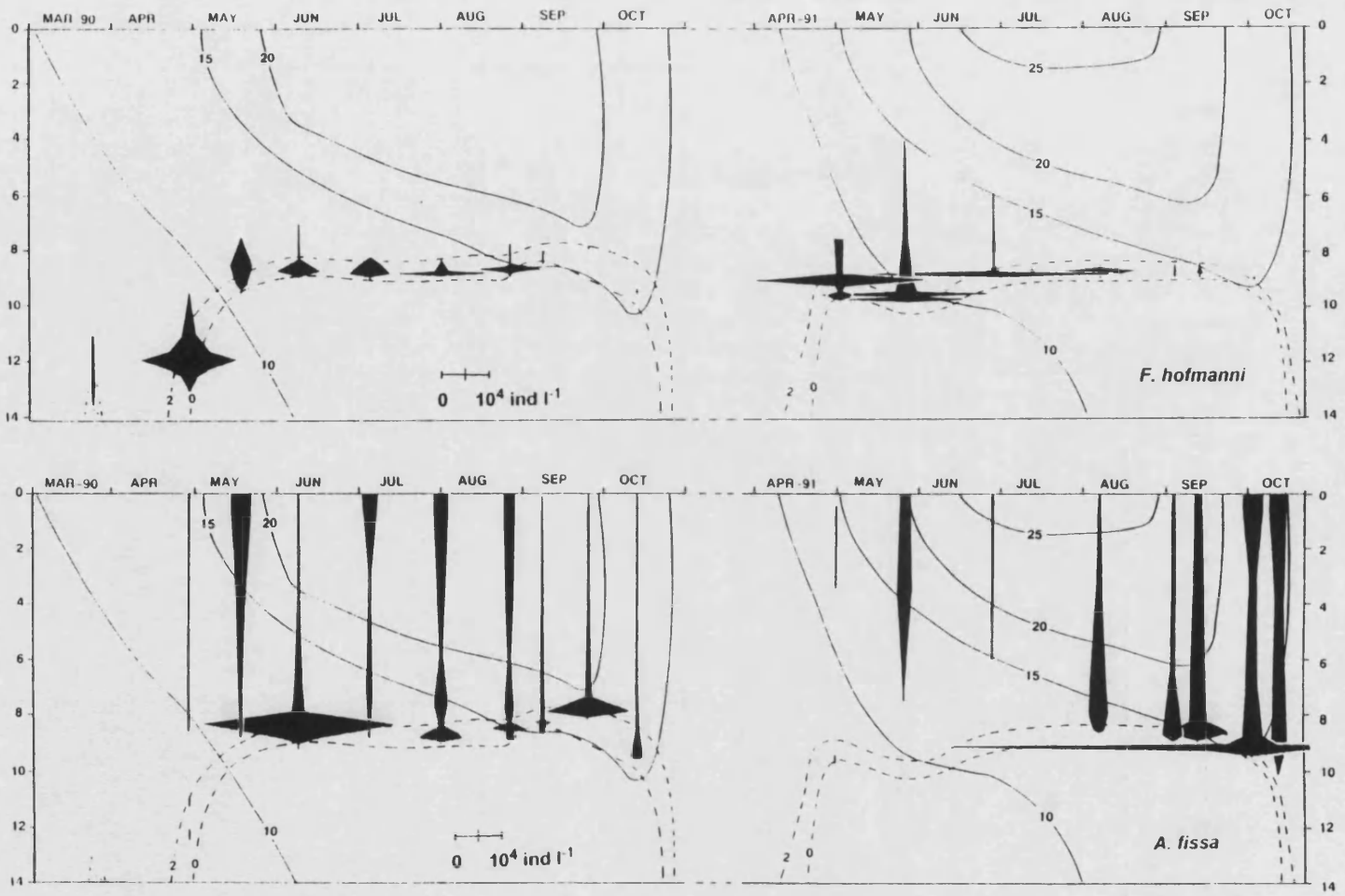

Fig. 2. Vertical profiles of *F. hofmanni* (top) and *A. fissa* (bottom) during the stratification period in 1990 and 1991. Abundance of these species is very low during the mixing period (November-March). Isotherms every 5°C are indicated with solid lines and the oxygen isopleths of 0 and 2 mg l^{-1}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

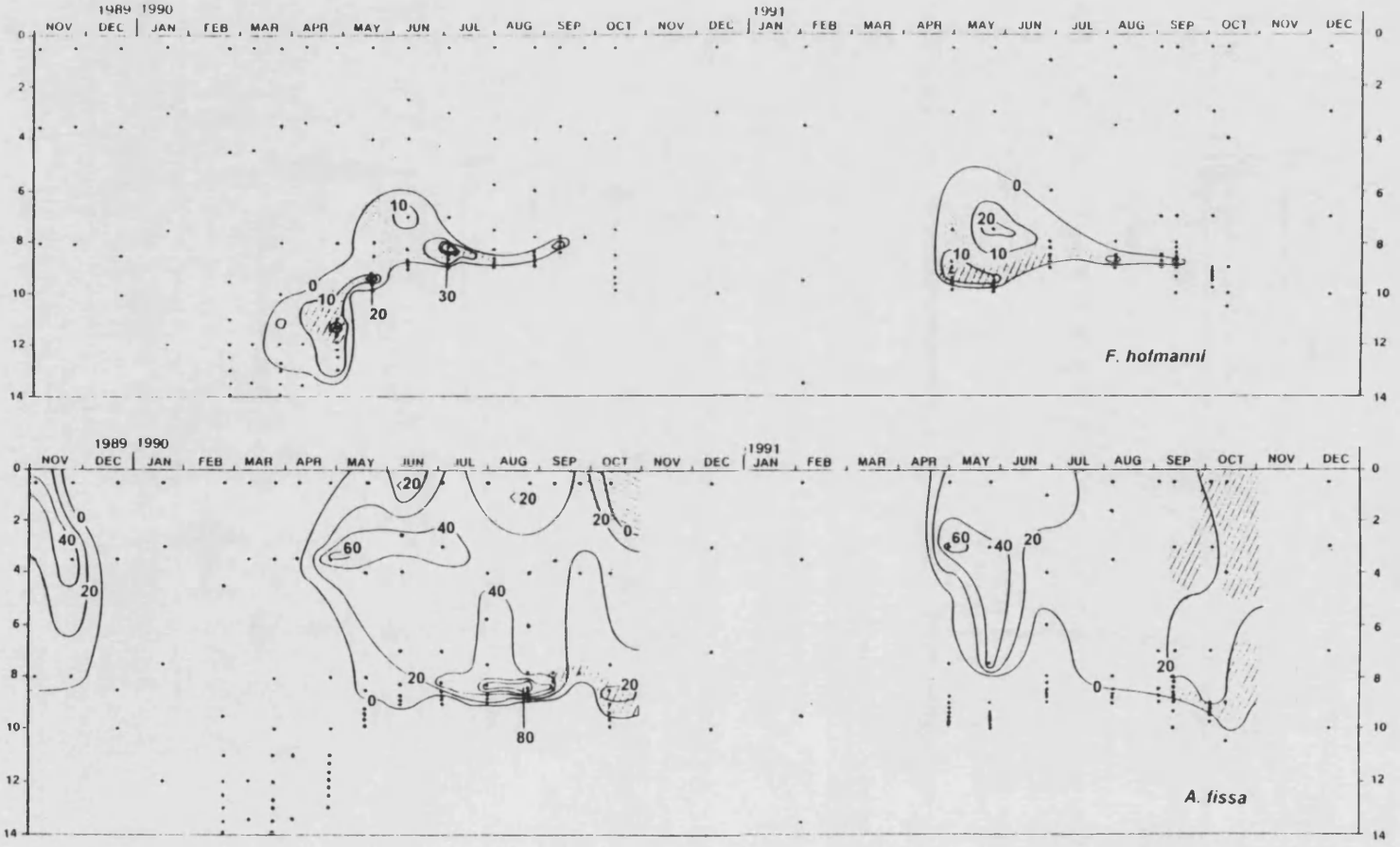

Fig. 3. Isopleths for *F. hofmanni* (top) and *A. fissa* (bottom) showing depth-time distribution of the amictic egg per female percentages, considered only when female densities were higher than 100 ind l^{-1}. The dots indicate the sampling points during the whole studied period and the shaded areas 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

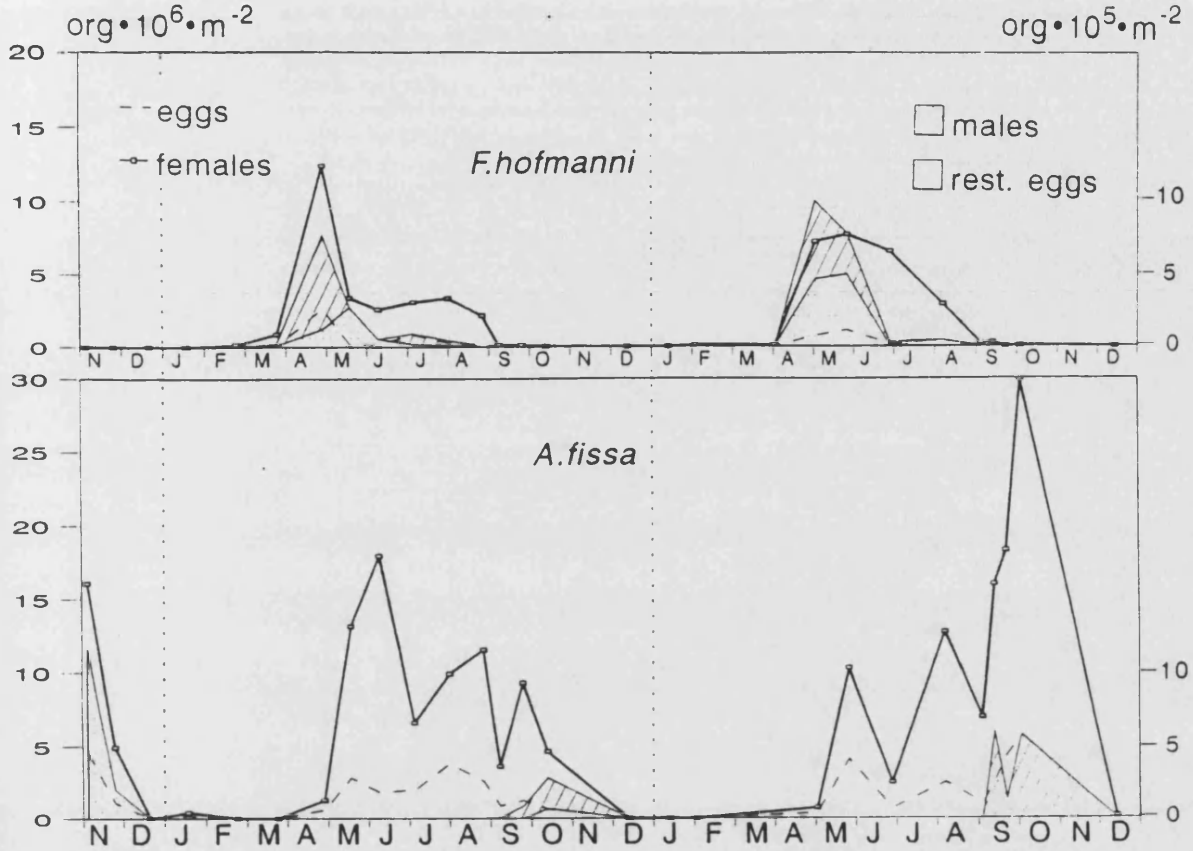

Fig 4. Integrated number per water column of females and of amictic eggs in 10^6 organisms.m^{-2} (left scale) and of the sum of male+male eggs+resting eggs in 10^5 organisms.m^{-2} (right scale) for *F. hofmanni* (top) and *A. fissa* (bottom) from November 1989 to October 1991. The different proportions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

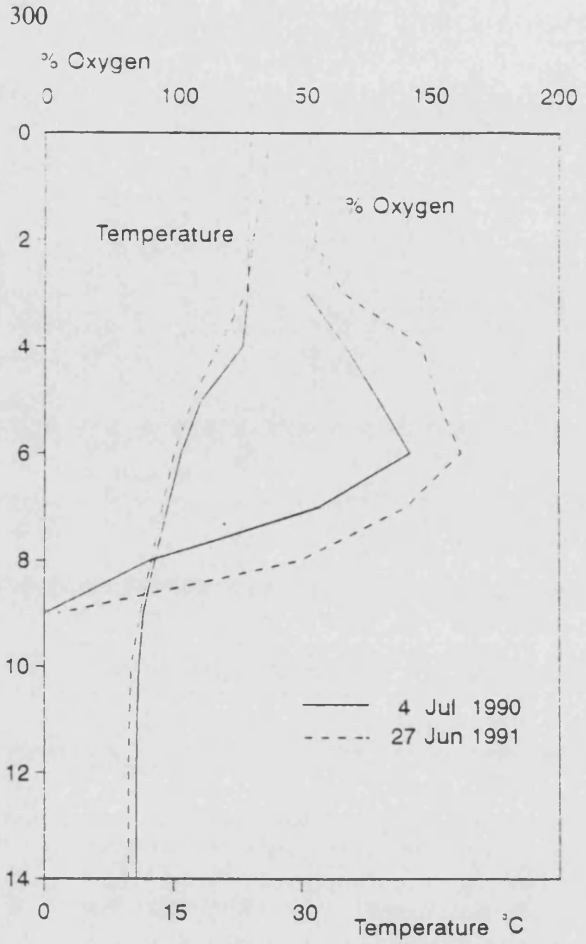

Fig 5. Comparison of temperature and oxygen vertical profiles between the beginning of summer of 1990 and that of 1991.

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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IV.- ARTÍCULOS POR PUBLICAR

IV.5 - Rotifer vertical distribution in a stratified lake: a multivariate niche analysis.

IV.6 - Diel vertical movement of zooplankton in lake La Cruz (Cuenca, Spain).

IV.7 - Zooplankton communities in doline lakes and pools, in relation to bathymetric and physico-chemical parameters.

[IV.5]

ROTIFER VERTICAL DISTRIBUTION IN A STRATIFIED LAKE: A MULTIVARIATE NICHE ANALYSIS

X. Armengol, A. Esparcia & M.R. Miracle

Departament de Microbiologia i Ecologia, Universitat de València, 46100 Burjassot, (Valencia, Spain)

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Armengol, X.; A. Esparcia and M.R. Miracle.

Departament de Microbiologia i Ecologia, Universitat de València, 46100 Burjassot, (Valencia, Spain)

Key words: rotifers, vertical distribution, temperature, oxygen, diversity, PCA, oxicline, karstic lake.

Abstract

The main sources of variation of rotifer species distributions in lake Arcas-2, a small karstic lake near Cuenca (Spain) were explored by means of Principal Components Analysis (PCA). Two PCA were performed, one with rotifer densities and the other with these rotifer densities plus physicho-chemical parameters. In the analysis with rotifers alone Factor 1 separates summer species from winter-spring species and Factor 2 accounts for the variation in the vertical profile. In the second PCA, Factor 1 is mainly related to temperature, and groups together three summer species of different food habits: *Polyarthra.dolichoptera, Hexarthra mira* and *Asplanchna girodi.* Factor 2 is mainly related to oxygen, pH and redox potential and separates hypolimnetic species, *Filinia hofmanni* and *Anuraeopsis fissa,* from the rest. The relative position of rotifer species in the space determined by the two Principal Component Analyses was the same, indicating that they respond to the annual cycle and vertical heterogeneity together with the abiotic factors. The most significant parameters affecting the rotifer distribution were oxygen and temperature. In relation with both parameters it is possible to separate epi-metalimnetic from hypolimnetic species. The niche separation of rotifer species is clearly seen in the principal components analysis and in the weighted means of the main abiotic parameters for each species.

The low diversity of rotifer species found in lake Arcas-2 is attributed to the reduced dimensions of the lake and its morphometry of a sink hole with abrupt slopes, which does not permit littoral development and favors stratification. Thus, the vertical structure of the oxygenated water column is simplified, due to that fact, from midsummer the oxic-anoxic boundary is located in the upper metalimnion. This low rotifer diversity contrasts with a high ciliate diversity in the anoxic waters.

Introduction

Many studies have been done to show the seasonal and vertical variation of the rotifer planktonic community within a lake. Rotifers show non-random specific distributions, but the question is how are the species combinations assembled from a common species pool? The planktonic rotifer community is a dynamic system of interacting populations and, at a given time and depth, a distinct assemblage occurs. In order to identify these patterns of change in space and time, the rotifers of a small lake, Arcas-2, with a high degree of stratification have been studied. In this lake, which has a high relative depth, stratification can be established early in the year and an anoxic hypolimnion can have already developed by early spring. When the thermocline descends in the second half of the summer, the oxicline coincides with it and this originates a lake with an epilimnion almost in contact with the anoxic hypolimnion. In this oxic-anoxic interface light is still available so photosynthetic organisms develop and a high diversity of ciliates is found (Finlay *et al.* 1991, Esteban *et al.* 1993). This contrasts with the low diversity of zooplankton in the oxygenated upper waters. The aim of this paper is to study the distributions of rotifers in a lake with these characteristics and to statistically explore the interrelationships of the rotifer species with the main physical and chemical parameters.

Site description and methods

Lake Arcas-2 (UTM 30SWK 732276) is a small dissolution lake located in a field of dolines near the town of Arcas (Cuenca, Spain). The origin of some of these dolines is relatively recent and developed by dissolution of gypsum- rich marls. Arcas-2 consists of two flooded circular dolines connected by a short channel 1 m deep. The larger doline, i. e. the main basin of the lake, is then quite isolated from the other. All samples were collected at the center of this main basin, which is very deep relative to its surface area (surface circular area: 0.16 ha and maximum depth: 14 m), and thus becomes easily stratified with the deeper layers becoming anoxic from early spring to early autumn. The water level is almost constant and is maintained by the water table and a small surface outflow. The special features of the main basin of Arcas-2 during the same sampling period have been described in Vicente *et al.* (1991), a study centered on the oxic-anoxic interface and the distribution of photosynthetic bacteria. It is a warm monomictic hard water lake, with a mean conductivity of 2.5 mS and an alkalinity of 4-5 meq l^{-1}. The waters are sulfate-carbonated (SO4:CO3:Cl approx. 100:10:1) and quite turbid (Secchi depth range: 2-3.6 m) due to the mentioned subterranean circulation.

The sampling site in the main basin of Arcas-2 was fixed at the intersection of two perpendicular ropes attached to the lake shores. This site corresponds with a small secondary sink hole sited near the center of this basin, which deepens the lake from 12 to 14 m. Detailed vertical profiles of temperature, conductivity and oxygen were obtained *in situ* using WTW meters. Secchi disk depth and light penetration were also measured. Redox and pH were measured in the boat by pumping the water through ORION meters and water samples were collected using a bi-conical inlet device connected to a peristaltic pump, as described in Miracle *et al.* (1992). In this way we were able to sample at short depth intervals (10 cm) when the lake was stratified. Zooplankton samples were obtained by filtering 2 to 4 liters of the pumped water through 30 μm nylon mesh. During mixing (November and February), zooplankton samples were taken by filtering through the same mesh the contents of a double Van Dorn bottle (5.6 l). In both cases, the water with living animals was filtered slowly, at low pressure. The samples were afterwards preserved in 4% formalin to be counted in the lab with an inverted microscope at 100 and 200X magnification.

Principal Components Analyses (PCAs) were performed on previously logarithmically transformed rotifer densities and physico-chemical parameters (with the exception of pH), using the 4M BMDP program, principal factors were extracted and a varimax rotation was applied (Dixon *et al.*, 1983).

Results

Rotifer diversity in Arcas-2 is very low. There are only six main species in the plankton: *Anuraeopsis fissa, Filinia hofmanni, Keratella quadrata, Asplanchna girodi, Hexarthra mira* and *Polyarthra dolichoptera*. Along with *P. dolichoptera* some individuals belonging to other species of the *P. dolichoptera-vulgaris* group were probably counted, however all the individuals of *Polyarthra* which have been studied for identification by means of morphometry, position of lateral antenna and resting eggs, belong to *P. dolichoptera*. Due to the difficulty of differentiating between the species of the *Polyarthra dolichoptera-vulgaris* group in the fixed specimens, we preferred to refer the counts in tables and figures to the group *P. dolichoptera-vulgaris*, even though *P. dolichoptera* was the dominant species.

Few other rotifer species appeared in the plankton samples, and always with very low densities. They were: *Cephalodella forficula, Colurella obtusa, Colurella uncinata, Lecane bulla, Lecane closterocerca, Lecane flexilis, Lecane luna, Lecane lunaris, Lophocharis salpina, Notholca acuminata, Synchaeta oblonga* and some bdelloides. Rotifers were always the dominant group, comprising more than 60% of the

total zooplankton densities most of the year, except in winter and midsummer. With respect to the crustaceans, copepods were the most abundant especially nauplii and copepodites of *Tropocyclops prasinus*, but *Cyclops abyssorum* was also present and *Macrocyclops albidus* very occasionally appeared. Cladocerans were very scarce, *Ceriodaphnia reticulata* occurred with low relative abundance during summer and autumn and in July 1987 some *Diaphanosoma brachyurum* also appeared.

The physico-chemical parameters showed marked gradients in the vertical profile (Figs. 1 and 2). In winter the temperature remained homogeneously distributed around 6.3°C in the coldest month and varied through the year to reach 24 °C at the surface in summer, showing a strong variation according to depth, with differences of 15°C between the top and bottom waters. Oxygen also remains homogeneously distributed in winter (around 9 mg l^{-1} during the mixing period), but during the early stratification period its concentration in the wide metalimnion raises to supersaturation (>140%) and then drastically diminishes to its extinction at the beginning of the hypolimnion. As summer advances the thermocline descends and becomes sharper, and at the end of the stratification the oxygen presents a typical clinograde curve, with the oxicline now located at the beginning of the thermocline. In this way an oxic-anoxic interface was established around 8 m in 1987, and 9 m in 1988. These solution lakes present high values of conductivity (mean conductivity around 2.5 mS/cm). Conductivity varied slightly in the vertical profile with a small relative increase in the anoxic hypolimnion, but showed a variation during the year with lower values during rainy periods, especially due to sulfate and calcium contents. A deep chlorophyll *a* maxima is characteristic of this lake (Fig. 1), consisting mainly of *Cryptomonas* and *Oscillatoria*, this algal biomass is practically untouched by the rotifer population, usually situated above it.

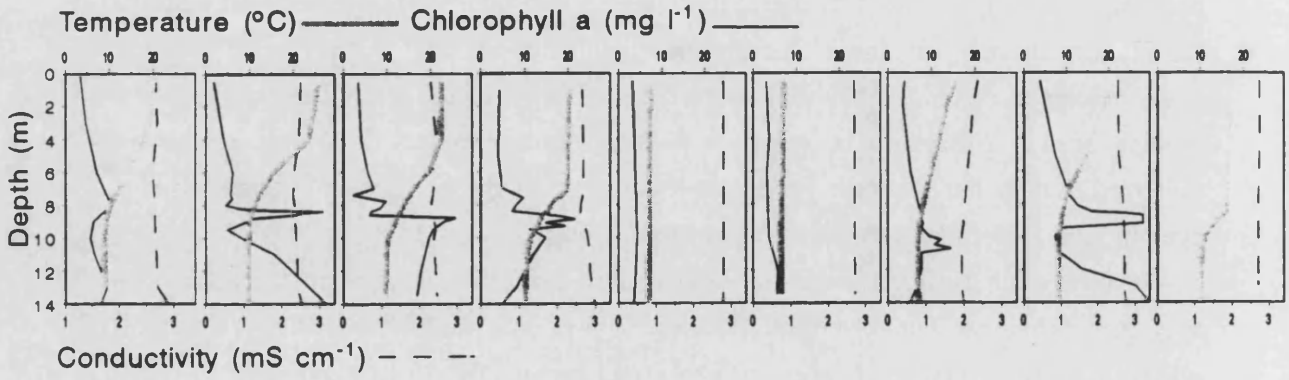

Figure 1: Vertical profiles of temperature, conductivity and chlorophyll *a* at the sampling dates of the years 1987 and 1988.

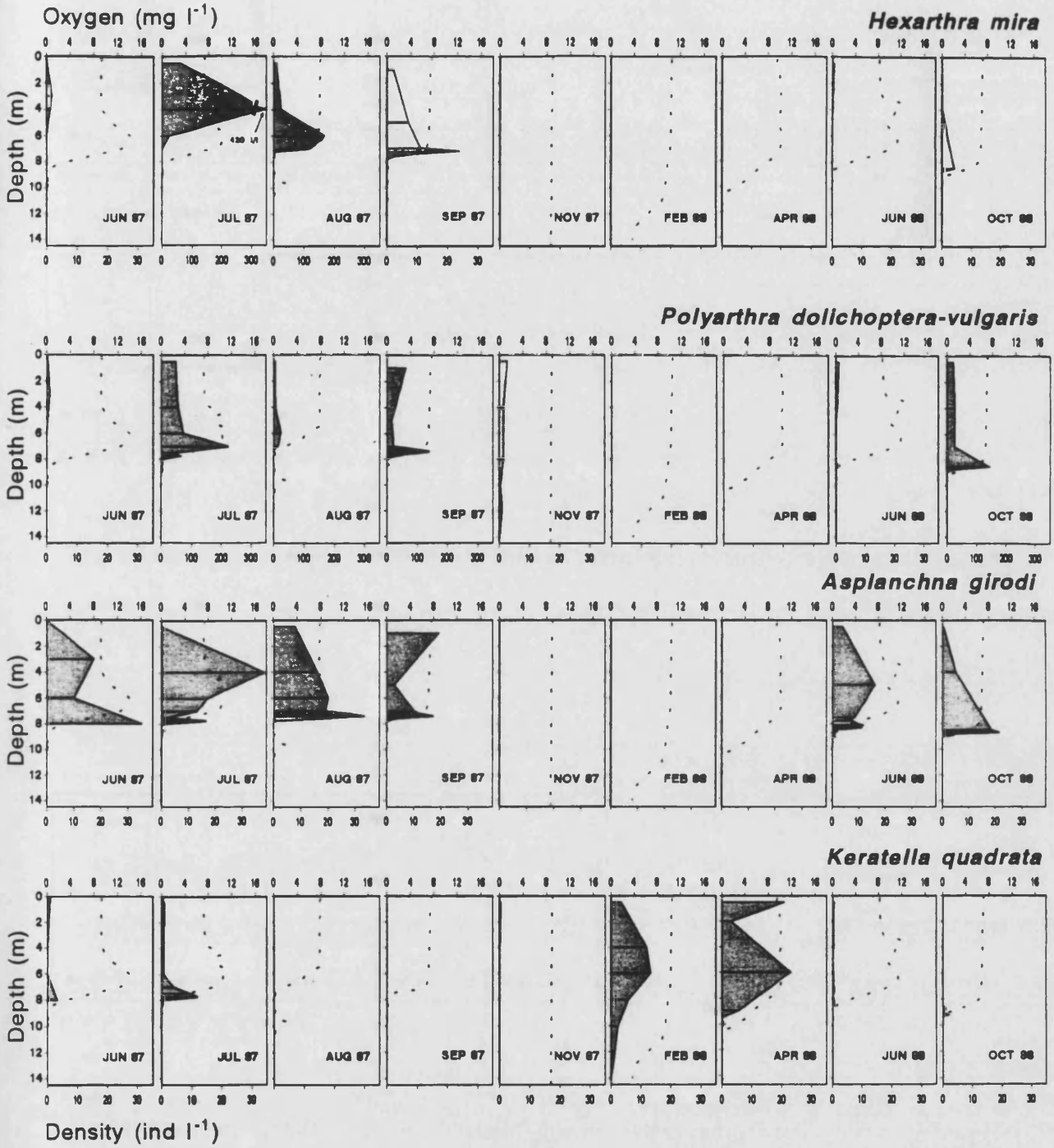

Figure 2: Vertical distribution of the main rotifer species at different dates from June 1987 to October 1988. For each species, non shaded areas indicate a smaller scale than the usual, absence of scale means that the species was not found in that date. Vertical profiles of oxygen are shown with dotted lines.

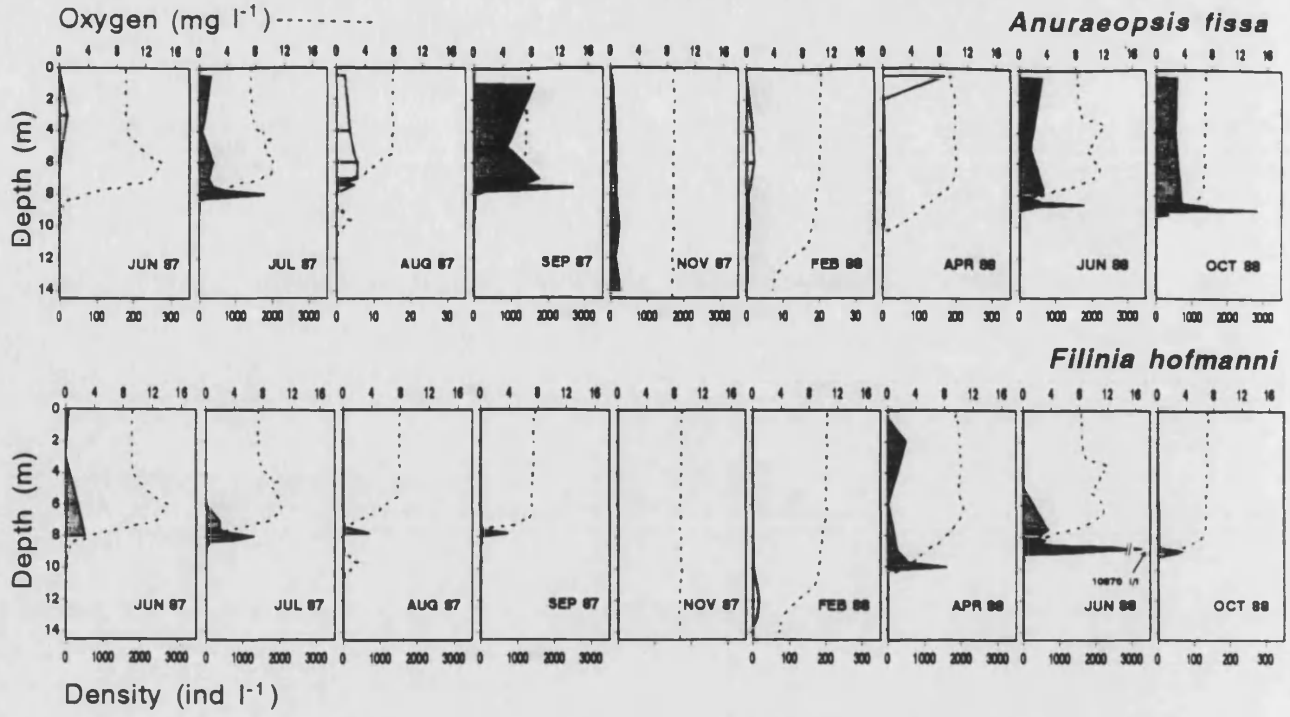

Figure 2: (Continuation, previous page for legend)

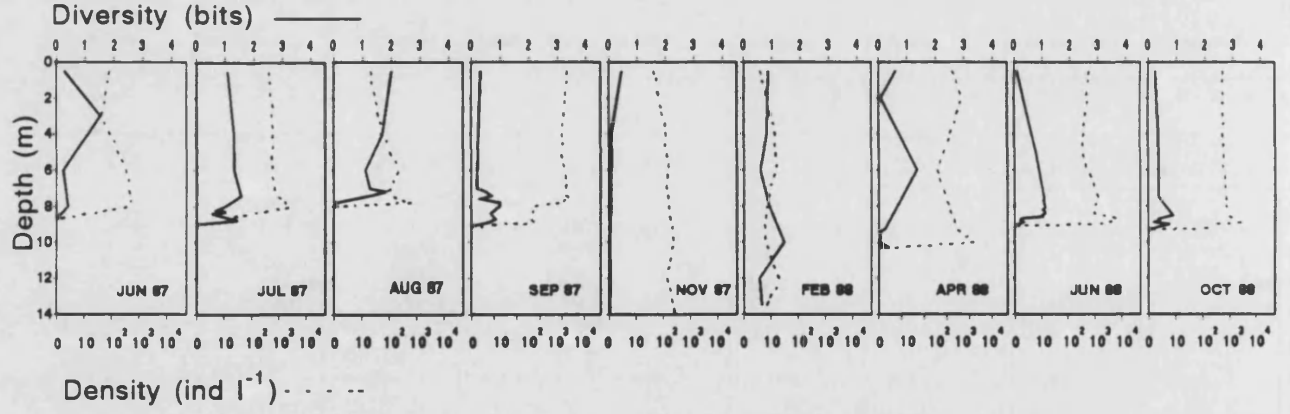

Figure 3: Vertical distribution at the sampling dates, from June 1987 to October 1988, of diversity (solid lines) and rotifer densities (dotted lines).

The vertical distribution of the six main rotifer species at several times of the years 1987-88 is shown in Figure 2, together with the oxygen profiles. The strong stratification of the lake waters in summer bears to an associated stratification of their planktonic populations, especially of rotifers. In this study most species showed a marked tendency to develop peaks near the oxic-anoxic boundary.

Filinia hofmanni and *Anuraeopsis fissa* were the most abundant species in this lake and formed important peaks at the oxicline layers. Nevertheless their distributions were quite segregated. *F. hofmanni* is a late spring-early summer species and it showed its maximal densities at the onset of stratification period, whereas *A. fissa* was present during all the studied period, but developed its density maxima at the end of the stratification period. *A. fissa* was also more widely distributed in the vertical profile while *F. hofmanni* was more restricted to the hypolimnion. Both species presented peaks at oxicline, but with the maxima slightly displaced; that of *A. fissa* was generally above that of *F. hofmanni.*

Polyarthra dolichoptera-vulgaris, next in order of abundance, also showed marked peaks at the oxicline in summer. Their densities were also relatively important during the autumn overturn. *Hexarthra mira* showed a distribution restricted to summer and in the upper metalimnetic waters. *Keratella quadrata* was the least abundant species, and was distributed in winter and spring covering all the oxic water column, it also occurred during early summer with very low densities and restricted to the upper oxicline, with peaks above *Anuraeopsis fissa.*

Asplanchna girodi was present from late spring until the autumn overturn. It dwelled mainly in epilimnetic waters but it also formed peaks in the hypolimnion during stratification. In order to see the interaction of this predator with other rotifers, we have studied the stomachal content of several individuals (10-15 per sample) obtained at different depths in June and July 1987 (Table 1a). It is striking that the relative abundances of ingested preys do not coincide with the relative abundances of rotifers, as potential preys, in the same samples (Table 1b). It is clear that *A. girodi* was feeding on *A. fissa* even if it was not dominant. The other prey ingested was *F. hofmanni* but only when it was very abundant. *Polyarthra* and *Hexarthra* although abundant were not observed in the stomach contents. The stomach contents also showed large phytoplankton cells such as *Peridinium spp.* and diatoms (*Cyclotella, Navicula, Cymbella*).

In Figure 3, we show the vertical distribution and seasonal variation of diversity compared with the density of rotifers. In each profile we can generally see an inverse relationship between both parameters. Diversity clearly increased in the bottom during stratification, although in the oxiclinal layers there were also marked decreases of

Table 1. (a) Relative abundances of preys in the stomach content of *Asplanchna girodi* at the indicated dates and depths. (b) Relative abundances of rotifer species, in the same water samples from which *A. girodi* was studied

(a)	*A. fissa*	*F. hofmanni*	*K. quad*	*P. dolich*	*H. mira*	*Phytoplan*
June 1987 8 m	**23.1**	**30.8**	0	0	0	**46.1**
July 1987 4 m	**40**	**0**	0	0	0	**60**
July 1987 7 m	**87.5**	**0**	0	0	0	**12.5**

(b)	*A. fissa*	*F. hofmanni*	*K. quad*	*P. dolich*	*H. mira*
June 1987 8 m	0	99.4	0.6	0	0
July 1987 4 m	13.1	0	0.2	10.2	76.5
July 1987 7 m	29.9	43.1	0.5	26.5	0

diversity in coincidence with the density peaks found at these layers. After the autumn overturn, diversity was very low probably due to the drop in temperature and the mixing of anoxic hypolimnetic waters. In winter, density diminished and diversity recovered its values to around 1 bit, although the number of species remains very low.

In table 2 correlations of rotifer species with the main physico-chemical parameters are shown. Temperature was the parameter which showed highest correlation coefficients with all the rotifer species (Table 2), being negative in the case of winter species (*K. quadrata*) and species restricted to the oxicline (*F. hofmanni*), and positive for summer species and for species mainly distributed in the epilimnion. Oxygen was correlated positively with more epilimnetic species (*K. quadrata* and *H. mira*) but negatively with *F. hofmanni*.

In table 3 weighted averages for the most significant physicho-chemical parameters are presented. Temperature and oxygen were the parameters with greatest differences between the species. *K. quadrata* -mostly a spring species- presented the lowest value for temperature, next to this we found the hypolimnetic species *F. hofmanni*. On the other hand *H. mira* -a summer species- had the highest value for temperature. The oxygen values clearly separated *F. hofmanni* from *H. mira* remaining the rest of species in a narrow interval around 6 mg l^{-1}. Also remarkable differences are found with respect to Chlorophyll *a*, once again we found opposition between *Filinia* and *Hexarthra*, while the rest are in intermediate positions, because of the high dependence of chlorophyll on depth.

Two PCAs were performed, one with rotifer densities and the other with these rotifer densities plus physicho-chemical parameters. In the PCA analysis (PCA-1) with

Table 2: Correlation coefficients (r) between the main planktonic rotifer species and some physicho-chemical parameters. Bold type corresponds to $p \geq 0.05$ and (*) corresponds to the significant values at 0.05 significance level with Bonferroni sequential test.

	KERA	POLY	ANUR	HEXA	FILI	ASPL
Temp	-0.218	**0.623***	**0.313**	**0.565***	-0.243	**0.497***
Oxyg	**0.370**	0.150	-0.143	0.239	**-0.568***	0.162
pH	**0.338**	-0.165	-0.207	-0.040	**-0.405**	0.011
Redox	0.114	0.180	0.087	0.202	-0.135	**0.281 ***
Cond	-0.174	0.065	**0.423***	-0.138	-0.252	0.100
Alcal	-0.110	**-0.284**	-0.061	-0.202	-0.005	0.037
Ca	0.031	**0.329**	-0.050	**0.317**	-0.017	0.131
Cl	**-0.509***	**0.361**	**0.476***	0.239	0.013	0.141
K	0.232	**-0.471***	**-0.370**	**-0.353**	-0.226	-0.217
Mg	0.040	0.150	-0.129	0.150	0.182	0.136
Na	-0.019	**0.318**	0.059	0.239	0.133	0.039
NH_3	-0.102	**0.492***	0.181	**0.415**	0.121	0.204
NO_2	-0.027	**-0.302**	-0.220	**-0.294**	**0.308**	**-0.431***
NO_3	**0.330**	-0.143	-0.182	-0.047	-0.188	-0.039
P solub	-0.222	-0.259	-0.108	**-0.369**	0.229	**-0.524***
Silic	0.163	**0.354**	0.231	**0.394**	**-0.336**	0.189

KERA: *Keratella quadrata*; POLY: *Polyarthra dolichoptera-vulgaris*; ANUR: *Anuraeopsis fissa*; HEXA: *Hexarthra mira*; FILI: *Filinia hofmanni*; ASPL: *Asplanchna girodi*.

Table 3: Weighted averages for several physicho-chemical parameters in relation to the densities of each rotifer species during the studied period.

	Temp	Oxyg	pH	Redox	Cond	Chlor *a*
A. girodi	13.6	6.0	7.65	366.2	2.61	6.21
K. quadrata	11.0	5.9	7.68	331.4	2.58	6.26
H. mira	17.6	7.3	7.55	370.0	2.58	4.67
P. dolich-vulg.	16.1	6.1	7.73	374.0	2.61	5.81
A. fissa	13.6	5.9	7.71	344.7	2.58	6.32
F. hofmanni	11.5	2.8	7.47	294.1	2.50	11.24

rotifers alone, Factor 1 accounted for 65% of the common variance (40 % of the total variance) and Factor 2 for the remaining 35% of the common variance (22 % of total variance). Factor 1 separates summer species from winter-spring species and Factor 2 accounts for the variation of rotifer species distribution in the vertical profile (Fig. 4).

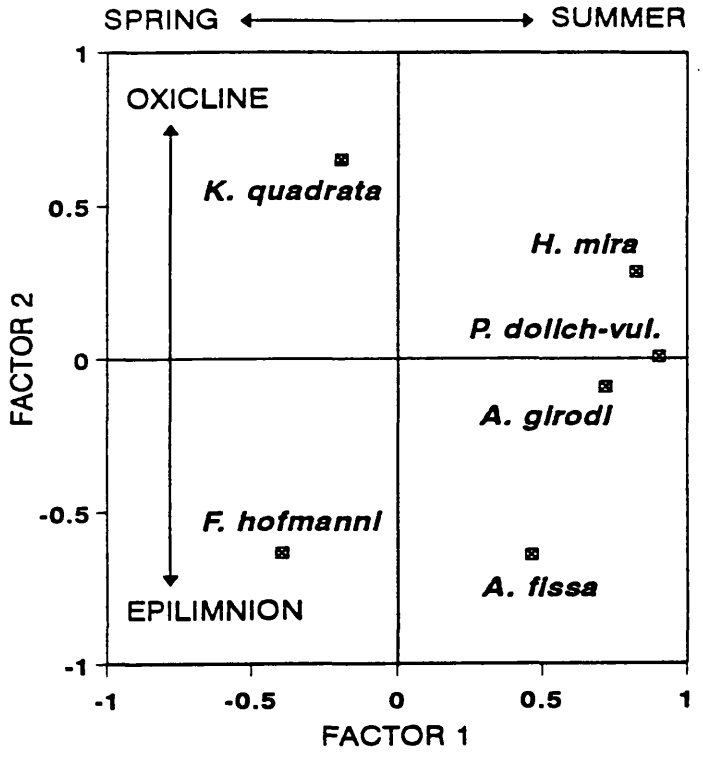

Figure 4: Relative position of each rotifer species in the plane dimensioned by the first and second factors extracted by PCA-1, performed on rotifer densities during the studied period.

The results of the second PCA (PCA-2) with the addition of abiotic factors were the same as the results of PCA-1, in relation to the distribution of rotifer species. In PCA-2, Factors 1 and 2 accounted respectively for 40 % and 30% of the common variance (30 % and 23 % of the total variance) and both factors revealed the same two main sources of variation: changes through the seasons and in the water column. Factor 1 is mainly related to temperature and groups together three summer species of different food habits: *Polyarthra.dolichoptera, Hexarthra mira* and *Asplanchna girodi.* (Fig. 5). Negatively related with temperature we have found *K. quadrata*, a typical winter-spring species in this work, and *F. hofmanni* a spring-summer species restricted to the

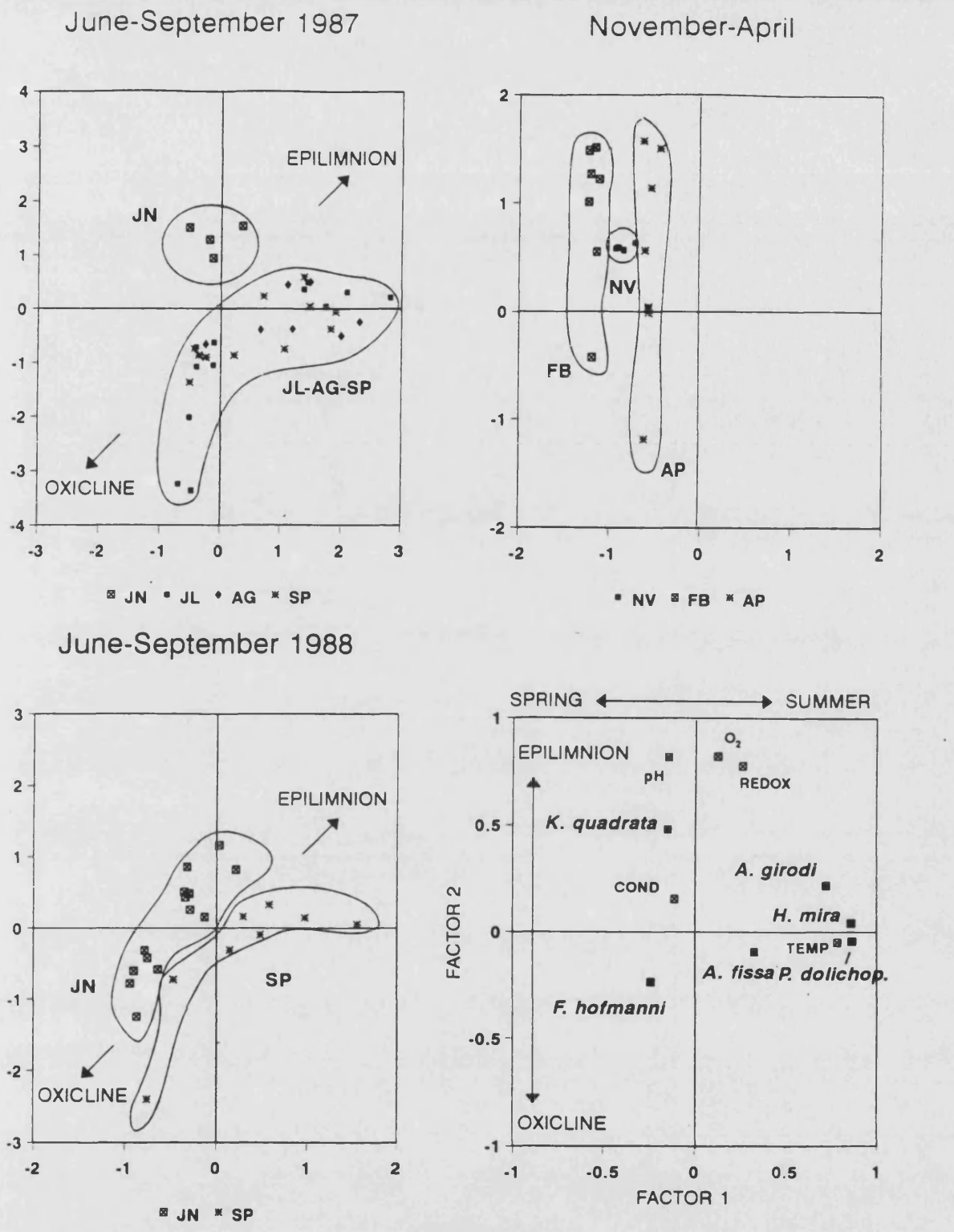

Figure 5a

Figure 5: *Graphs at the bottom right corner:* Relative position of each species and physicho-chemical parameters in the plane dimensioned by the first and second principal factors (a),and by the first and third principal factors (b) extracted by PCA-2, performed on rotifer densities and physicho-chemical parameters. *Other graphs*: Ordination of the samples in the plane dimensioned by the first and second principal factors (a), and by the first and third principal factors (b). The samples are plotted in three graphs to facilitate identification of the points.

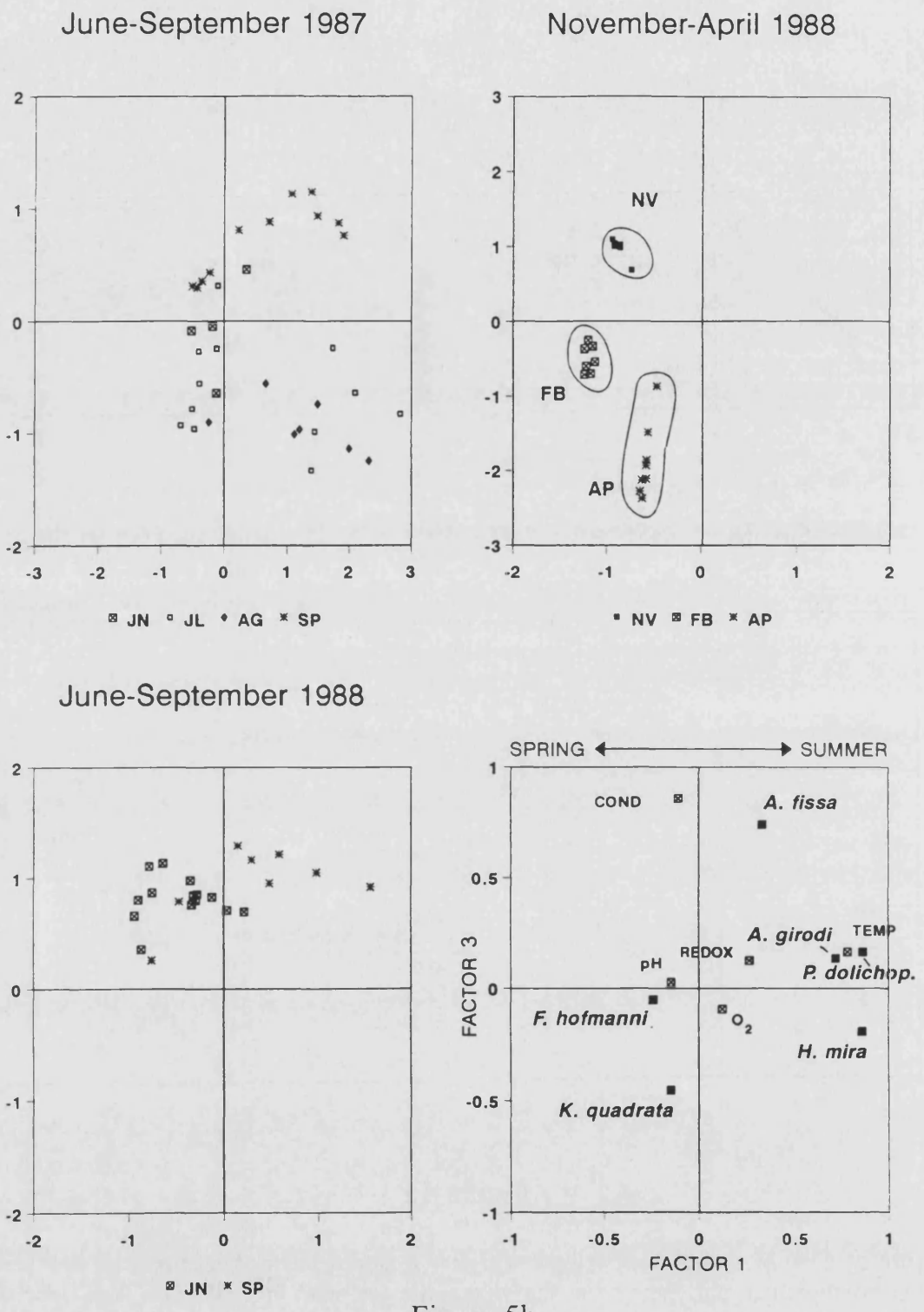
June-September 1987
November-April 1988
NV
FB
AP
JN JL AG SP
NV FB AP
June-September 1988
JN SP
SPRING
SUMMER
COND
A. fissa
A. girodi
TEMP
REDOX
pH
P. dolichop.
F. hofmanni
O2
H. mira
K. quadrata
FACTOR 3
FACTOR 1

Figure 5b

hypolimnion. Temperature varies through the year but also presents a strong variation through the vertical profile in summer when thermal stratification occurs; so in the positive part of this axis are located summer epi-metalimnetic samples and in the negative part oxiclinal and winter samples.

Factor 2 is mainly related to oxygen, pH and redox and separates hypolimnetic species from the more superficial ones. *F. hofmanni* and *A. fissa* are negatively related to this factor as is *P. dolichoptera,* although very close to zero, whereas the other species, especially *K. quadrata,* are in the positive part. The samples in the space dimensioned by the first two factors from this analysis become clearly ordered by temperature in the first axis and by depth in the second axis.

A third factor was also important in this analysis accounting for 17% of the common variance (13% of the total variance). This Factor 3 was highly correlated with conductivity, integrating a component of seasonality which is the main source of variation for this parameter. It separates *A. fissa* from the rest of species, especially from *K. quadrata.*

DISCUSSION

Most of the rotifer species tend to develop higher concentrations in the metalimnetic waters near the oxicline. The vertical heterogeneity during stratification promotes an increase in diversity in the gradient layers even if they are sampled with a fine-layer sampler as in this study (Fig. 2). The species distributions are however, clearly separated seasonally or in the vertical profile. The steep gradients of the main abiotic parameters in the lower metalimnion allows a separation of the maxima of the different coexisting species. The niche separation of rotifer species can be clearly seen in the principal components analysis results (Fig. 4 and 5) and in table 3 where it is shown that the weighted mean of the main abiotic parameters is different for each species. The species relative position in the space dimensioned by the first two factors from Principal Components Analysis is practically the same whether the analysis is done exclusively with rotifer species or also including physico-chemical parameters. This indicates that the underlying factors which account for most of the variability of the rotifer distributions are the same determinants of the seasonal and vertical variation in abiotic conditions. The different species which have a slightly different optima may exclude each other in the space or succeed each other in time and are positioned on opposite sides of the principal components space. The same results were obtained in other lakes (Miracle, 1974).

The first two factors obtained through PCA are correlated mainly with temperature and oxygen, both parameters are the main markers for explaining winter-summer and surface-oxicline variations. Temperature and oxygen have also been found to be the most important parameters for the explanation of rotifer distribution variation throughout the vertical profile and the seasons (Mikschi, 1989; Bogaert & Dumont, 1989). These parameters were also seen as determinants in the segregation of congeneric species of rotifers (Esparcia *et al.* 1991; Armengol *et al*, 1993). They are however, only markers of the seasonal and vertical variation, which have other changes associated, derived from succession and from the separation between production and decomposition in the water column. May (1983) studied the relation between the seasonal occurrence of rotifer species and found that temperature had a net effect on the temporal segregation of species. However, among stenotherms there were also eurytherms showing seasonal variations e.g. *Keratella quadrata* which normally occurred in winter-spring and in some years also in summer. This species in Arcas-2 always shows a winter-spring occurrence forming a small hypolimnetic peak in early summer. In other lakes of the same region, the species also occurs in late summer and with maxima at the oxic-anoxic interface (Armengol *et al.*, 1993; Miracle *et al.*, 1993). May (1983) points out that other factors, like food availability, should be involved, and we can also add the competition with other species. This may be true for other rotifers such as *A. fissa*, which is almost always present in the plankton, but with greater abundances at the end of summer when the oxicline reaches its highest temperature and *A. fissa* can outcompetes *F. hofmanni.*

This structure of the rotifer populations is quite constant, the same species composition and distributions and low diversity were found during the years 1990-1991, in which this lake was studied again (Miracle & Armengol, 1995). This study was centered on the population dynamics of *A. fissa* and *F. hofmanni.* The basic features of these main species were also coincident in both periods when the two species presented a time and depth segregation. *F. hofmanni.* appears in the bottom waters at the end of winter in any incipient stratification that may develop in the small hole of the center of the lake, and peaks in the oxicline at the onset of stratification with a high production of resting eggs (Miracle and Armengol, 1995). It maintains a development in the oxicline which drastically declines from midsummer to disappear at the end of the stratification period. *A. fissa* is howerver, continuously in the plankton although with very scarce densities in winter, it initially grows in surface waters and later occupies the hypolimnion forming peaks a few centimeters over the peaks of *F. hofmanni.* It has maximal densities at the end of stratification with the production of resting eggs restricted to this time.

The study of the stomach contents (Table 1) suggests that *Asplanchna girodi* ingests the easiest to catch among the most abundant rotifer species. It preyed preferentially on *A. fissa,* and only when this species was scarce was *F. hofmanni* used as a food source. In the years 1990-91 the same preys were found (Miracle & Armengol, 1995), however in other lakes where *Keratella quadrata* was more abundant and coincident with *A. girodi, K. quadrata* was also found in its gut (Miracle *et al.*, 1993). *K. quadrata* and *A. girodi* in Arcas-2 presented a very different distribution and when both coexisted *K. quadrata* never reached high densities. *Keratella* is one of the main food organisms of *A. girodi* when it is abundant (Pourriot, 1965; Pontin, 1989). We did not find this species preying on *H. mira* or *P. dolichoptera*, although they were somewhat coincident, as the principal components indicate, placing the three species relatively close to each other (Figs. 4 and 5). This confirms the experimental results of other authors who report that *Hexarthra* (Sarma, 1993) and *Polyarthra* (Gilbert, 1980) were not captured by *Asplanchna* due to their rapid escape movements. The presence of this predator can affect the development of the *Keratella* population as well as other species such as *Anuraeopsis* or *Filinia* although the densities observed for these two species do not suggest that effect. Nevertheless strong population reduction can be affected by physicho-chemical conditions as well as by *Asplanchna* and other predators. The species distributions vary following a habitat template but finally are the result of the interaction between themselves. Lake Arcas-2 shows a low diversity in rotifer species, the following factors could account for this: (1) its conditions of mineralization with high sulfate contents, (2) the isolation of the wetland within a dry region, (3) human impact with the establishment of agricultural land almost to its shore and the introduction of fish and (4), the most important, its reduced dimensions and particular morphometry. This morphometry with steep slopes does not allow the full development of macrophytic vegetation, and promotes the onset of stratification from early spring. As the lake is not very deep the hypolimnion easily becomes anoxic and is from mid-summer when the thermocline deepens and becomes sharper, a situation where the upper part of the themocline coincides with an oxicline is established. Then the conditions of the metalimnion are very special and the anoxic water is almost in contact with the epilimnion, this favors microphagous, r-strategist species, such as *A. fissa* and *F. hofmanni*, which can attain high densities in the layers of the oxicline rich in nutrients and organic particulate matter. This simplification of the oxygenated water column could be one of the main reasons for the low diversity. We should point out especially the almost complete absence of congeneric species with pronounced niche specificity, so frequent in most lakes (Miracle, 1977). Furthermore, a wide layer of anoxic water could make colonization through resting eggs in summer difficult, and

restrict the development of the typical succession of summer species, some of which belong to congeneric clusters (*Polyarthra, Hexarthra, Synchaeta*). The low rotifer diversity contrasts with a high ciliate diversity in the anoxic waters, due to the important development of photosynthetic stratifying alga and bacteria which show small scale vertical distributions in the oxic-anoxic boundary (Vicente *et al.*, 1991; Finlay *et al.*, 1991; Esteban *et al.*, 1993).

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[IV.6]

DIEL VERTICAL MOVEMENTS OF ZOOPLANKTON IN LAKE LA CRUZ (CUENCA, SPAIN)

X. Armengol, & M.R. Miracle

Departament de Microbiologia i Ecologia, Universitat de València, 46100 Burjassot, (Valencia, Spain)

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X. Armengol & M.R. Miracle.

Departament de Microbiologia i Ecologia, Universitat de València, 46100 Burjassot, (Valencia,Spain)

Key words: vertical migration, diel cycle, zooplankton, rotifers, freshwater, plankton traps

ABSTRACT

Different samples were taken along the vertical profile at different hours in a diel cycle, to study vertical migration of rotifers in the highly stratified lake La Cruz (Cuenca, Spain). Additionally some plankton traps were located at different depths to catch organisms going upwards and downwards to confirm the results obtained from the samples. The results indicate an almost general movement in epilimnetic waters corresponding to the "normal" pattern of migration (ascendent movement at dusk and descendent at dawn), in meta and hypolimnetic waters, vertical movements are reduced to few meters but exist. This also confirms that the dense populations at these levels of the oxic-anoxic boundary are constitued by active animals.

INTRODUCTION

Vertical migration is an extended phenomenon observed in many taxa of freshwater and marine zooplankton. The "normal" or most frequent pattern consists of an upwards movement around dusk to stay near the surface at night, and a downwards movement in the morning to spend the day in deeper waters, but a "reverse" pattern has also been described. In the sixties research was directed at looking for the proximate cause of vertical migration, and relative changes in light intensity were identified as this cause. Today research is mainly focused on identifying the ultimate cause (Lampert, 1989). Several hypotheses try to explain the facts involved in this phenomenon but it seems that light-dependent predation mortality plays an important role in crustaceans, nevertheless some other hypotheses could also play secondary roles.

The majority of studies in freshwater have been performed on cladocera and copepoda because they are bigger animals, better swimmers and easier to be observed resulting in a higher amplitude of their movements and easier design of laboratory experiences. Vertical migration has also been described in rotifers (Pennak, 1944; Larsson, 1971, George and Fernando, 1970; Stewart and George, 1987; Cruz-Pizarro, 1978; Dumont, 1972), nevertheless most of these studies compare mean residence depths of animals sampled at different times of the diel cycle, a method that presents some difficulties.

The aim of this work was the study of the vertical movements observed in the zooplankton of lake La Cruz connected with the diurnal cycle; not only an ascent and descent in the epilimnion but also the movements at the oxicline layers. With this objective we took samples from the vertical profile at different times of a diel cycle, and furthermore we placed several plankton traps in the water column to support the interpretation of mean residence depth variations obtained from the diel cycle.

This lake is flooded doline with the water level occupying only lesser than its lower half; the morphometry -i.e. small surface/depth ratio- and its situation -well protected from wind action- provide great stability to the water column wich renders it meromictic. These characteristics make this lake a very adequate site to for testing vertical migration of zooplankton in a diel cycle, especially of rotifers which dominate in number, but also to confirm the presence of vertical movements which could occur in the hypolimnion to profit the dense population of procariotes and nutrients remaining at the oxicline layers.

METHODS

Vertical profiles of temperature, oxygen, light and conductivity were previously obtained at the sampling point to select sampling depths (Fig.3). Samples were taken at aproximatedly the center of the lake at its deepest point, from a boat fixed at the intersection of two perpendicular wires attached to the banks of the lake.

The study can be divided into two parts which were carried out simultaneously. The first part was the collection of samples through the vertical profile at differents times of the daily cycle. Succesive samples were taken at 0h, 7h, 13h, 18h and 22h on the 16th september 1989, at local time (2 hours advanced from U.T.). Eight points were selected on the vertical profile: 0.5, 4.5, 8.5, 10.5, 12, 12.5, 13 and 13.7 m. The distribution of these points was not uniform along the vertical profile with greater sampling intensity at the oxicline layers. Water samples were collected with a peristaltic pump connected to a thin layer inlet sampler as described in Miracle *et al.* (1992), by filtering 1 or 2 liters of water *in situ* with 30 μm nytal mesh (at the oxicline layers 1 liter was enough due to the high density of organisms). At some samples two replicates were also taken. To diminish the impact on rotifer populations the sampling point was modified at the different sampling times by changing the position one or two meters, always around the intersection of the wires.

The second part was the installation of several traps, consisting of a funnel coupled with an Erlenmeller (Fig. 1) similar to the ones used in Salonen *et al.* (1993). Twelve of these traps were used in the experiment by situating them at different depths; three replicated pairs placed with the opening of the funnel towards the bottom of the lake (to catch organisms going upwards); and three replicated pairs opened to the surface (to catch organisms going downwards). Traps were mantained in the vertical position by means of an iron bar that could be placed at the different depths using a system of ropes attached to a group of four buoys at the surface. These buoys were also attached to the wires crossing the lake close to the sampling point. The traps were maintained for three periods of aproximatedly 8 hours to cover the diel cycle (see Table 2). In order to avoid interference due to the different quality of water at the various depths, the traps were filled, before being placed, with filtered water (30 μm nytal mesh) previously extracted from the corresponding depth . Traps were placed from bottom to surface with approximately one hour delay from the first placed at 13.8 to the last placed at 4.5 m. To avoid the escape of organisms, traps oppened to the bottom were reversed before collection from the surface.

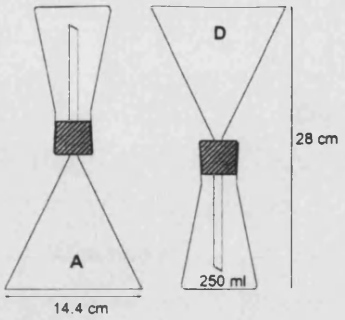


Figure 1: Outlined drawing of funnel traps showing their size. Traps marked with an "A" were located to catch ascent organisms. Traps marked with a "D" were located to catch descent organisms.

From the data mean residence depth (MRD) was calculated as

$$MRD = \Sigma(N_i \times d_i)/ \Sigma N_i$$

where N_i = concentration of individuals at depth i, and d_i = depth of the *i*th sample.

To evaluate the intensity of the vertical movements for each species we used an index calculated as the percentage of individuals caught in the traps in relation to the number of individuals estimated from the counts in a hypothetical cylinder of water -1 m in height and 14.4 cm in diameter- located inmediatly below or above the trap, depending on the orientation of the funnel.

Organisms from filtered water samples and trap contents were fixed in formalin 4 % and counted with an inverted microscope at 100X or 200X magnification, some trap contents were fractioned for counting due to the high density of organisms. Eggs were also counted and an *egg ratio* was calculated as the percentage of parthenogenetic eggs with respect to adult females (Paloheimo, 1974).

Since rotifers are the dominant group, especially in hypolimnetic layers, this experiment was designed to address rotifer populations vertical migration. Consequently the size of the traps and sampling procedure adapt better to the body sizes of this group of organisms. Data on copepods and cladocera were also obtained and presented, however such results must be taken with reservations.

Site description

Lake La Cruz (UTM 30 SWK 962272) is a small dissolution lake located at 1000 m altitude, in a karstic area near the town of Cuenca (Spain). It is a closed circular sink hole with a mean diameter of 121 m and a maximum depth of 23.5 m at the sampling

date. Its morphometry, -i.e. small surface/depth ratio- and its location -inside a basin having steep walls rising 20-30 m above the water surface- (Fig. 2), produce a reduction in the wind mixing; the lake also presents iron meromixis so part of the anoxic hypolimnion is never mixed. These factors are to a large extent responsables for the great stability of the water. At the sampling time, the lake presented a marked oxicline with an oxygen extinction depth of 13.8 m. Fish were introduced artificially many years ago with the american perch (*Micropterus salmoides*) being abundant. The zooplankton is dominated in number by rotifers, reaching very high populations in hypolimnetic layers; the most abundant crustaceans were *Daphnia longispina* and *Tropocyclops prasinus*. Rotifer vertical distribution was studied during the annual cycle 1987-88 (Armengol- Díaz *et. al.*, 1993; Esparcia,1993).

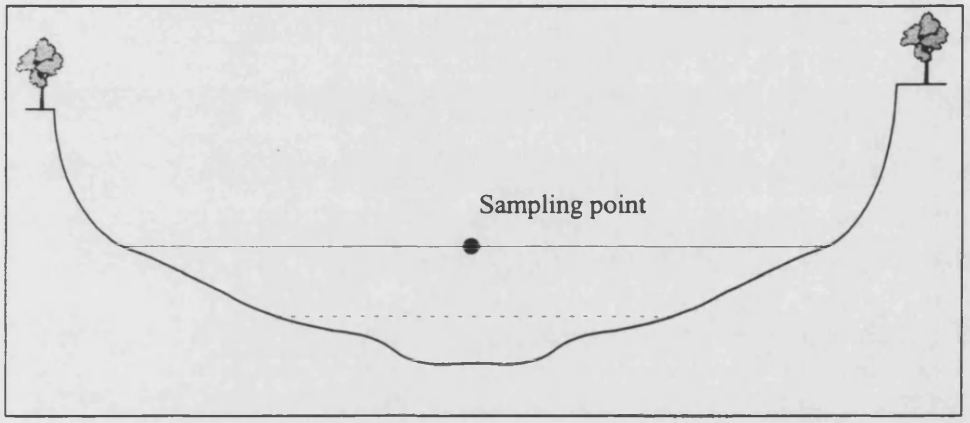


Figure 2. Cross-section of lake La Cruz showing the relative dimensions as well as the steep walls protecting it from wind action. Dashed line indicates annual oxicline average position. Same vertical and horizontal scales.

RESULTS

At the time of the study (September 16th, 1989) the lake presented a steep stratification, as indicated by the strong gradients (Fig. 3). Between aproximatedly 9 and 12 m we found a marked thermocline with a thermic reduction of more than ten degrees. Oxygen was super saturated (206 % and 19.2 mg l^{-1}) at 10.25 m, from this point a sharpe reduction of oxygen concentration produced the oxygen depletion at 13.9 m. Conductivity was also stratified but in the lower part of the monimolimnion, witn the rest of the water column being quite homogeneous. Secchi disk transparency was 9.25 m.

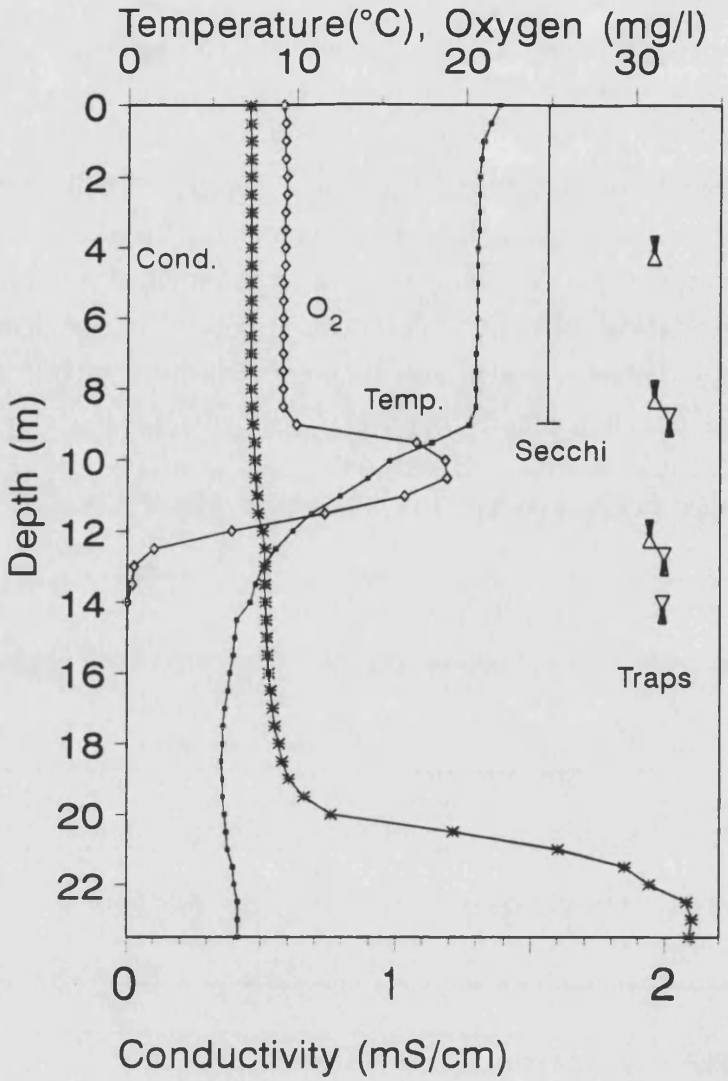


Figure 3: Vertical profiles of Oxygen, Temperature and Conductivity together with Secchi disk depth at the sampling site on 16th September 1989. Place of traps location is also indicated.

Figure 4 shows the diel changes in the vertical distribution of the main planktonic rotifer species (8), the copepod *Tropocyclops prasinus* (larval and adult phases), and the cladoceran *Daphnia longispina*. In table 2 we present the results obtained in the experiment with traps. Both results will be described for each species in the following sections.

Asplanchna girodi

During our experiment the distribution of this rotifer was clearly epilimnetic with very low numbers of individuals in the metalimnetic waters. The observed population density was low but the *egg ratio* was high (~32 %). The irregularity

between day and night captures was characteristic for this species, with very few organisms captured during day time.

The variation of mean residence depth along the vertical profile through the day indicates that this species presents a "normal" migratory pattern (Fig. 4a). The greatest difference between residence depths was observed between 18 h and 22 h, and was of 4 m. The trap results support this fact, with a high percentage of catches for this species at the III-4.5-A trap collecting organisms going upward during evening. In traps situated at 8.5 m we also had some captures but the low density observed in the lower meter does not permit the use of our index. Only one animal was captured in the traps catching downwards at 8.5 m in contrast to 17 going up at this depth.

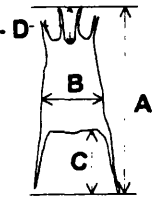
Keratella quadrata

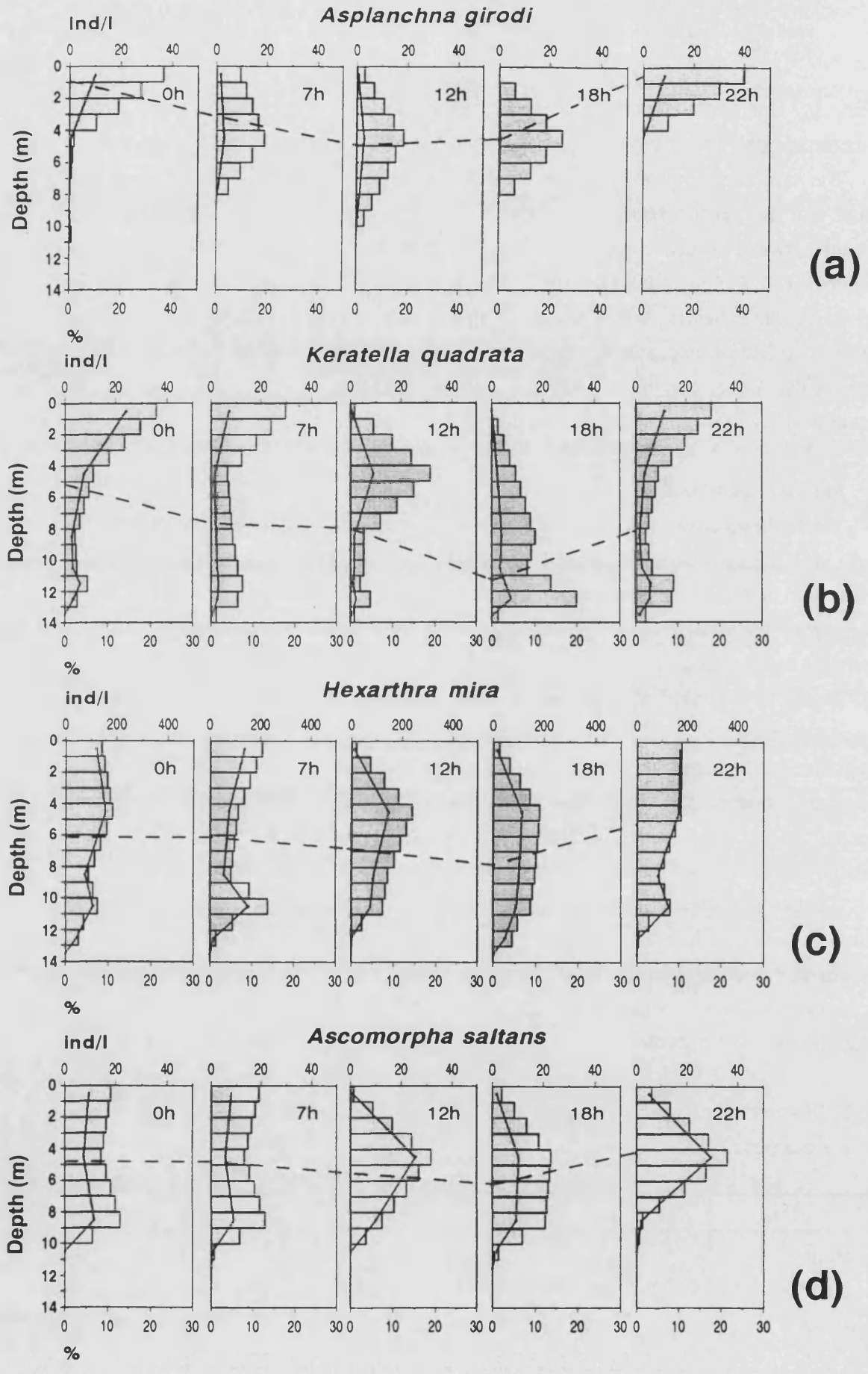
The highest density recorded during our experience was low, with a maximum of 24 ind/l, and the *egg ratio* was around 11 %. The vertical distribution of this species presented two peacks, one epilimnetic and the other at the hypolimnion (12 m) in all the samples from the diel cycle (Fig. 4b). Moreover, two different morphotypes were observed in the samples, one having long caudal spines and the other short spines (see Table 1 for a biometrical comparison between both morphotypes). The two morphotypes presented a differential distribution with the short spined dominating in the hypolimnetic samples and the long spined in the epilimnetic samples. The variation in the mean residence depth was the highest one, with a maximum amplitude of 6.1 m between 0 h and 18 h. Great differences were observed between the numbers of organisms estimated from the daylight samples and those from night samples.

Catches in traps amounted to a low amount of organisms, but as the density in the samples was also low this corresponds to a relatively high percentage of catches. The higherst percentages in this case were also in the evening for the 4.5 trap and at night for the I-8.5-A trap, whereas in traps situated at 12.5 m percentages lower than 10 % were obtained. As with the majority of species, catches in D traps were very scarce.

Table 1: Biometrical comparision between long and short spined morphotypes of *Keratella quadrata.*

	A	B	C	D
K.quadrata (short spines)	149.7 ± 8.6	69.6 ± 4.9	25.7 ± 4.6	27.6 ± 3.3
K.quadrata (long spines)	225.7 ± 8.7	82.4 ± 3.2	73.1 ± 6.2	39.8 ± 4.1




Asplanchna girodi
Ind/l
Depth (m)
0h
7h
12h
18h
22h
%
(a)
Keratella quadrata
ind/l
(b)
Hexarthra mira
(c)
Ascomorpha saltans
(d)

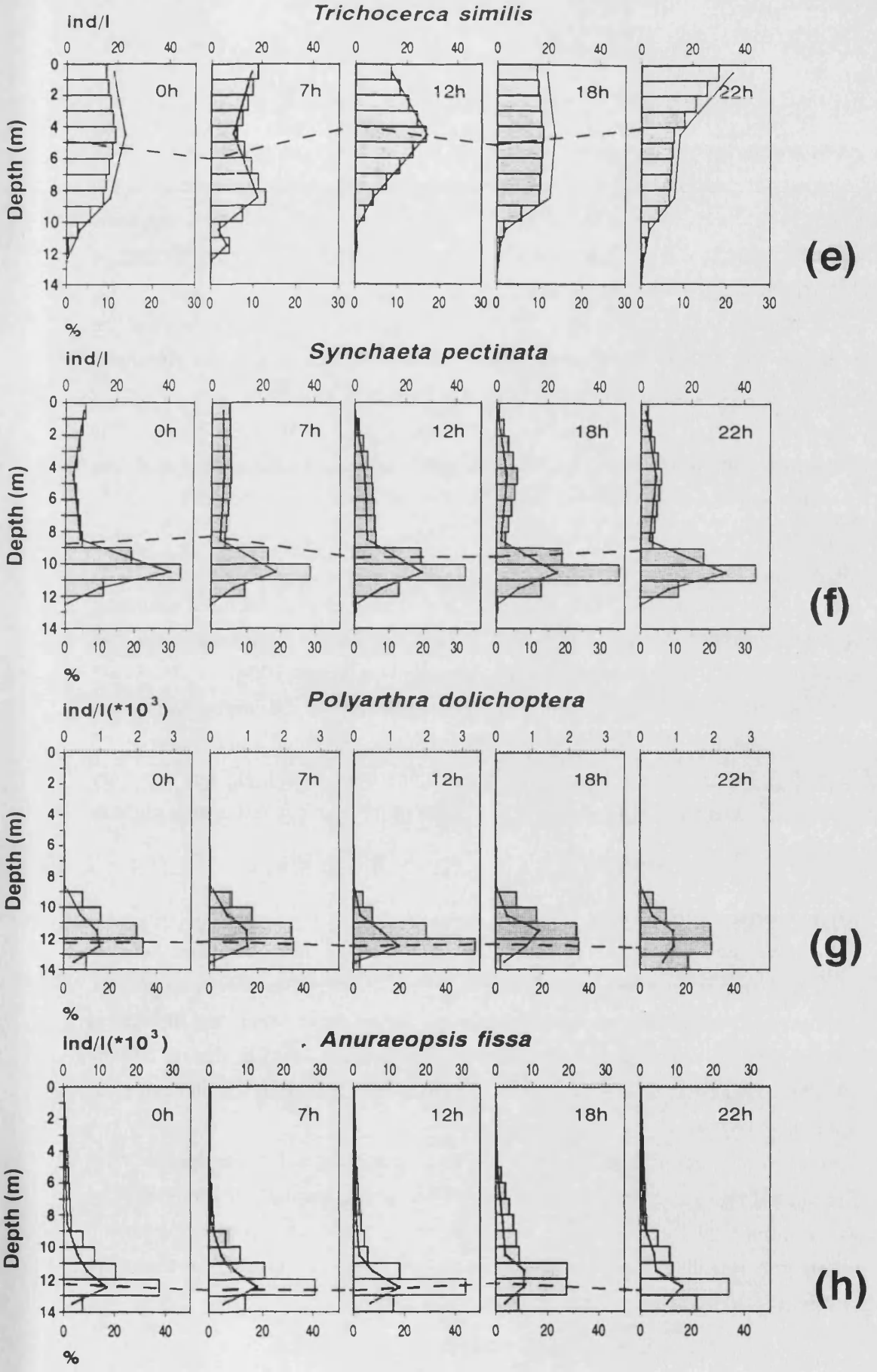


Figure 4 (a-h): Vertical profiles of different rotifer species at different times of diel cycle. Dashed line indicates mean residence depth of each species

Ascomorpha saltans

During our experience this species was one of the least abundant species in the samples taken for the daily cycle but otherwise was the second in number of organisms catched in the 4.5 m and 8.5 m traps, depths where the species was present because of its epilimnetic vertical distribution (Fig 4c).

The highest variation observed for the mean residence depth was between the samples at 18 h and 22 h, with only two meters; although the variation of this parameter was low the vertical movement fits with the normal pattern of migration.

This species registered the highest percentage of catches in the A traps, at the same times as observed in *Keratella*. The maximum number of catches was at 4.5 m during evening and at 8.5 m during the night. D traps had a very low efficiency.

Hexarthra mira

Among the species of the epi-metalimnion this species was the most abundant, reaching densities of between 100-200 ind/l. During our diel cycle a secondary peak was observed at the thermocline (Fig. 4d), and the *egg ratio* was around 10 %.

The surface samples presented high densities during the night and lower densities during the day. Changes of mean residence depth presented a maximum of 2.5 m between the 18 h and 22 h samples. Catches in some traps were high, but with very low percentages, especially in 4.5-A and 8.5-A traps, in the evening and also at night as in the preceding species.

Trichocerca similis

This species also presented an epi-metalimnetic vertical distribution. In this case the migration pattern reported is not normal and can be considered as reverse migration, with a rise of the mean residence depth (of 2.08 m) during the morning and another in the evening with high densities and percentages in the surface samples during the day (Fig. 4e). The average *egg ratio* was close to 25 % in the samples from the diel cycle but much lower in the traps.

Numbers of organisms in the traps and catch percentages for this species were high. The highest percentage of catch was in III-4.5-A trap (evening), nevertheless trap II-4.5-A (morning) had a percentage of 56%, supporting the result of a morning ascent. *T. similis* together with *P. dolichoptera* were the only two rotifer species that were caught in significant numbers in traps going downwards.

Synchaeta pectinata

This species showed a tendency to occupy the lower part of thermocline. In fact a density peak at 10.5 m was observed throughout all the diurnal cycle, whereas at the epilimnion we observed the normal pattern of migration, althogh there were always lower densities. The variation of mean residence depth was very low -1.3 m-(Fig. 4f).

Not many organisms were catched in the traps, the highest percentage was in trap III-4.5-A, in the evening.

Polyarthra dolichoptera

Densities over 1000 ind/l were found in oxyclinal layers, between 12 and 13.7 m, but these densities drastically decreased at the epilimnion (around 3 ind/l at superficial levels) as showed in figure 4g. A close relationship was found between egg ratio and density distributions along the vertical profile (Fig 6a). Changes in mean residence depth were very low with maximum variation around 0.35 m.

With respect to the catches in traps, the highest number of catches was obtained in the 12.5 m traps, with very low numbers at the epilimnion. Nevertheless the percentages over the upper/lower meter were always low. This species presented the highest percentage of catches in the D traps.

Anuraeopsis fissa

Thia was the dominant species in our study, presenting by far the highest relative abundance in the epilimnion, and moving downwards towards the oxicline the densities strongly increased reaching around 13000 ind/l in the 13 m samples (Fig. 4h). Also in the year 1988 densities of this order of magnitude and higher were found at the hypolimnion at the end of summer. In contrast with this vertical distribution of densities the *egg ratio* was highest in the 8.5 m sample, decreasing very much in deeper layers - changing from 50-60% to 0.1% - (Fig. 6b). A similar vertical distribution pattern was found for the total number of eggs.

Oxicline layers presented very high densities during the entire diel cycle, a fact which displaces the "gravity center" of population to these layers greatly reducing the variation of mean residence depth (0.37 m of maximum amplitude), nevertheless strong variatons were observed in surface waters. The trap with the highest percentage was the III-4.5-A trap, but this species also showed high percentages of catches in the 8.5 and 12.5 m traps, especially at the latter level, and the percentage of catches was constant and high through all the diel cycle.

Crustacea

Below we present the results for nauplii, copepodites and adults for the copepod *Tropocyclops prasinus* and also for the cladoceran *Daphnia longispina*. All the nauplii were computed together, thus a low percentage of them could belong to other species of copepods. Only a few adults belonging to the genera *Cyclops abyssorum* were obtained but the low numbers made it imposible to include them in our study. Some cladocerans belonging to *Diaphanosoma sp.* and *Ceriodaphnia sp.* appeared in a few samples, but here also numbers were too low.

Tropocyclops prasinus

nauplii: We found nauplii distributed in epi-metalimnetic waters, maximum densities being around 100 ind/l. Changes in mean residence depth follow the normal pattern. They almost desappeared at the 12 h surface sample, otherwise at 8.5 m samples their density increased at 7 and 12 h (Fig. 5a). Catches in traps were very uniform throughout the diel cycle and the percentages quite low.

copepodites: They presented a normal pattern of migration, similar to that presented in nauplii, but they did not present the peack at noon in the 8.5 m sample, and the maximum variation of mean residence depth was of only 1.37 m. Densities of copepodites were lower than in nauplii and closer to the densities of adults (Fig. 5b). Low percentages of catches in traps were obtained except in I-4.5-A and I-8.5-D traps. From this result, as well as from the vertical distribution at 7 h, it seems that at night part of the population migrates upwards and part downwards.

adults: These also presented the normal pattern with a maximum variation of 2.5 m. The highest densities were around 15 ind/l and corresponded to the samples taken at night (Fig. 5c). Only trap I-4.5-A presented a high percentage of catches, near 50 % of the estimated population in the lower meter. Males and females were considered together due to the low densities obtained.

Daphnia longispina

The highest density was 10 ind/l, but the result of samples was irregular with absence of organisms in the samples taken at 12 h and 18 h (Fig. 5d). Results from the traps revealed a strong migratory behaviour. Trap I-8.5-A catched an average of 76 individuals, this amount being higher than the amount of organisms expected below this depth in the water column. D traps catched several individuals at all the depths, and particularly traps II-8.5-D and III-8.5-D presented very high numbers of moulds.

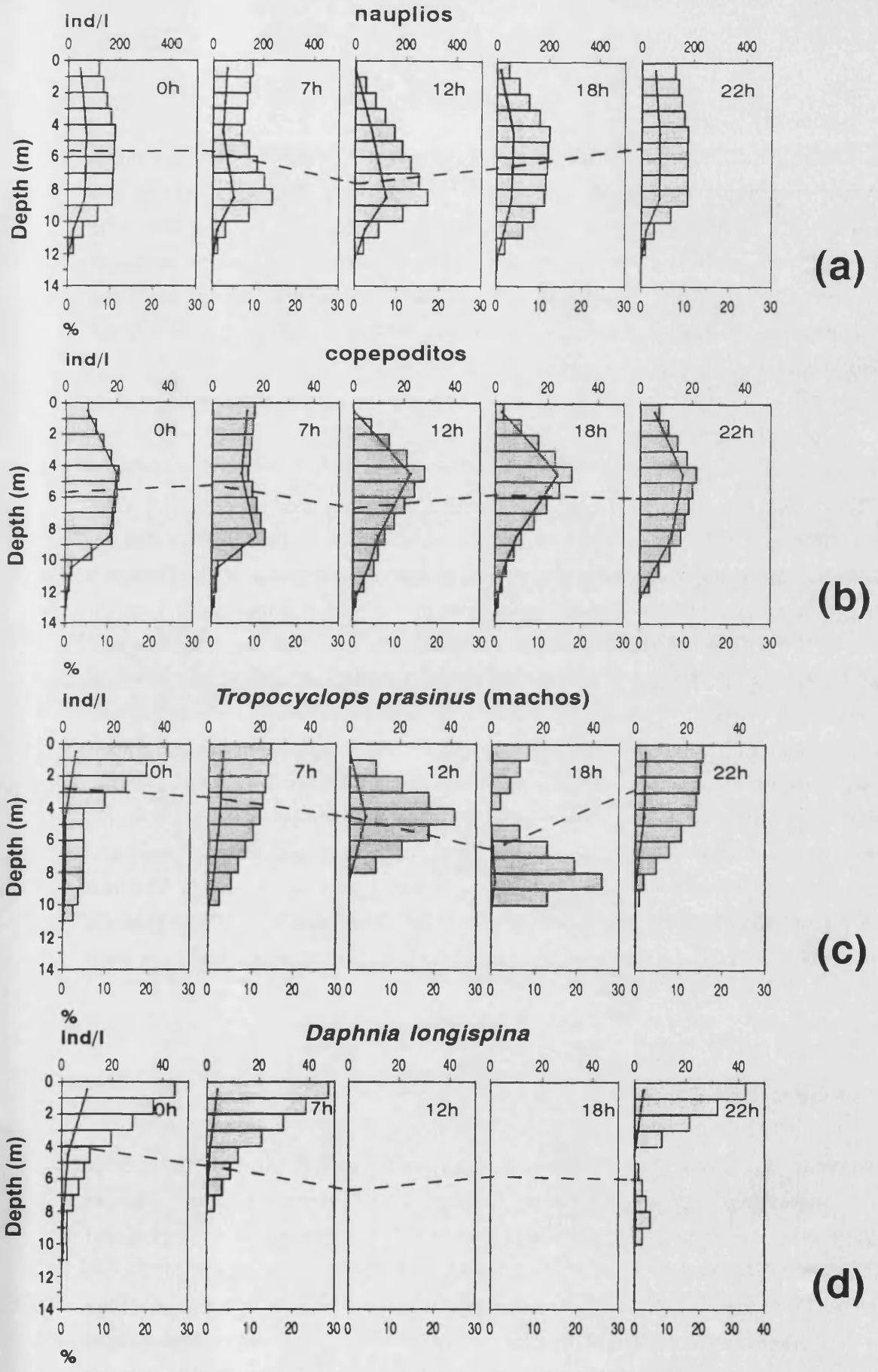


Figure 5 (a-d): Vertical profiles of the copepod (larval and adult stades) *T. prasinus* and the cladoceran *D. longispina* at different times of diel cycle. Dashed line indicates mean residence depth of each species.

Other organisms:

Some more crustacea such as *Ceriodaphnia reticulata, Diaphanosoma brachyura, Cyclops abyssorum,* as well as some ostracods were catched in samples and traps; Gastrotricha were also present in our samples but appeared sporadically. The presence of some larvae and pupae of the diptera *Chaoborus sp.* is remarkable although the number of individuals in samples was low as a consequence of the sampling procedure. The presence of this organism is very interesting because it is a great predator in surface waters at night, resting below the oxicline during the day.

Catches in traps:

Results of catches in traps are presented in Table 2. Generally they support the results obtained from the diel cycle samples as has been pointed out for the different species. Nevertheless some comments can be aded: (1) In general, efficiency of the D traps - catching descent animals- was much lower than that of the A traps-catching ascent animals-. (2) The III-4.5-A trap was the most efficient trap in almost all cases, followed by the I-8.5-A and III-8.5-A traps. These times correspond to an upward movement at dusk especially below 4.5 m depth, while below 8.5 m this movement seems to begin at dusk and continues through the night. Only copepods, especially copepodites and adults, showed an upwards movement at night as shown by results from I-4.5-A trap. In the traps from 12.5 m movement seems to be more uniform throghout the diel cycle. (3) Some species such as *T. similis* presented great differences between the *egg-ratio* estimated from the diel cycle samples and that obtained from the traps. (4) Variance between some replicates was high, although these variations were much lower than the variations observed among the three different periods of time at which the traps were set.

DISCUSSION

Zooplankton of lake La Cruz exhibit diel migration behaviour. Most of the species depicted the normal pattern of migration, but one case of reverse migration was also observed. The amplitude of the vertical movements at the epilimnion was consistent with the results obtained for rotifers by other authors, but generally it was lower than in migratory movements reported for other groups of zooplankton with better swiming capacity. George and Fernando (1970), obtained variations for the mean residence depth ranging from 3 to 0.2 m for *K. quadrata* and from 5.6 to 1.1 m for *P. vulgaris*

depending on the season. Stewart & George (1987), reported 2 m of maximum amplitude of migration for *K. quadrata* in a hypereutrophic tarn. In our study the maximum amplitude of migration was observed for *K. quadrata* and *A. girodi* being of 6.1 m and 4.4 m respectively. Other authors (Pennak, 1944; Larson, 1971; Bogaert and Dumont, 1987) found similar magnitudes for rotifers. In contrast, longer migrations - measured in tens of meters- have been described for copepods and cladocerans (Worthington, 1931, Cushing 1951, Lampert and Stich, 1981; Harding *et al.*, 1986).

The amplitude of the vertical migration can be influenced by the transparency of the water and food conditions (Lampert and Sommer, 1997). Thus, we chose September for this experiment because at this time of the year transparency is high in lake La Cruz and this is one of the main abiotic factors affecting intensity of vertical migration (Dodson, 1990). At this time of the year, moreover, oxicline layers of these stratified lakes are especially rich in nutrients, because these layers work as a trap faciliting the development of high densities of cryptophytes and procariote populations (Miracle and Vicente, 1983) which can be used as a nutritional source by some zooplanktonic organisms (e.g. recent studies of this lake using flourescence techniques have shown the presence of dense populations of the cyanobacterium *Synechococcus sp.*). Nevertheless oxicline layers are a particular environment with some peculiarities such as low oxygen content, low temperatures and low intensity of light; not all species or populations are adapted to such environmental conditions.

Vertical distributions of rotifers along the vertical profile in lake La Cruz during an annual cycle has been reported in previous studies (Esparcia *et al.*, 1991; Armengol *et al.*, 1993). Results from these studies showed how some rotifer species which are widely distributed in the water column in spring were able to occupy the hypolimnetic layers at the end of summer,such species were, *P. dolichoptera*, *K. quadrata* and *A. fissa. A. miraclei* (a new species described for this lake; Koste, 1991) and *F. hofmanni* (Koste, 1980) were considered as hypolimnetic species *sensu stricto*, meaning capable of occupying hypolimnetic layers permanently, being almost totally absent from the epilimnion. However in September 1989, these two most typical hypolimnetic species were not present. Results of vertical distribution from the current study are in agreement with the previous studies, showing the same spatial segregation. Epilimnetic, metalimnetic and hypolimnetic zooplankters corresponded with these defined in such works. During the diel cycle we have observed variations in mean residence depth (MRD) that occurred mainly in epi-metalimnetic waters. In contrast, movements of the organisms at the hypolimnion and metalimnion were very small, and produced very low variations in the mean residence depth. Species with maximum at these layers but also abundant at the epilimnion showed a migratory behaviour in the epilimnetic waters

Table 2a: Catches in A traps (animals going up) at differents times and depths

A Traps	22:20 to 6:55 I-4.5-A	7:05 to :14:15 II-4.5-A	14:50 to 21:05 III-4.5-A	21.50 to 6:40 I-8.5-A	6:55 to 14:35 II-8.5-A	14:45 to 20:55 III-8.5-A	21:20 to 6:25 I-12.5-A	6:40 to 14:25 II-12.5-A	14:35 to 21:15 III-12.5-A
Rotifera									
Anuraeopsis fissa	9.5 + 3.5	27.0 + 9.9	1533 + 350	2129 + 1141	694 + 134	4489 + 1679	32393 + 1758	35161 + 9954	291301 + 699
eggs A.f.	0.5 + 0.7	1.0+ 1.4	470 + 35	698 + 532	263 + 119	1858 + 845	21.2 + 15.2	49.3 + 7.5	80.0+ 33.9
Ascomorpha saltans	0	1	371 + 79	252 + 52	15.5 + 4.9	89.5 + 20.5	0	0	0
Asplanchna girodi	0	0	20.0 + 1.4	2	5.0 + 2.8	1.5 + 0.7	0	0	0
Hexarthra mira	0.5 +0.7	0.5 + 0.7	158 + 10	95 + 33	16.5 + 4.9	79 + 34	0	0.5 + 0.7	0.5 + 0.7
eggs H.m.	0	0	25.5 + 10.6	5.0+ 7.1	4.5 + 6.4	8.0 + 1.4	0	0	0
Keratella quadrata	0	0	19.0 + 5.7	24.0 + 5.7	3.0 + 1.4	6.0 + 4.2	5.0 + 2.8	3.5 + 4.9	3
eggs K.q.	0	0	2		0.5 + 0.7	0	1.0+ 1.4	0	0
Polyarthra dolichoptera	0.5 + 0.7	1	10.0 + 2.8	19.5 + 10.6	5.0 + 4.2	8.0 + 2.8	849 + 286	145 + 35	100 + 21
eggs P.d.	0.5 + 0.7	0.5 + 0.7	1.5 + 2.1	4.5 + 2.1	1.5 + 2.1	0	124 + 47	42.6 + 6.2	14.5 + 10.6
Synchaeta pectinata	0	0.5 + 0.7	20.5 + 0.7	20.5 + 3.5	3.0 + 1.4	5	0.5 + 0.7	0	0
Trichocerca similis	1	1.0 + 1.4	285 + 100	112 + 25	119 + 13	66.5 + 20.5	0.5 + 0.7	1.0 + 1.4	3.0 + 2.8
eggs T.s.	0	4.0 + 5.7	7.5 + 2.1	3.0 + 4.2	4.0 + 5.7	1.0 + 1.4	0	0	0
Crustacea									
nauplia	13.0 + 2.8	7.0 + 4.2	10.5 + 2.1	22	14	21.5 + 2.1	0	2.0+ 1.4	0.5 + 0.7
copepodita	37	6.0 + 1.4	3	0.5 + 0.7	3.5 + 0.7	0.5 + 0.7	1.5 + 2.1	1.5 + 2.1	0
Tropocyclops prasinus (ad)	33	1	0.5 + 0.7	0.5 + 0.7	0.5 + 0.7	0	1	0.5 + 0.7	0
Daphnia longispina	0	0.5 + 0.7	9.5 +2.1	76 + 36	8.5 + 4.9	4.5 + 0.7	0	0	0
Otros									
Chaoborus sp.	0	0	0	2	0	0	3.0 + 1.4	2.5 + 0.7	3.5 + 2.1

Table 2b: Catches in D traps (animals going down) at differents times and depths

D Traps	21.30 to 6:10 I-8.5-D	6:25 to 14:05 II-8.5-D	14:15 to 20:45 III-8.5-D	20:50 to 5:45 I-12.5-D	6:00 to 13:45 II-12.5-D	14:00 to 20:40 III-12.5-D	20:40 to 5:30 I-13.8-D	5:45 to 13:15 II-13.8-D	13:45 to 20:30 III-13.8-D
Rotifera									
Anuraeopsis fissa	672 +85	221 + 103	345 + 98	641 + 21	192 + 53	230 + 78	243 + 129	61 + 27	125 + 40
eggs A.f.	33.5 +7.8	22.5 + 7.8	11.5 + 3.5	6.5 + 0.7	4.5 + 2.1	14.0 + 7.1	1	1.0 + 1.4	2.5 + 0.7
Ascomorpha saltans	0.5 + 0.7	1.5 + 0.7	0	0	0	0	0	0	0
Asplanchna girodi	0	0	0.5 + 0.7	0	0	0	0	0	0
Hexarthra mira	2	2.5 + 0.7	2	1	0.5 + 0.7	0.5 + 0.7	0.5 + 0.7	0	0
eggs H.m.	0	0	0.5 + 0.7	0	0	0	0	0	0
Keratella quadrata	2.5 + 0.7	0	0.5 + 0.7	0.5 + 0.7	0	1.5 + 2.1	0	0	0
eggs K.q.	0	0	0.5 + 0.7	0	0	0	0	0	0
Polyarthra dolichoptera	7.5 +2.1	3	15 + 5.7	774 + 40	485 + 94	1636 + 119	5.5 + 2.1	1	4.5 + 3.5
eggs P.d.	0.5 + 0.7	0	0	10.5 + 0.7	13.0 + 7.1	36.5 + 0.7	1	0.5 + 0.7	0.5 + 0.7
Synchaeta pectinata	2.0+ 1.4	0	1	0	0	0	0	0	0
Trichocerca similis	23.5 + 2.1	1.5 + 2.1	14.5 + 0.7	0.5 + 0.7	1.0 + 1.4	2.5 + 2.1	0	0	0
eggs T.s.	0.5 + 0.7	0	1.0 + 1.4	0.5 + 0.7	0	0	0	0	0
Crustacea									
nauplia	8.5 + 4.9	28.5 + 20.5	10.0 + 2.8	1	0.5 + 0.7	0	0	0.5 + 0.7	0
copepodita	46.5 + 0.7	13.0 + 2.8	3	0	0	0	0	0	0
Tropocyclops prasinus (ad)	1.5 + 0.7	0	0.5 + 0.7	0	0	0	0	0	0
Daphnia longispina	8.5 + 0.7	5.0 + 4.2	4.0 + 2.8	7.5 + 0.7	6	4.5 + 3.5	3	5.0 + 1.4	1
Otros									
Chaoborus sp.	0	0	0	0.5 + 0.7	1 ninfa	0	0	1	1.0+ 1.4
Ciliados	0	0	0	0	0	0	810 + 14	3300 + 2404	1400

related to the daily cycle. Moreover, not only vertical distribution of densities along the cycle, but also catches in the traps, showed this effect. However, in the hypolimnion, movements were either negligible as in *S. pectinata,* or asynchronic with respect to those in the epilimnion as in *A. fissa.*

The vertical profile of plankton samples only allows us to see the changes in the density of organisms at particular depths (Lampert and Sommer, 1997). Shifts in mean residence depth are usually interpreted as movements of the population, and day-night differences as measures of the vertical range of migration (Lampert, 1989). However, an indirect analysis such as this depends on synchronous movement by most members of a population, otherwise it could lead to erroneous conclusions about the strength and even the existence of vertical migration (Pearre, 1979). The use of traps helps in the interpretation of variations in mean residence depth, and thus variations in the vertical distributions could be corroborated through catches in traps (Harding *et al.*, 1986). The use of traps was also relevant in our study because they showed a large amount of catches in hypolimnetic waters. These catches were independent from diel variations and support the consideration of these populations as active ones, and not as decaying sedimenting individuals.

High densities of rotifers obtained in previous studies dealing with hypolimnetic layers (Armengol *et al.*, 1993; Miracle and Armengol, 1995), led us to concentrate our samples on these layers. Moreover, for a higher accuracy, we have used a fine layer sampler with a pump. This device, effective for rotifers and nauplii, can understimate organisms such as copepods and cladocerans because they are better swimers and can swim away from the water flow. Traps were also designed for rotifer sizes, so the results for other groups must be considered with care.

Results from the traps show a general trend of movement upwards during dusk and night. Catches in traps mean that the organisms must cover at least 260 mm, which is a significant distance in animals of between 0.1-0.4 mm in size, and moreover the presence of the funnel is an additional difficulty. In spite of this, organism density in some traps was several times higher than the highest density found in our samples (around 14 10^4 ind l^{-1} compared with a maximum density of 12644 ind l^{-1}) so the presence of organisms in traps indicates a strong tendency to go upwards. A very different result was obtained in traps catching organisms moving downwards ("D" traps), where a lower amount of catches was obtained for almost every species (see Table 2). Eventhought in the absence of strong water currents, as is the case of this lake, an equilibrium between upwards-downwards catches over the daily cycle seems reasonable, horizontal movements could interfere in this equilibrium. For instance Carrillo *et al.* (1989), found strong differencies in day/night horizontal distribution of

Hexarthra bulgarica in a mountain lake. These authors atributed the horizontal movements to light changes, but also wind-induced water currents could be important in explaining this result. However the steep slopes and the strong wind protection of lake La Cruz make such an interpretation unlikely. A more reliable explanation for differences between "D" and "A" traps is to consider that animals move downwards in a passive way. The animals stop swiming and feeding activities which produces a passive sinking, a behaviour that could be bioenergetically very positive because it implies a saving of energy when going down, and the energetic cost of swiming is high in these animals (Epp, 1984). This behaviour has been reported in other groups, in which direct observation is easier, such as cladocerans (Dawidowicz, 1992; De Meester, personal communication). This strategy may considerably hinder the entrance in our funnel traps, because in a passive descent a mechanical contact against the funnel walls could act as an stimulus for the organism to begin to swim away, thus avoiding the trap. Harding *et al.* (1986) using similar traps found the same effect in a study on copepods in St. Georges Bay. These authors attributed this effect to passive sinking and upward avoidance reaction caused by contact with funnel walls. Only *P. dolichoptera* had a higher number of captures going downwards which can be attributed to an active descent by this species since the presence of paddles could impede passive sinking.

After the discussion of these general aspects, some particularities of the different species are discussed in the following paragraphs.

Asplanchna girodi and Keratella quadrata (Figs. 4a and 4b) showed the normal pattern of variation with the highest amplitude of migration. *K. quadrata* is one of the typical preys of *Asplanchna* as is supported by our observations in the meromictic lake El Tobar (Miracle *et al.*, 1993). Differential development of *Keratella*'s caudal spine has been correlated with differences in temperature (Pejler, 1962), but also with predatory preasure by *Asplanchna* (Gilbert and Stemberger, 1984; Conde-Porcuna, 1993). In our samples we have found two different morphotypes of this species, one having long caudal spines and the other with short spines; both morphs presented a marked segregation in the vertical profile. In *Keratella,* cases of simultaneous presence of several morphs are known (Green, 1981; Galkovskaya and Mityanina, 1989). As hypolimnetic conditions seem inadequated for *A. girodi* (Esparcia, 1993; Armengol *et al.*, 1993) segregation of both morphs may be related to the predation presure of *Asplanchna*. Thus, there could be two different populations of *K. quadrata,* one living at the hypolimnion with short spines and low predation presure, the other living at the epi-metalimnion with long spines and higher predatory presure produced by *A. girodi.* Nevertheless the migratory behaviour of *K quadrata* does not seem to be a very adaptative behaviour for avoiding predation. In fact, one of the effects of vertical

Table 3. Amount estimated of each rotifer species in the lower/upper meter of the trap. Among parenthesis is shown the percentage of catches in traps with respect to this estimation is indicated. (*) indicates no significant percentages due to the low amount of rotifers estimated. (---) Indicates catches in the trap where there not were estimated rotifers, so the percentage can not be calculated.

Hexarthra mira

	Ascent			Descent		
Depth	I	II	III	I	II	III
4.5	1895 (0.03)	1812 (0.03)	2384 (6.7)			
8.5	1069 (8.9)	1168 (1.4)	1501 (5.3)	1069 (0.2)	1168 (0.2)	1501 (0.1)
12.5	244 (0)	66 (0.8)	140 (0.4)	735 (0.1)	413 (0.1)	496 (0.1)
13.7				244 (0.2)	66 (0)	140 (0)

Trichocerca similis

	Ascent			Descent		
Depth	I	II	III	I	II	III
4.5	264 (0.4)	305 (0.3)	361 (79.1)			
8.5	295 (38.0)	211 (56.5)	224 (29.7)	295 (8.0)	211 (0.7)	224 (6.5)
12.5	1 (48.5)*	1 (96.9)*	6 (48.5)*	31 (1.6)	28 (3.6)	15 (16.5)
13.7				1 (0)	1 (0)	1 (0)

Ascomorpha saltans

	Ascent			Descent		
Depth	I	II	III	I	II	III
4.5	107 (0)	256 (0.4)	358 (103.7)			
8.5	169 (148.9)	157 (7.3)	116 (77.4)	169 (0.3)	157 (1.0)	116 (0)
12.5	0	0	0	0	0	0
13.7				0	0	0

Asplanchna girodi

	Ascent			Descent		
Depth	I	II	III	I	II	III
4.5	29 (0)	50 (0)	19 (103.8)			
8.5	0 (---)	8 (60.6)	6 (27.3)	0	8 (0)	6 (9.1)
12.5	0	0	0	0	0	0
13.7				0	0	0

Synchaeta pectinata

	Ascent			Descent		
Depth	I	II	III	I	II	III
4.5	66 (0)	74 (0.7)	77 (26.6)			
8.5	78 (3.8)	70 (7.1)	56 (0.9)	78 (2.6)	70 (0)	56 (1.8)
12.5	0 (---)	2 (0)	2 (0)	90 (0)	80 (0)	85 (0)
13.7				0	2 (0)	2 (0)

Keratella quadrata

	Ascent			Descent		
Depth	I	II	III	I	II	III
4.5	74 (0)	87 (0)	80 (24.4)			
8.5	39 (61.9)	29 (10.4)	37 (16.3)	39 (6.4)	29 (0)	37 (1.4)
12.5	26 (19.4)	24 (14.7)	48 (6.2)	60 (0.8)	36 (0)	74 (2.0)
13.7				26 (0)	24 (0)	48 (0)

Polyarthra dolichoptera

	Ascent			Descent		
Depth	I	II	III	I	II	III
4.5	37 (1.4)	29 (3.5)	39 (26.0)			
8.5	105 (18.6)	107 (4.7)	85 (9.4)	105 (7.2)	107 (2.8)	85 (17.6)
12.5	9545 (8.9)	9680 (1.5)	10735 (0.9)	15841 (4.9)	16167 (3.0)	15941 (10.3)
13.7				9545 (0.1)	9680 (0.01)	10735 (0.04)

Anuraeopsis fissa

	Ascent			Descent		
Depth	I	II	III	I	II	III
4.5	5090 (0.2)	2815 (1.0)	4494 (34.1)			
8.5	12323 (17.3)	11444 (6.1)	19144 (23.5)	12323 (5.5)	11444 (1.9)	19144 (1.8)
12.5	125940 (25.7)	138203 (25.4)	126532 (23.0)	152570 (0.4)	150506 (0.1)	134302 (0.2)
13.7				125940 (0.2)	138203 (0.04)	126532 (0.1)

migration is the concentration of the organisms in surface waters during night, and *A. girodi* is a non-visual predator whose efficency is higher when the density of preys increases (Sarma, 1993). The same is true for another potential predator of *K. quadrata* in lake La Cruz, *Chaoborus* larvae, wich usually come to surface only at night staying in anoxic waters during the day (Lewis, 1977) avoiding visual predation by fish.

Ascomorpha saltans and Hexarthra mira also presented the normal pattern of migration. The first species, in spite of the low numbers counted in diel cycle samples, presented very high numbers and percentages of captures in the traps. This result can be explained in two ways: (1) a large amount of individuals migrate, so we find more than 100 % of the organisms estimated for the lower meter; or (2) estimations of organism abundance along the vertical profile could be biased as a consequence of patchiness. *H. mira* presented very low percentages in the traps. Regarding the vertical distribution along the diel cycle, we can observe a similar behaviour to that described for the other two species mentioned before. This species presented a normal pattern of migration, however they had a very low percentage of catches in traps. An explanation for this disagreement between these results could lie in the particular behaviour of this species. *H. mira* presents six appendages capable of an escape response to predation, so it is possible that this species could react against the contact of the funnel wall with the susequent decreasse of trap efficency. In fact, genera *Hexarthra* has such a rapid escape response that it makes it difficult for the predator to capture, as has been supported by several studies; for instance, results from a feeding experiment using *Asplanchna* as predator showed that *Hexarthra* was never captured (Sarma, 1993), and in field studies the absence of *H. mira* in gut contents of *A. girodi* in samples in which *H. mira* was the dominant species further strengthens the supposition (Armengol *et al.* in press.).

The reasons for the migratory behaviour in both species could be related to feeding and activity cycles. *A. saltans* has been described as a raptorial species, feeding usually on dinoflagellate populations. This group was also abundant in our samples but we do not have a quantitative estimation. Nevertheless, the fact that they were also captured in traps suggests vertical movements for this group, as has been previously reported in the literature (Reynolds, 1984; Bayly, 1986). *A. saltans* could follow these vertical movements.

In rotifers, especially filter-feeders, swimming and feeding are closely related through the use of the ciliated corona in both actions (Nogrady *et al.*, 1993). *H. mira* is a filter feeding organism, a higher feeding activity during the night could also imply higher swiming activity. This would explain the migratory behaviour we found for this species. Connell (1978), also found weak vertical migration in *H.mira*.

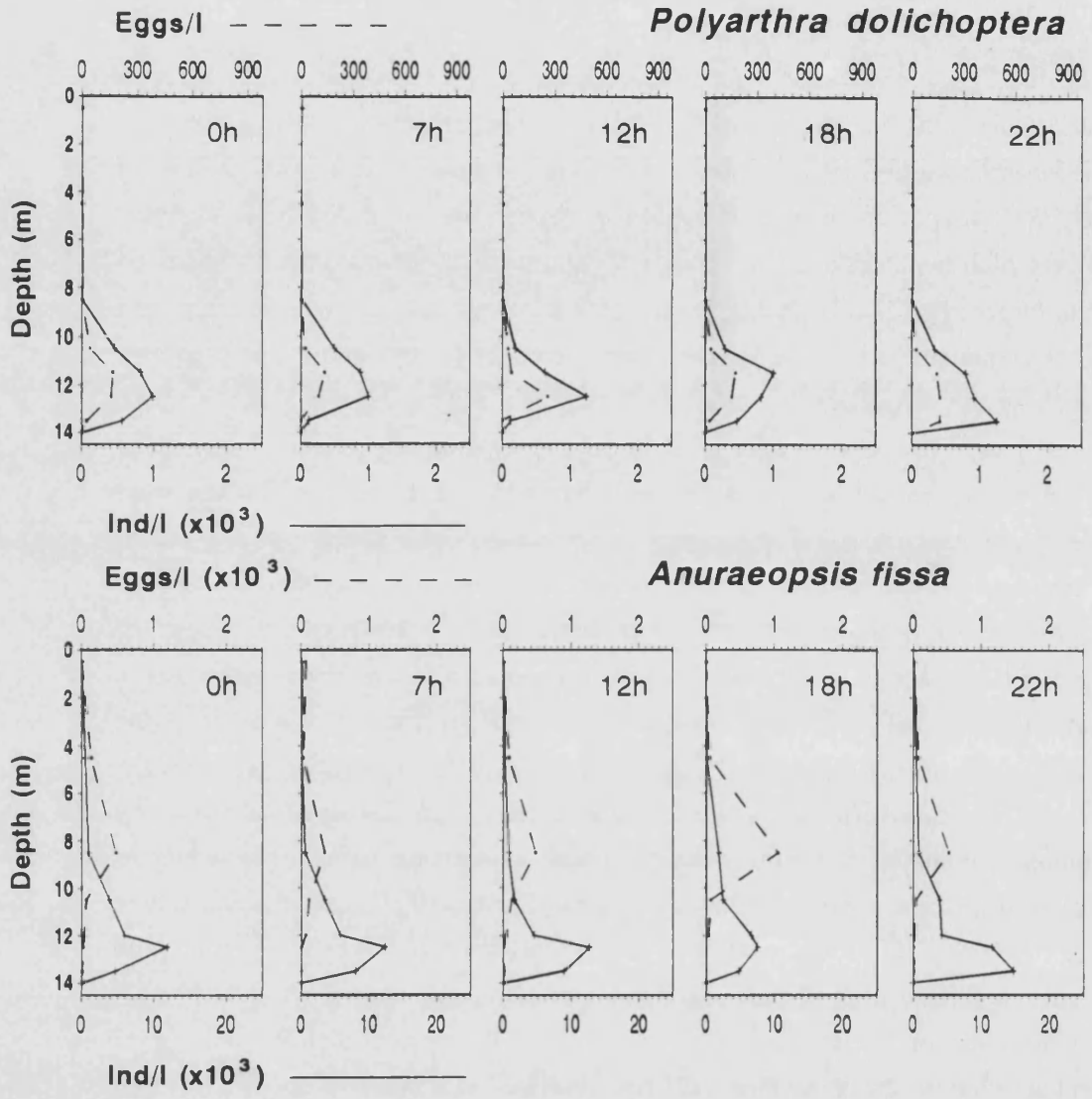


Figure 6: Comparision between egg densities and rotifer densities along the vertical profile during a diel cycle, for two rotifer hipolimnetic species : *P. dolichoptera* and *A. fissa*.

Only *T. similis* showed a weak reverse migratory pattern. Reverse vertical migration has been interpreted as a way of avoiding competition (Dumont, 1972) but also as a way of diminishing predation by *Chaoborus* larvae (Fedorenko, 1975). Both mechanisms could explain the behaviour of *T. similis* but in our observation intensity of migration was very low.

S. pectinata showed a very weak movement, always presenting a density peak at the same depth -the lower part of thermocline-, whch corresponds to an oxygen peak generally correlated with high phytoplankton density. High concentrations of phytoplankton in the thermocline, with maximum oxygen is probably the reason for their distribution. At the epilimnion, some movements were observed but implying a few individuals. Ruttner-Kolisko (1977), also found this species in an alpine stratified lake, always in conditions of high oxygen concentration.

P. dolichoptera behaved in our experiment as a true hypolimnetic species. Diel cycle samples and catches in traps support this result. The low number of catches in traps could also be related to the largely documented escape behaviour of this species (Gilbert, 1980). In relation to *Polyarthra*'s escape response (Armengol *et al.*, in press.) did not find remains of *Polyarthra* in *Asplanchna*'s gut contents. These results were atributed to its rapid escape response. In spite of the low percentage of captures in both "A" and "D" traps, "D" traps presented the highest efficiency for this species. We consider this effect to be due to *Polyarthra's* particular morphology -especially the presence of paddles- that could impede passive sinking. It could then be reasonable to think that sinking in this species would require active swimming which could facilitate entrance in "D" traps.

Together with the MRD of this species, the *egg ratio*'s vertical distribution confirms its consideration as an hypolimnetic species. The highest *egg-ratio* was aproximatedly coincident with the gravity center of population (i.e. MRD) situated at the hypolimnion (Fig 6a).

The most abundant species was *A. fissa* -as is common at the end of summer in this lake (Armengol *et al.*, 1993)-. This species occupies hypolimnetic waters reaching its maximum densities at these layers. Furthermore it is the dominant species all along the vertical profile, this fact could give us an idea of their eurioic characteristics. *A. fissa* has been considered as a filter feeding species being able to feed on bacterial populations (Pourriot, 1977; Esparcia, 1993 and Gasol *et al.*, 1995). In our samples their migratory behaviour can be considered as normal in the epilimnetic samples.

Results from the traps are consistent with the samples from the diel cycle. In spite of it being the most captured species in the traps, percentages of catches were low. The "A" traps from 12.5 m presented percentages around 20 % over the three periods of

trap catches. These high p p ntages could be considered as an evidence of the high activity found at these llayayay*A. fissa* is also a filter feeding rotifer but in this case cycles of activity (swiimimmand feeding) and inactivity (passive sinking) were asynchronous with the liggghghhle.

In contrast with h ı *lolichoptera*, *A. fissa* presented a different vertical distribution of *egg-rattio'oio* density. *Egg-ratio* presented its maximum at the epilimnion, while the graavavavinter of the population was clearly hypolimnetic. *A. fissa* has been considered in pprererres papers (Armengol *et al.*, 1993; Miracle and Armengol, 1995) as a facultative hyypypypnetic species, and our results support this consideration. Differential distribution cofofof: and organisms, together with the catches in traps, might be explained in two waysss.s.s. his species could present their maximum egg production in epilimnetic waters wvhvhvhtorditions are optimal, whereas high concentrations in hypolimnetic waters wooububul due to the accumulation of weaker organisms. These organisms would sink aiftiftiftheir reproductive period ending their lives at these layers. (2) This species could feeeeeeedypolimnetic layers where food is abundant but due to the special conditions of lowowwpe:ature and low oxygen, the egg production would be reduced, and so they wcovotouigate upwards to higher temperature layers in order to facilitate egg developmmeneneDu data are consistent with the second explanation, especially the results frcororon 12.5 m A-traps which showed a high activity in these layers, difficult to expldailaiaiithi case of being inhabited by weak animals. Morales-Baquero *et al.* (1995)),),), id that changes in temperature could stimulate egg production, as betweenı a ı end hipolimnion we find great thermic differences, this effect could facilitate suachclchavour.

With respect to ı cı cıcreas we have found two different behaviours. The first one is represented by ccococopdswhich were studied in their three different stages of development (Fig. 5a-cc)c)c). ncmal" pattern was found in nauplii, copepodites and adults, attending the vanriiriiriz oiMRD, but traps showed some differences. In nauplii, catches in traps were off tf tf tlm order of magnitude at the different depths all through the diel cycle, but copeppepcpo ad adults presented a night ascent (trap I-4.5-A). while catches in the other trappspsos · lcv. This night ascent of copepodites and adult copepods constituted the main diiiiiifificewith respect to rotifers. The copepodites were also catched in I-8.5-D trap ı ii ir irh numbers. These results together with the changes in the vertical distributions (FFiFiginicate that part of the population migrates up and other part migrates down.

The second behaaaaay, caracterised by the absence in the daylight samples and presence, especially in ı sı sı sıe vaters, at night, is represented by *D. longispina*. In this case, we found a high ı n n ner f catches in I-8.5-A trap but only III-4.5-A trap had a

significant number of catches. Taking into consideratichee e fact that methodological aspects limit our interpretation of results related to :anlss ł bigger than rotifers, this result could be interpreted as a consequence of the ɔuhlalation concentration in a methalimnetic layer. Later when it is completely dark asssisive migration occurs and the population remains widespread throgh the vertic:al,fifilele, but presenting highest percentages in surface waters.

Finally *Chaoborus sp.* were found in too low nbbeɔers to allow an accurate description of their movements, but we did find a regulunmmber of catches along the diel cycle in the traps from 12.5 m. This may indicate *CChaoborus* - which during dayligth occupies anoxic layers- could go up to feed otyyclclinal rotifer populations, independently from the diel cycle. Several studies haveowwvn the importance of this especies as a rotifer predator (Fedorenko, 1975; Lewis, 1).

CONCLUDING REMARKS

Vertical movements related with the diel cycle in epheetiɔtic waters seem to be a general behaviour in rotifers. Several reasons could explsuuclch movements. From our results, in most rotifer species, predation does not seem mnoost important due to: (1) At the time of the year in which our study was conduc ahlelewives of dominant fish *Micropterus sp.* are too large to feed mainly on rotifers, (2) i) concentration in surface waters at night could be disadvantageous to rotif boeecause of interferential competition with *Daphnia*, and predation by *Chaoborus Asspspilanchna.*

As in rotifers, especially filter-feeders, swimiannchdl feeding are strongly connected through the "rotatory apparatous", to consi vvevertical movements as a consequence of diel regulation of activity cycles better einnsis our results. During the night, higher activity (swiming and feeding) produces noovvement mainly directed upward; during the day, passive sinking could be associavititihth lower feeding rates. In these cases light would be an important factor in regulatire ɛ acactivity of such animals.

For the predatory rotifer *Asplanchna girodi* verticiggrgration to spend the night in surface waters, could be advantageous. They are biggiinmmals, thus this behaviour could diminish visual predation risk. Furthermore highenaccecentrations of rotifers in surface waters at night facilitate the predatory behaviour *ephlalainchna.*

The use of traps is important in supporting the rɛ f fr:from the diel samples of the vertical profile. Traps indicate that vertical moveme>f f a a certain magnitude are also important in hypolimnetic layers, probably correspog t tc to cycles of activity, but in this case independent from the diel cycle.

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[IV.7]

ZOOPLANKTON COMMUNITIES IN DOLINE LAKES AND POOLS, IN RELATION TO BATHYMETRIC AND PHYSICO-CHEMICAL PARAMETERS

X. Armengol & M.R. Miracle

Departament de Microbiologia i Ecologia, Universitat de València, 46100 Burjassot, (Valencia, Spain)

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X. Armengol y M.R. Miracle

Departament de Microbiologia i Ecologia, Universitat de València, 46100 Burjassot, (Valencia, Spain)

Key words: Zooplankton communities, diversity, bathymetry, abiotic factors, trophic gradient, multivariate statistics.

ABSTRACT

The zooplankton communities from several lakes and pools in three zones of a karstic area in central Spain have been studied in two different seasons, spring and autumn, and in relation with bathymetrical and other physico-chemical characteristics of the lakes. This study, performed by means of different multivariate statistical methods, showed that the trophic state and mineralogical conditions were very important in determining species occurrence. Some morphometrical characteristics were also seen to be correlated to the structure of the communities.

INTRODUCTION

Zooplankton communities are generally composed of ubiquitous species capable of colonizing a wide array of water bodies. Abiotic features of the lake together with biotic interactions among the different organisms living in the water determine a community composition in a particular geographic zone.

Several studies have been performed with the purpose of comparing zooplankton communities in particular zones (Tonolli and Tonolli, 1951; Patalas, 1971; Miracle, 1978; Coussement and Dumont, 1980), some other studies have been focused on classifying different water bodies on the basis of their planktonic communities by means of multivariate statistical methods; Jersabeck (1995), applied these methods to the study of rotifer commuinities from different alpine water bodies in Austria. Pontin and Langley (1993) and Langley *et al.* (1995) also applied multivariate methods -in this case Two-Way Indicator Species Analysis (TWINSPAN)- to the classification in England of small water bodies or several urban ponds in London on the basis of their rotifer communities. These and other studies attempt to identify the main abiotic factors responsible for such zooplankton assemblages.

In previous works we have studied the principal factors influencing rotifer communities over an annual cycle (Armengol *et al.*, 1993; Miracle and Armengol, 1995, Armengol *et al.*, in press.) finding temperature and oxygen to be the most important factors in the explanation of changes in rotifer communities throughout the year and in the vertical profile. In this case we have studied samples of zooplankton taken over a short period of time when the differences in temperature between lakes were low and the morphometrical and mineralogical conditions of each lake were more important to explain variations in zooplankton communities. Something similar occurred with oxygen content, a parameter which often separates surface and bottom samples. In our case several samples were taken along the vertical profile but the study was performed by averaging the zooplankton densities to obtain an averaged density for each species in each lake. The aim of this work is to identify the factors responsible for the main source of variance in the distribution of the zooplanktonic community in 27 karstic lakes by means of multivariate statistic methods, considering the same season and integrated depth abundance values in order to characterize the communities according to the different types of lakes. We have used correlations, PCA and Twinspan to explore the effects of morphometry and substrate of these solution lakes on the composition and structure of zooplankton communities.

MATERIAL AND METHODS

Samples were taken from 27 flooded dolines of the karstic area of Cuenca over two periods of three weeks, one at the end of April-beginning of May 1992 (spring), and the other at the end of September-beginning of October 1992 (early autumn, before turnover). An additional trip was made in winter 1993 to obtain the morphometric and bathymetric data of the different lakes.

At every sampling site, the different physico-chemical parameters (Temperature, Oxygen, Conductivity, pH, and Secchi disk depth) were measured *in situ*. Water samples were collected with a 5.4 l Van Dorn bottle and filtered through 30 μm nytal to concentrate zooplankton. Other water samples were collected with a 3l Ruttner bottle for chemical and pigment analyses. The samples were collected from three different points on the vertical profile chosen in function of the lake status and, in addition, a plankton net was used to identify the more scarce species. Zooplankton samples were counted in the laboratory by means of an inverted microscope. Chemical analyses were performed according to Golterman *et al.* (1978). For characterization of the different sites, physicho-chemical data and zooplankton densities taken along the vertical profile were averaged to a single value for each site.

Zooplankton diversity was calculated for each depth and values were averaged (H'mean), the same was also calculated for the integrated water column (H'); using the Shannon-Wiener function (Shannon and Weaver, 1949):

$$H' = - \Sigma p_i \log_2 p_i$$

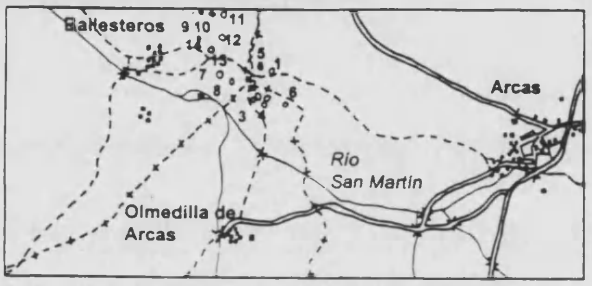
Evenness or equitability (E%) was calculated as 100 H'/H'max, where H'max = log2 S. (S = number of species). An Index of Floral Originality was used to evaluate the different zooplankton fauna among the lakes (Puchalski, 1987):

$$IFO = \frac{\Sigma 1/M}{S}$$

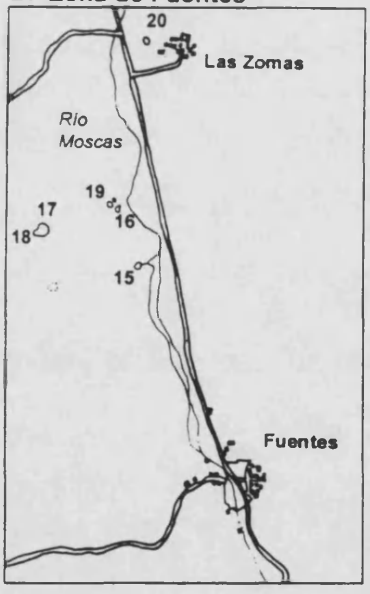
where: M = number of samples in which a species occurs and S = number of species in a sample.

A number of statistical methodologies have been used in the processing of the data. The spring and autumn data on physical and chemical features and densities of main planktonic or semiplanktonic species were transformed logarithmically -with the exception of pH-, and linear correlations and Principal Component Analysis (PCA)

A.- Zona de Arcas-Ballesteros



B.- Zona de Fuentes



C.- Zona de Cañada del Hoyo

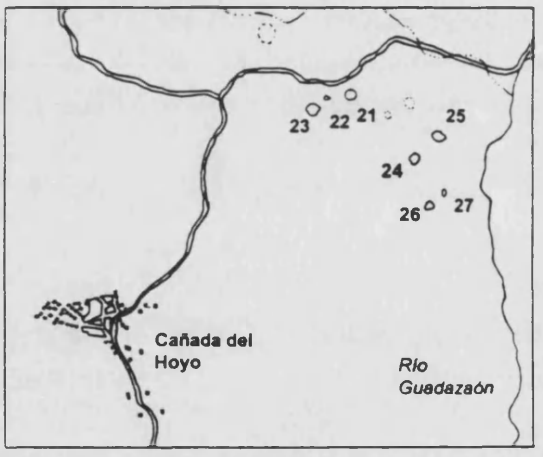


Figure 1: Maps of the three main study areas in the province of Cuenca, showing the location of the sampling sites.

were performed (see Appendix 1). These analyses were carried out using the program SPSS for windows version 6.1.3. Two-Way Indicator Species Analysis (TWINSPAN, Hill, 1980) was used to analyze data from spring only, recording the presence/absence in each sampling site of all the species present in the bottle samples, also taking into account the littoral species.

Study site

The different water bodies studied are distributed along three main river valleys in a karstic area (A, B and C, Fig.1) close to the city of Cuenca (central Spain) These zones present different mineralogical compositions. Zone C is located near the village of Cañada del Hoyo where the lakes are flooded dolines, situated on the right margin of the river Guadazaón, and developed on a cretacic dolomitic substrate, where carbonates are dominant in the mineralogical composition of water. The system consists of seven permanent and three temporary lakes, but only the permanently flooded dolines were studied. Zone B is near the village of Fuentes, from where six flooded dolines situated on both margins of the river Moscas were studied. Zone A consists of the greatest number of flooded dolines, a total of 21 pools located on the right margin of the river San Martín. Fifteen of these, which have been permanent in recent years, were studied. Zones A and B are situated on a tertiary marls substrate rich in gypsum, especially zone A.

RESULTS

The morphometric-bathymetric data obtained from the different lakes considered are presented in table 1. The marked differences between the sizes of the different lakes are interesting, as are the shapes of the cross-sections (represented by the slopes). Differences in trophic gradient were also observed among these lakes and pools. The mean densities of each zoplanktonic species for each lake/pool basin at two times of the year are summarized in Appendix 1 and the different community indexes derived from them are shown in table 2.

The distribution of the diversity values in the doline lakes or basins in autumn and spring is shown in figure 2. In autumn diversity was higher than in spring, and furthermore the range of diversity values was wider in autumn than in spring. In figure 3 we show the relation of diversity to maximum depth (Zmax) and mean diameter (Mean diam) for both periods. In spring both morphometrical parameters showed a positive

Table 1: Some morphometrical characteristics measured in metres at the different lakes or basins. Maximum diameter, Mean diameter, Perimeter and Maximum depth (Z max). Surface is measured in square metres. Relative depth (Z rel) is given as a percentage and slope is also given as a percentage ± standard deviation, (--) absence of data.

lakes (basins)	Max. diam	Mean diam	Surf	Perimet	Z max.	Z rel	slope 5m (% ± sd)	slope 10m (% ± sd)
1.- Arcas-1 (Ar 1)	24.0	23.0	389.2	74.0	11.5	51.7	149 ± 18	111 ± 14
2.- Arcas-2 (I) (Ar2-I)	45.0	45.3	1581.2	145.7	14.0	31.2	99 ± 28	88 ± 14
3.- Arcas-2 (II) (Ar2-II)	34.0	30.0	629.0	97.2	4.4	15.5	32 ± 17	32 ± 8
4.- Arcas-3 (II) (Ar3-II)	45.0	45.0	1134.1	148.6	7.4	22.1	36 ± 50	36 ± 28
4'.- Arcas-3 (I) (Ar 3-I)	38.0	38.0	1590.4	119.4	8.4	16.4	65 ± 41	66 ± 10
5.- Arcas-4 (Ar 4)	17.0	16.0	257.0	59.9	1.9	11.9	sd	sd
6.- Rincón (Rinc)	54.5	50.8	1427.8	140.0	5.7	13.4	73 ± 48	39 ± 21
7.- Barraganes 1 (Bar 1)	42.0	42.0	1612.7	147.0	14.3	31.6	109 ± 14	94 ± 25
8.- Barraganes 2 (Bar 2)	24.8	22.7	283.5	62.5	7.9	41.6	86 ± 45	83 ± 19
9.- Ballesteros-1 (Bll 1)	17.0	16.8	141.3	43.7	4.4	32.8	99 ± 36	67 ± 21
10.- Ballesteros-2 (Bll 2)	36.5	33.3	509.1	84.6	2.6	10.2	21 ± 7	28 ± 9
11.- Ballesteros-3 (Bll 3)	58.0	57.0	1592.4	147.6	1.5	3.3	18 ± 5	15 ± 1
12.- Ballesteros-4 (Bll 4)	68.0	67.0	3351.4	214.5	7.4	11.3	11 ± 2	10 ± 5
13.- Ballesteros-5 (Bll 5)	73.0	73.0	3381.9	213.5	7.0	10.7	9 ± 2	6 ± 0
14.- Ballesteros-6 (Bll 6)	35.0	28.0	394.3	77.2	5.6	25.0	52 ± 52	38 ± 10
15.- Fuentes-1 (Fu 1)	60.0	59.5	3327.0	216.8	6.6	10.1	82 ± 30	55 ± 8
16.- Fuentes-2 (Fu 2)	56.0	46.5	664.6	102.4	9.9	34.0	91 ± 97	53 ± 35
17.- Fuentes-3 (I) (Fu3-I)	141.0	128.5	13011.4	395.2	3.3	2.6	38 ± 6	24 ± 3
18.- Fuentes-3 (II) (Fu3-II)	46.0	50.5	1700.0	159.0	4.1	6.3	44 ± 6	36 ± 1
19.- Fuentes-4 (Fu 4)	35.0	34.5	667.6	95.2	7.0	23.8	95 ± 29	76 ± 13
20.- Las Zomas (Zoma)	39.0	39.0	960.3	113.9	8(15.1	17.4	90 ± 8	80 ± 12
21.- La Cruz (Cruz)	135.8	132.0	11816.3	399.2	24.0	19.9	78 ± 15	75 ± 7
22.- Lagunillo del Tejo (ltej)	86.0	83.0	5253.7	266.1	11.0	13.3	42 ± 5	35 ± 3
23.- El Tejo (Tejo)	150.0	145.0	16245.9	469.2	32.0	22.1	sd	sd
24.- La Parra (Parra)	112.0	105.0	8987.2	351.8	16.0	15.2	sd	sd
25.- La Llana (Llan)	105.0	100.0	8603.1	343.5	6.6	6.6	sd	sd
26.- Cardenillas (Card)	98.0	90.0	6921.3	315.0	12.0	13.3	sd	sd
27.- Lagunillo de las Cardenillas (lca	80.0	65.0	2363.7	185.6	6.0	9.2	sd	sd

Table 2: Diversity and density of zooplankton communities calculated from spring and autumn data for the different lakes. H' = whole diversity of the water column, H' mean = averaged diversity in the vertical profile, S = number of species of zooplankton, E = Equitability.

	Spring				Autumn			
	H'	H' mean	S	E	H'	H' mean	S	E
1.- Arcas-1	1.45	1.43	10.00	0.44	2.26	2.25	13.00	0.61
2.- Arcas-2 (I)	1.84	1.01	14.00	0.48	0.69	0.80	11.00	0.20
3.- Arcas-2 (II)	0.95	0.95	12.00	0.26	1.26	1.26	12.00	0.35
4.- Arcas-3 (II)	1.69	1.65	11.00	0.49	1.61	1.78	18.00	0.39
4'.- Arcas-3 (I)	--	--	--	--	1.37	1.37	13.00	0.37
5.- Arcas-4	0.36	0.36	10.00	0.11	1.86	1.86	17.00	0.46
6.- Rincón	0.89	0.72	16.00	0.22	2.35	2.18	19.00	0.55
7.- Barraganes-1	1.01	1.26	11.00	0.29	1.74	1.65	5.00	0.75
8.- Barraganes-2	1.30	1.46	16.00	0.33	2.47	2.23	17.00	0.60
9.- Ballesteros-1	1.51	1.48	16.00	0.38	1.54	1.83	14.00	0.40
10.- Ballesteros-2	1.83	1.77	13.00	0.49	3.09	2.95	14.00	0.81
11.- Ballesteros-3	1.67	1.69	9.00	0.53	1.78	1.78	16.00	0.45
12.- Ballesteros-4	1.71	1.40	10.00	0.51	1.90	1.75	17.00	0.46
13.- Ballesteros-5	1.49	1.52	16.00	0.37	1.99	2.15	24.00	0.43
14.- Ballesteros-6	0.29	0.30	8.00	0.10	1.30	1.51	14.00	0.34
15.- Fuentes-1	1.88	1.60	7.00	0.67	2.50	2.38	9.00	0.79
16.- Fuentes-2	0.54	1.05	8.00	0.18	2.03	1.92	17.00	0.50
17.- Fuentes-3 (I)	0.91	1.25	7.00	0.32	2.11	2.11	7.00	0.75
18.- Fuentes-3 (II)	1.33	1.14	7.00	0.47	1.63	1.59	13.00	0.44
19.- Fuentes-4	1.31	1.17	8.00	0.44	2.16	1.84	13.00	0.58
20.- Las Zomas	1.48	1.53	6.00	0.57	2.24	2.06	15.00	0.57
21.- La Cruz	2.26	1.34	10.00	0.68	1.27	1.56	26.00	0.27
22.- Lagunillo del Tejo	1.21	1.30	19.00	0.28	0.31	0.90	20.00	0.07
23.- El Tejo	2.07	1.57	9.00	0.65	1.73	1.42	24.00	0.38
24.- La Parra	1.86	1.26	9.00	0.59	2.41	1.83	12.00	0.67
25.- La Llana	2.41	2.24	16.00	0.60	2.97	2.96	18.00	0.71
26.- Cardenillas	2.36	1.09	12.00	0.66	1.04	1.76	14.00	0.27
27.- Lagunillo de las Cardenillas	0.99	0.99	13.00	0.27	1.81	1.69	14.00	0.48

correlation with diversity (see table 3) but in early autumn these parameters were uncorrelated.

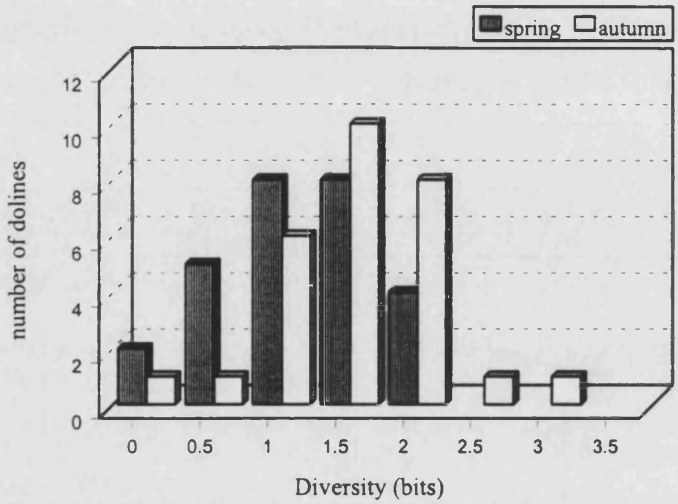


Figure 2: Frequency of diversity index values in the different lakes/basins in spring and early autumn.

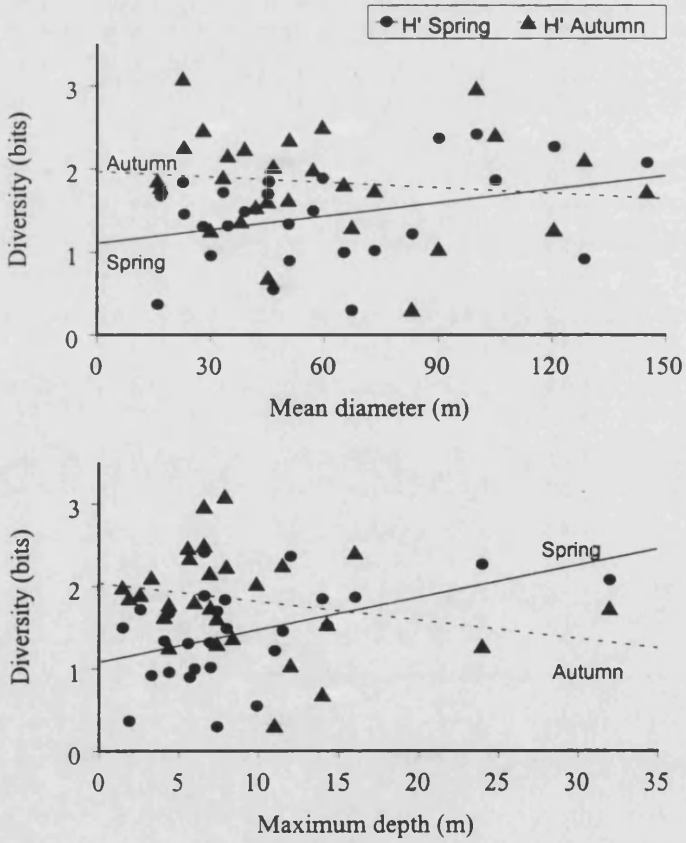


Figure 3: Relations between zooplankton diversity and mean diameter (upper graphic) or maximum depth (lower graphic) for the different dolines in spring and early autumn. Lines show correlations for both periods.

Correlations

Significant correlations ($p \geq 0.05$) between several parameters derived from the zooplanktonic communities and other biological and lake morphometry features are shown in tables 3 and 4.

Table 3: Significant correlation coefficients ($p \geq 0.05$) among several biological features and trophic indicators in two seasons; in autumn (upper hemimatrix) and in spring (lower hemimatrix). Non significant coefficients are not printed.

	APR	ALR	AEg	AZo	AH'	AEq	AIFO	Asp	ACh	ASe	Autumn
Spring Pl Rot	1				**-0.73**	**-0.68**					Autumn Pl Rot
Spring Lit Rot		1	**-0.32**						**0.86**	**-0.43**	Autumn Lit Rot
Spring Eggs			1				**-0.36**	**-0.48**			Autumn Eggs
Spring zoopl				1	**-0.74**	**-0.68**					Autumn zoopl
Spring Div					1	**0.90**					Autumn Div
Spring Equit	**-0.37**	**-0.33**		**-0.39**	**0.94**	1		**-0.45**			Autumn Equit
Spring IFO			**-0.43**				1				Autumn IFO
Spring n° spp.								1	**0.39**		Autumn n°spp.
Spring Chlo a	**0.37**			**0.38**					1		Autumn Chlo a
Spring Secchi					**0.44**	**0.38**				1	Autumn Secchi
Spring	SPR	SLR	SEg	SZo	SH'	SEq	SIFO	Ssp	SCh	SSe	

Table 4: Significant correlation coefficients ($p \geq 0.05$) among several biological features and some morphometrical characteristics of the lakes. (ns) means non-significant correlation coefficient. SPR, SLR, SEg, SZo, SIFO, Ssp, SCh (from spring); and, APR, AEg, AZo, AH', AEq, Asp, ACh (from autumn) did not show significant coefficients, (see table 3 for abbreviations).

	Mean diam	Volume	Perim	Z max	Z rel	slope 10m	slope 5m
Spring Diversity	**0.34**	ns	**0.40**	**0.47**	ns	**0.51**	ns
Spring Equitability	**0.34**	**0.37**	**0.40**	**0.48**	ns	**0.50**	**0.37**
Spring Secchi	**0.54**	ns	**0.56**	ns	ns	ns	ns
Autumn litt rot	ns	ns	ns	**-0.37**	**-0.39**	ns	**-0.54**
Autumn IFO	**0.57**	ns	ns	ns	ns	ns	ns
Autumn Secchi	**0.45**	ns	**0.47**	ns	ns	ns	ns

Chlorophyll a, and Secchi disk depth are among the main indicators of trophic degree, although in our study there was no significant correlation between them. The values of Secchi depth in spring and autumn were correlated with one-another, and in both seasons there was also correlation with lake depth. In autumn, moreover, correlation also existed with lake diameter and perimeter. Secchi depth was positively correlated with diversity and equitability in spring, but not in autumn when the only significant correlation was with littoral rotifers. Chlorophyll a was positively correlated with total zooplankton and planktonic rotifer abundance in spring, whereas in autum it was only correlated with littoral rotifer abundance (Table 3).

Due to steep stratification in autumn, which in the largest and deepest lakes promotes the presence of a high number of organisms and strong chlorophyll a concentration in the bottom/oxicline layers, the results of these correlations are not so interesting as in spring. In this season diversity and equitability were significantly correlated with most morphometric parameters (Table 3).

Principal Component Analysis (PCA)

Several PCA's have been performed in order to analyze the data, one each on the physico-chemical variables measured in the lakes or basins in spring (PCA-1) and in autumn (PCA-2), and a further two on the zooplankton densities in the lakes or basins, one with data of spring and autumn (PCA-3) and the other with only the spring data (PCA-4). The variance explained by each of the main factors extracted by means of PCA in the different analyses performed is shown in Table 5. In the two analyses performed on physico-chemical parameters (spring and autumn, Fig.4), the first principal component clearly differentiated two groups of lakes or basins; namely the lakes with the dolomite solution (zone C), from the rest of lakes (zones A and B). In this second group a weaker segregation between zones A and B can also be observed, especially in the analysis with autumn measurements (PCA-2), where the zone A lakes are situated in the more negative part of this axis, opposite those from zone C. This component (Table 6) is positively related to alkalinity, pH and diameter, and negatively related to conductivity, sulphates and calcium. The second principal component is also related to the ionic composition of the lakes.in spring when data on concentrations of main cations were available, whereas in autumn without those variates it was related to oxygen concentrations. The third principal component was mainly related to the trophic status of the lakes in both analyses (Table 6).

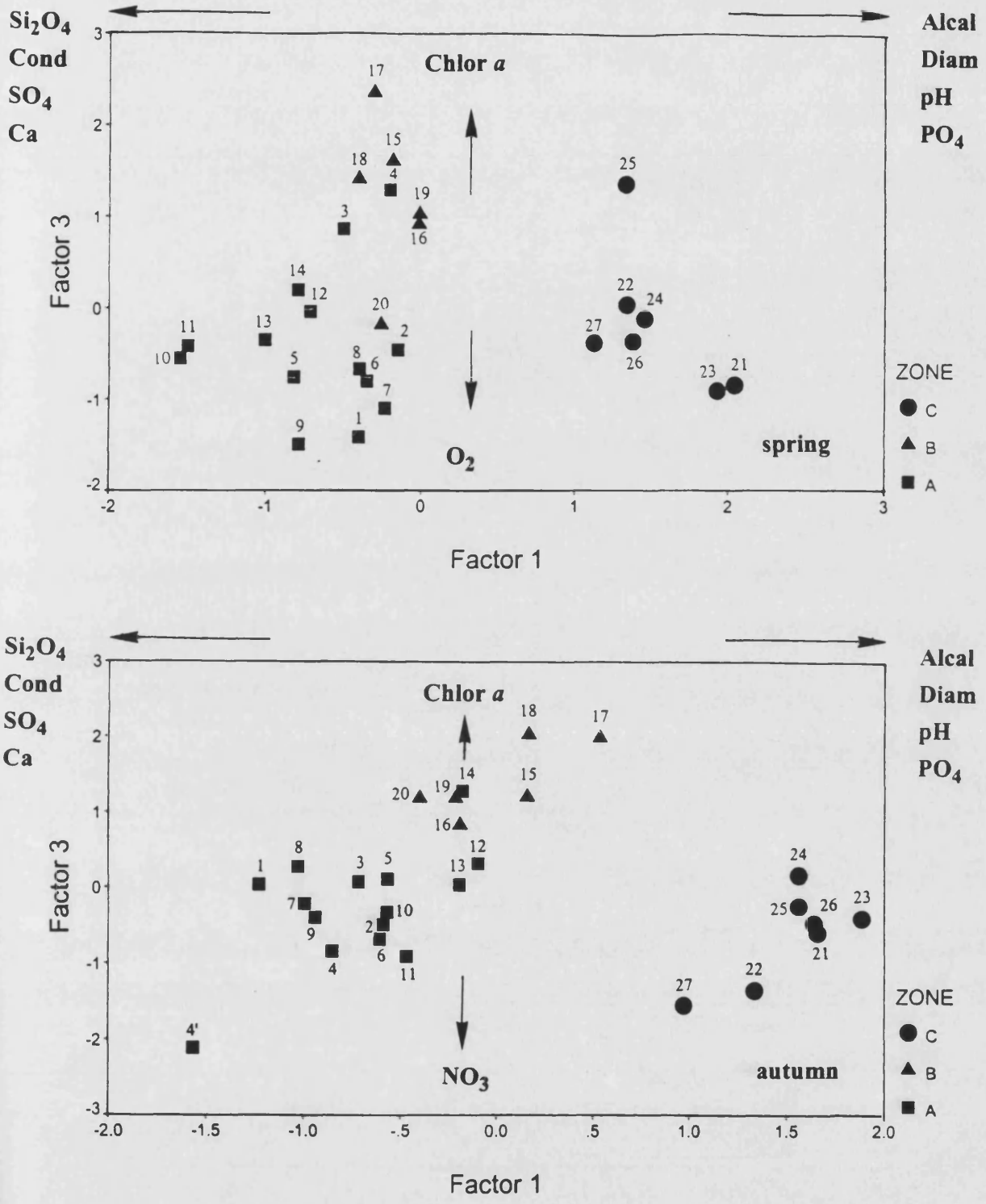


Figure 4: Upper graph: Relative position of each lake or basin in the plane determined by the first and third principal factors extracted by PCA-1 (Physicho-chemical parameters from spring). Lower graph: Relative position of each lake or basin in the plane determined by the first and third principal factors extracted by PCA-2 (Physicho-chemical parameters from early autumn). Principal component scores as coordinates.

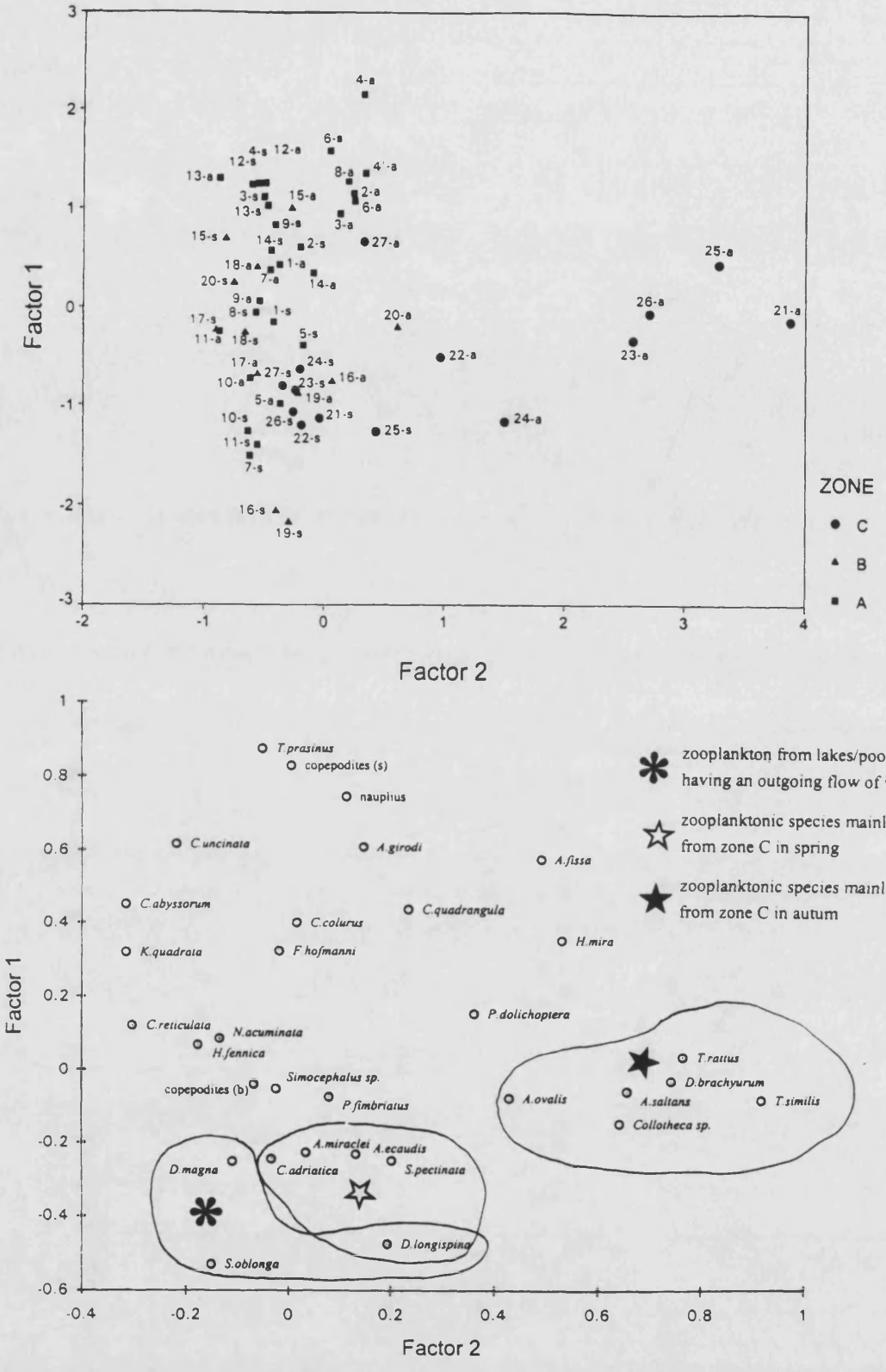


Figure 5: Upper graph: Relative position of each lake or basin in spring (s) and autumn (a) in the plane determined by the first and second principal components extracted by PCA-3 (zooplankton densities from spring and autumn together). Principal component scores as coordinates. Lower graph: Relative position of each zooplankton species in the plane determined by the first and second principal components extracted by PCA-3 (zooplankton densities from spring and autumn together). Component loadings as coordinates.

Table 5: Percentage of variance explained by the first three factors extracted in each of the different PCAs performed; PCA-1, on physico-chemical parameters from spring; PCA-2, on physico-chemical parameters from autumn; PCA-3, on species densities from spring and autumn together; and PCA-4, on species density from spring. Cum pct corresponds with the percentage of variance accumulated.

	Factor 1	Factor 2	Factor 3	Cum pct
PCA-1	33.3	21.9	16.4	71.6
PCA-2	32.1	19.6	16.6	68.3
PCA-3	15.2	13.3	8.1	36.6
PCA-4	21.7	12.4	10.8	45

Table 6: Loadings or correlation coefficients of the first three factors of PCA-1 and PCA-2, physical and chemical features with the highest coefficients for each factor are indicated in bold.

	Spring (PCA-1)			Autumn (PCA-2)		
	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
Alcalinity	**-0.63**	-0.13	0.05	**0.44**	-0.21	0.11
Cl	0.32	**0.64**	0.14	-0.10	0.37	**0.80**
Chlor a	-0.13	-0.10	**0.47**	-0.20	-0.05	**0.65**
Cond	0.96	-0.15	-0.03	**-0.92**	0.31	0.17
Mean diam	**-0.67**	0.44	-0.29	**0.79**	0.17	0.06
NH3	-0.25	-0.28	-0.13	0.26	**0.51**	-0.12
NO2	-0.01	-0.08	**0.45**	-0.10	**0.67**	-0.37
NO3	0.13	**-0.74**	-0.33	-0.25	0.10	**-0.92**
O2	-0.33	0.08	**-0.66**	0.37	**0.69**	-0.13
O2 Sat	-0.26	0.30	**-0.76**	**0.48**	**0.55**	-0.17
pH	**-0.75**	**0.56**	0.05	**0.87**	-0.09	0.37
PO4	**-0.83**	0.21	0.22	**0.68**	**0.52**	0.08
SI2O5	**0.69**	-0.28	-0.02	**-0.82**	-0.05	0.34
SO4	**0.96**	-0.15	-0.04	**-0.94**	0.27	-0.03
Temp	**0.88**	0.01	-0.25	**0.40**	**-0.71**	0.26
Zmax	**-0.74**	-0.26	0.26	**0.48**	**-0.51**	**-0.40**
Zrel	-0.08	**-0.64**	**0.51**	-0.26	**-0.64**	**-0.44**
Ca	**0.92**	-0.31	-0.10	--	--	--
K	0.40	**0.73**	0.28	--	--	--
Mg	**0.48**	**0.77**	0.27	--	--	--
Na	**0.50**	**0.74**	0.26	--	--	--
Slope5	-0.25	**-0.85**	0.26	--	--	--

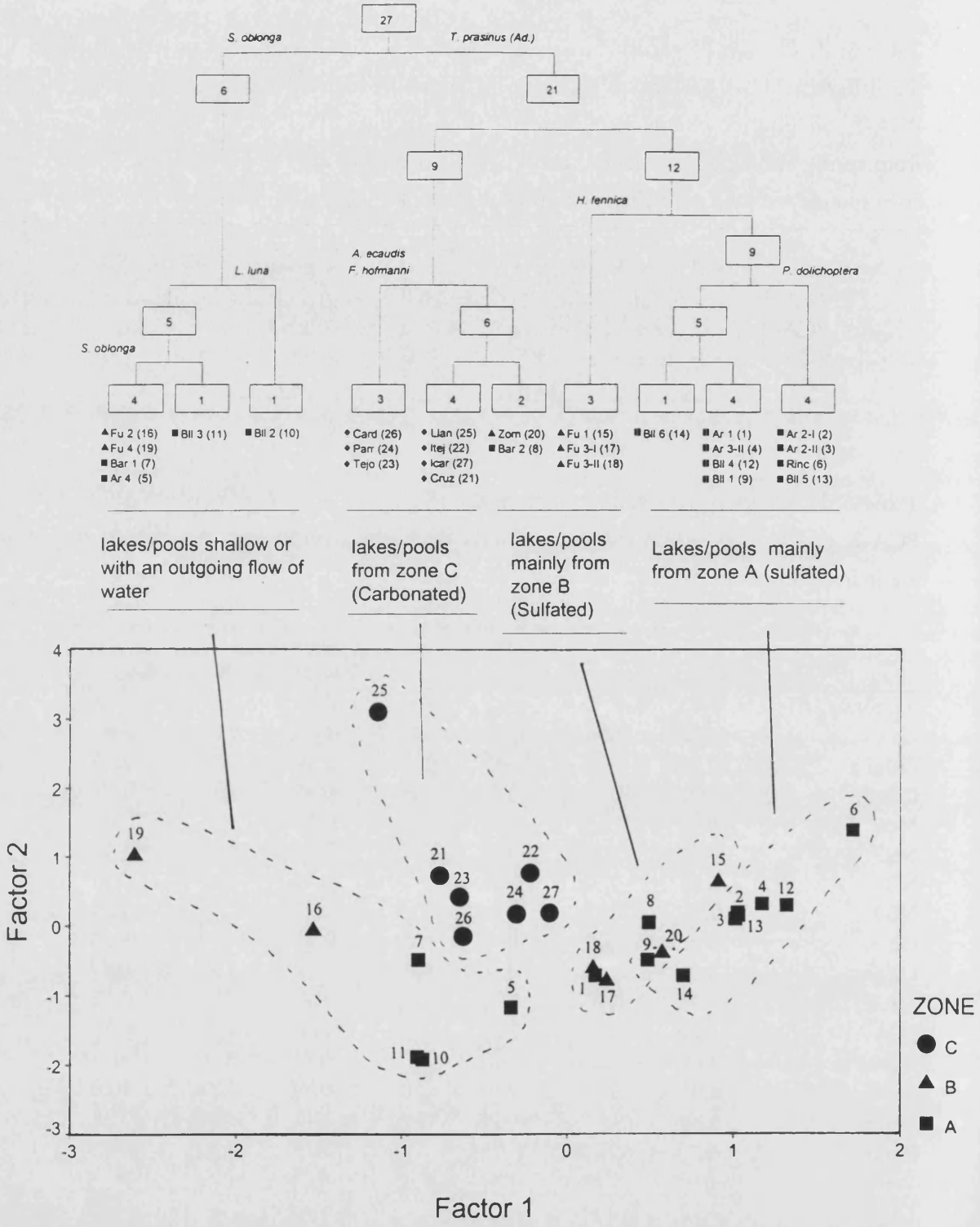


Figure 6: Cluster obtained by TWINSPAN performed on planktonic and littoral species from spring samples of the different lake basins. The main groups of lakes obtained in this analysis as well as the indicator species responsible for each clustering are shown on the graph.

Figure 7: Relative position of each lake or basin in the plane determined by the first and second principal components extracted by PCA-4 (zooplankton densities from spring). Principal component scores as coordinates.

The first factor of PCA-3, performed on all zooplankton samples from spring and autumn together, clearly separated from the rest (in the negative part of the axis) the very shallow lakes plus the lakes having subaquatic water sources giving an appreciable outflow (Fig.5). The second factor separated the distinct zones as well as autumn from spring samples, especially samples from the dolomitic substrate (zone C) in autumn, by situating autumn and zone C samples mainly in the positive part of this axis. Figure 5, shows the relative position of the different planktonic species considered in this analysis in the plane defined by the first and second factors of PCA-3. Several groups of species can be recognized with respect to these factors: (1) a group of species characteristic to zone C in early autumn, (2) a group of two species characteristic to lakes with water sources, (3) a group of species from zone C in spring and (4) a general group of widespread species which are more frequent in zone A (zone A contains the largest amount of lakes/pools). Thus the first principal component could separate the more general species from the more indicative or local species and order the communities of zone A. The second principal component differenciates the species assemblages of zone C from the rest of the zones, especially in autumn.

An additional analysis, PCA-4, was performed on zooplankton densities but only from spring (Fig. 6). Species assemblages from zone C (lakes with dolomitic substrate), which in the analysis of the total number of samples came very close together, are again ordered by the second principal component in PCA-4 and discriminated from the communities of the rest of the zones. Principal component 1, then, orders assemblages in zones A and B and also segregates these two zones into two main groups.

TWINSPAN

The data on spring zooplankton densities was also analyzed by means of clusters formed with TWINSPAN. In this case, the data used was the presence/ausence matrix corresponding to all the species found in the samples, also including littoral species. Planktonic species were, however, dominant due to the way the samples were collected (see Methods). The results of this analysis are remarkably similar to those obtained with PCA-4 (Fig. 7).

The primary division separates out a group formed of six lakes/pools characterized by their shallowness or by their having an outgoing flow of water; the species characteristic of this division was *Synchaeta oblonga*, while the copepod *Tropocyclops prasinus* (adults) -a widespread species- characterized the rest of lakes (21). The next division separates two sets of lakes, in the first set we can separate a group formed by the lakes from zone C (carbonated waters) among which a subgroup of

three lakes was characterized by the presence of *Ascomorpha ecaudis* and *Filinia longiseta*. The other division is made up of 12 lakes. In this group (12 lakes) the following division separated out a set of lakes from zone B characterized *by Hexarthra fennica*. The last group is composed of the majority of lakes from zone A, including a subgroup of 4 lakes showing the presence of *Polyarthra dolichoptera*.

Apart from the first division separating shallow lakes and lakes with outflowing water, the rest of the lakes can be grouped approximately according to the different zones sampled. This may then be an indicator of the importance of the mineralogical composition of the substrate.

DISCUSSION

Samples integrating the vertical profiles and taken over a short period of time from a number lakes within a quite homogeneous area could help to identify the main factors involved in the distribution of the zooplankton communities. When seasonal variation is eliminated, changes in temperature and oxygen are more related to the morphometrical characteristics of the lakes.

Chlorophyll a has been considered to be the most relevant parameter for defining the trophic state of a lake (Schröder, 1991), and it usually has a great effect on Secchi disk depth. In our samples, however, these two parameters were not significantly correlated. This fact could be explained by one of several reasons: (1) turbidity due to mineral matter is important in these lakes (2) most of the lakes are stratified, showing a deep chlorophyll maximum far below Secchi depth (Miracle *et al.*, 1993) and (3) in the shallow lakes Secchi disk depth may not be readable due to the limited depth of the lake. In spite of the latter considerations, it is remarkable that Secchi depth should be correlated with morphometrical parameters. Greater dolines showed, in general, higher transparency, whereas on the other hand only the mean depth was positively correlated to chlorophyll content, indicating the important effect of stratification which promotes the formation of a deep chlorophyll maximum.

Correlation coefficients furthermore revealed some interesting relationships with morphometric parameters; such parameters (Hakanson, 1990) are very important since they affect eutrophication and thus the planktonic community. In fact, Patalas (1971) in a study of 45 lakes in the experimental lake area, Ontario (Canada), distinguished 4 types of zooplankton communities, each of them characteristic of a group of lakes of specific size and depth. In our karstic lakes, diversity and evenness of spring communities increase along with the size of the lakes, i.e. with diameter, surface, perimeter and also with depth. In autumn, however, this is not true since high

stratification in the larger and deeper lakes favours the formation of peaks of abundance of given species in the interfaces, which reduce eveness, even though the number of species is higher. If we were to consider lakes as islands, the theory of islands (McArthur & Wilson, 1967) can be applied to our data when littoral species are not taken into consideration, since there is a trend towards a higher number of species in larger lakes. Nevertheless, this relationship is not a simple one, as has been discussed elsewhere (Fryer, 1985). Diversity in spring was lower than in autumn, with the autumn diversity showing a greater variability. This is consistent with the theory of plankton succession and the wider degree of vertical heterogeneity attained at the end of the stratification period which increases niche availability for zooplankton (Miracle, 1977).

Table 7: Correlation coefficients between first and second factor obtained in PCA-4 (species from spring and autumn together) and the different physico-chemical parameters measured in spring and autumn. (ns) means non-significant correlation. Cl, K, Mg, Na, NH3 and NO2 showed non-significant correlations with factors 1 and 2.

	spring		autumn	
	Fac1ssp	Fac2spp	Fac1ssp	Fac2spp
Alcalinity	**-0.3811**	**0.6076**	ns	**0.588**
Ca	**0.4233**	**-0.5871**	ns	ns
Chlor_a	**0.3947**	ns	**0.4183**	ns
Cond	**0.3926**	**-0.5734**	ns	**-0.7131**
Mean diam	ns	ns	ns	**0.5431**
NO3	ns	**-0.442**	ns	ns
O2	ns	ns	**-0.4691**	ns
pH	ns	**0.5153**	ns	**0.6906**
PO4	**-0.439**	**0.6081**	**-0.4504**	**0.4277**
O2 Sat	ns	ns	**-0.5057**	ns
SI2O5	ns	ns	**0.6411**	**-0.4889**
SO4	**0.3928**	**-0.5609**	ns	**-0.8071**
Temp	ns	**-0.4119**	ns	**0.3725**
ZMax	ns	ns	ns	**0.5492**

Cl, K, Mg, Na, NH3, and NO2 were non significantly correlated.

The density of planktonic rotifers and zooplankters in spring was not in general significantly correlated with morphometry, whereas in autumn it was correlated with the average depth (Z med), this can be explained if we assume that, by the end of stratification, lakes with higher Z med have probably been strongly stratified developing

higher populations in their oxicline layers. The littoral rotifer abundances were negatively correlated with depth and slope in autumn, but this did not happen in spring; this effect could be explained through the possibility that in spring the macrophytic community might be underdeveloped. The samples used for this work, collected in the centre of the lakes, were dominated by planktonic species, and only a few littoral species appeared in the samples from some water bodies with macrophytes, but these were never significant even in the shallow sites. Thus, in our results littoral fauna does not have the importance that it has in other works using net samples (Morales-Baquero *et al.*,1989; Jersabeck, 1995; Langley et al ,1995)

The clusters grouping our doline lakes obtained with Twinspan are quite similar to the ordering of these lakes by PCA. Lakes characterized by zooplankton species abundances become grouped according to the different zones which harbour waters of different ionic composition. When a PCA is performed with physico-chemical parameters, the most important source of variation is that corresponding to a different composition of the substrate, and mainly with the carbonated versus sulphated-silicated waters. Next, to a secondary extent, trophic gradients also play an important role in explaining variances between lakes. When we performed the PCA with species densities, the order of importance of these two sources of variation was reversed. This is clearly seen in table 7 where we present the correlation coefficients between the principal components extracted from the species-sites matrix, and their correlations with the physico-chemical parameters. The first of these principal components is mainly correlated positively with chlorophyll and negatively with dissolved phosphate, and the second is strongly correlated with the main features which differenciate the larger dolomite solution lakes from the rest, mainly the carbonate-sulphate dichotomy, as well as diameter and depth. Thus, for zooplankton communities of these lakes trophic factors are more important than mineralization. The importance of trophic state has also been shown in other works (Karabin, 1983; Radwan & Popiolek, 1989; Langley *et al.* 1995). The aforementioned correlations of the first principal component are weaker than those of the second component. This means than other factors beside those measured influence the ordering of zooplankton assemblages in this first component. One of these factors is the presence of bottom springs in several dolines which provoke turbulence and also a large amount of suspended sediment (in fact these lakes presented a different colour -clear blue- at the sampling time), this situation lends special characteristics to the zooplanktonic communities of these dolines. This factor, together with shallowness, was responsible for the first division of the lakes with the Twinspan analysis and seems to be important in the PCA with species abundances. The first component of this analysis mainly reflects the bipolarity between the more infrequent species in our data

(those typical of the more scarce shallow water bodies and spring pools) and the more common species found in almost all the lakes. Among the latter, those with higher loadings, such as *Tropocyclops prasinus, Anuraeopsis fissa* and *Asplanchna girodi* are the indicators of a higher trophic level in the study sites.

It is clear from these results and from those of other authors (e.g. Pontin and Langley, 1993; Jersabek, 1995) that the ordering of sampling sites according to their zooplankton species abundances matches the ordering obtained with limnological parameters alone. The parameters associated with trophic level (chlorophyll) and mineralization (pH and conductivity) are always important factors which in many cases are influenced by variability of lake/pool size and depth.

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APPENDIX

Appendix : Density of planktonic and littoral organisms found in plankton samples from the different dolines in spring

	Afis	*Amir*	*Aeca*	*Agir*	*Bdel*	*Bdep*	*Bqua*	*Cgib*	*Ccat*	*Cfor*	*Cadr*	*Cunc*	*Cobt*	*Edil*	*Fhof*	*Hfen*	*Hmir*	*Kqua*	*Lacu*	*Lbul*	*Lclo*	*Lfle*	*Lfur*	*Luna*	*Lris*	*Lnan*	*Lohi*	*Lpat*	*Lsal*	*Mmuc*	*Nacu*
1.- Ar 1	0.3	0.0	0.0	0.0	1.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	69.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2.- Ar2-I	1212.9	0.0	0.0	0.0	16.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	1879.2	0.0	0.3	552.8	0.0	0.0	0.0	0.3	0.0	0.3	0.0	0.0	0.0	0.3	0.0	0.0	0.0
3.- Ar2-II	3332.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	6.0	7.0	0.0	11.0	0.0	0.0	152.0	0.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4.- Ar3-II	177.3	0.0	0.0	40.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	8.3	1.3	0.0	2.0	0.0	0.0	775.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4'.- Ar 3-I																															
5.- Ar 4	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
6.- Rinc	32345.0	0.0	0.0	59.0	5.0	0.3	0.3	0.0	0.0	0.0	0.0	5.3	0.3	0.0	5048.7	0.0	5.7	416.7	0.0	0.0	1.7	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.3	0.0	0.0
7.- Bar 1	0.0	0.0	0.0	0.0	0.3	0.7	0.0	0.3	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
8.- Bar 2	44.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	0.7	0.0	5.7	2.7	0.0	0.0	0.0	0.0	2.7	690.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.3
9.- Bll 1	2.5	0.0	0.0	0.0	33.0	0.0	0.0	0.0	0.0	0.0	0.0	5.5	14.0	0.0	1.5	0.0	0.0	6.0	0.0	0.0	0.0	0.0	0.0	0.5	5.5	0.0	0.0	0.5	1.0	0.0	0.0
10.- Bll 2	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.5	0.0	1.0	0.5	0.5	0.0	0.0	0.0
11.- Bll 3	0.5	0.0	0.0	0.0	2.5	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12.- Bll 4	773.3	0.0	0.0	13.7	33.7	0.0	0.0	0.0	0.0	0.0	0.0	5.0	0.3	0.0	1.0	0.0	0.0	1807.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0
13.- Bll 5	83.7	0.0	0.0	7.3	0.7	0.0	0.0	0.0	0.0	0.3	0.0	9.3	0.0	0.0	0.7	0.3	0.0	1317.3	0.3	0.0	1.7	0.0	0.0	2.3	0.0	0.0	0.0	10.3	0.0	0.0	0.0
14.- Bll 6	3.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	64.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15.- Fu 1	16.7	0.0	0.0	14.0	1.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.7	290.7	0.0	48.7	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
16.- Fu 2	2.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
17.- Fu3-I	0.5	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.0	0.0	821.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18.- Fu3-II	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	3.0	0.0	230.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
19.- Fu 4	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0
20.- Zoma	0.0	0.0	0.0	9.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	481.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
21.- Cruz	2.3	91.5	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	91.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
22.- Itej	37.7	33.0	0.0	0.0	10.7	0.0	0.0	0.7	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	3.3	2526.0	0.0	0.3	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.7	18.0	0.0	0.0
23.- Tejo	4.5	0.0	38.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
24.- Parra	20.0	0.0	36.3	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
25.- Llan	50.7	0.0	35.3	12.7	1.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	199.7	0.0	0.0	1.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
26.- Card	10.7	0.0	0.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
27.- Icar	3.5	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.5	1815.9	0.0	0.0	1.0	0.0	0.0	0.5	0.0	0.0	0.0	17.0	13.5	0.0	0.0

	Pdol	*Sobl*	*Spec*	*Tpat*	*Tsim*	*Tsp1*	*Tpoc*	*Ttre*	*cicn*	*cicp*	*cicg*	*Caby*	*Pfim*	*Tpra*	*dian*	*diac*	*Cqua*	*Cret*	*Csph*	*Dlon*	*Dmag*	*Dbra*	*Lqua*	*Sisp*	*chyd*	*chao*	*gast*
1.- Ar 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	34.0	0.0	1.0	0.0	5.3	0.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.3	0.0
2.- Ar2-I	7.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	309.9	89.0	0.0	0.5	0.0	10.8	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
3.- Ar2-II	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	422.0	201.0	0.0	8.0	0.0	36.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4.- Ar3-II	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	238.7	93.7	0.0	7.3	0.0	77.7	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4'.- Ar 3-I																											
5.- Ar 4	8846.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0	394.0	84.0	2.0	0.0	0.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	6.0	0.0
6.- Rinc	580.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	486.0	98.7	0.0	1.0	0.0	39.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
7.- Bar 1	0.3	124.0	0.0	0.0	0.0	0.0	1.0	0.0	21.0	1.7	0.0	0.7	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
8.- Bar 2	0.3	0.0	0.0	0.0	0.0	0.3	1.0	0.0	162.3	107.3	0.0	0.0	0.0	12.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0
9.- Bll 1	253.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	431.0	294.0	0.0	1.0	0.0	79.5	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0
10.- Bll 2	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	71.5	1.5	6.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	8.0	0.0	0.0	0.0	0.0	2.5	0.0
11.- Bll 3	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	122.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	64.5	0.0	0.0	0.0	0.0	2.0	0.0
12.- Bll 4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	603.7	137.3	10.7	7.0	0.0	263.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13.- Bll 5	45.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	741.0	280.7	12.7	0.7	0.0	117.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14.- Bll 6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15.- Fu 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	170.3	72.3	5.7	11.0	0.0	67.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0
16.- Fu 2	0.7	530.7	0.0	0.0	0.0	0.0	0.0	0.0	11.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	34.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
17.- Fu3-I	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	123.5	28.0	1.0	1.0	0.0	7.5	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18.- Fu3-II	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	144.5	39.0	1.0	0.0	0.0	12.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0
19.- Fu 4	3.5	161.5	0.0	0.0	0.0	0.0	0.0	0.0	9.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	126.5	0.0	0.0	0.0	0.0	0.0	0.0	0.5
20.- Zoma	18.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	393.7	0.0	0.0	28.0	0.0	67.7	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
21.- Cruz	179.3	0.0	0.0	0.0	2.8	0.0	0.0	0.0	60.8	6.3	12.0	0.3	0.0	1.3	0.0	0.0	0.0	0.0	0.0	6.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
22.- Itej	500.3	24.7	21.0	0.0	0.0	0.0	0.0	0.0	63.7	10.3	0.0	0.3	0.0	0.3	0.7	0.3	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
23.- Tejo	55.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0	72.5	2.5	11.0	4.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
24.- Parra	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	137.0	15.0	43.7	2.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
25.- Llan	33.0	0.0	5.3	0.0	2.7	0.0	0.0	0.0	0.0	21.3	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0	7.0	0.0	3.7	0.0	0.0	0.0	0.0	0.3
26.- Card	6.7	0.0	0.3	0.0	0.3	0.3	0.0	0.0	25.3	0.0	11.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
27.- Icar	0.0	0.0	60.0	0.0	0.0	0.0	0.0	0.0	242.0	20.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix : Density of planktonic and littoral organisms found in plankton samples from the different dolines in autumn

	AFIS	AMIR	AECA	AOVA	ASAL	AGIR	BDEL	BDEP	BQUA	CEGI	CECA	CEFO	CEME	CEPH	COAD	COOB	COUN	COLL	EUDI	FIHO	HEEH	HEFE	HEMI	KEQU	LEAC	LEBU
1.- Ar 1	26.3	0.0	0.0	0.0	0.0	13.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0	190.7	0.0	0.0
2.- Ar2-I	7637.7	0.0	0.0	0.0	0.0	50.7	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	3.3	0.0	0.0	59.3	0.0	0.0	39.7	0.0	0.0	0.0
3.- Ar2-II	2124.0	0.0	0.0	0.0	0.0	9.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.0	0.0	0.0	0.0	0.0	0.0	68.0	0.0	0.0	1.0
4.- Ar3-II	4607.7	0.0	0.0	0.0	0.0	11.0	0.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	4.3	9.7	0.0	0.0	0.0	0.0	0.0	238.7	15.0	0.0	2.3
4'.- Ar 3-I	3660.0	0.0	0.0	0.0	0.0	6.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	4.0	0.0	0.0	0.0	0.0	0.0	356.0	16.0	0.0	1.0
5.- Ar 4	6.0	0.0	0.0	0.0	0.0	0.0	8.0	0.0	0.0	8.0	0.0	0.0	0.0	4.0	0.0	2.0	10.0	0.0	1.0	0.0	0.0	0.0	0.0	4.0	0.0	12.0
6.- Rinc	4.7	0.0	0.0	0.0	0.0	36.3	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	446.0	18.7	0.0	6.0
7.- Bar 1	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.3	0.0	0.0
8.- Bar 2	1046.7	0.0	0.0	0.0	0.0	21.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	2.7	0.0	0.0	0.0	0.0	0.0	161.3	509.7	0.0	0.0
9.- Bll 1	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	11.5
10.- Bll 2	0.5	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.5
11.- Bll 3	1.0	0.0	0.0	0.0	0.0	0.0	76.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	26.0
12.- Bll 4	1066.7	0.0	0.0	0.0	0.0	7.3	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	5.3	0.0	0.0	6.0	0.0	0.0	0.7	6.0	0.0	0.0
13.- Bll 5	16.3	0.0	0.0	0.0	0.0	0.3	4.3	0.7	0.7	0.0	0.0	0.0	0.0	0.3	0.0	6.3	24.0	0.0	0.0	0.0	0.0	0.0	1.3	350.0	0.0	8.3
14.- Bll 6	1310.3	0.0	0.0	0.0	0.0	1.7	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	3.3	0.3	0.0	0.3	0.0	0.0	0.0	24.7	0.0	0.0
15.- Fu 1	415.0	0.0	0.0	0.0	0.0	4.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	260.3	5.3	0.0	0.0
16.- Fu 2	0.0	0.0	0.0	0.0	0.0	4.0	4.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	1.0	0.0	0.0	0.0	0.0	0.0	0.0	26.0	0.0	0.0
17.- Fu3-I	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	19.4	50.4	0.0	0.0
18.- Fu3-I	0.0	0.0	0.0	0.0	0.0	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.6	0.0	0.0	23.0	768.2	0.0	0.0
19.- Fu 4	0.3	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	2.3	1.7	0.0	0.0	0.3	0.0	0.0	1.0	49.0	0.0	0.0
20.- Zoma	0.7	0.0	0.0	0.0	0.0	5.7	3.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	1.3	11.3	0.0	0.0	0.0	0.0	0.0	0.0	660.0	0.0	0.0
21.- Cruz	5526.8	0.8	0.0	0.0	88.8	0.6	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	5.0	0.0	0.0	1.2	0.0	113.0	11.0	0.0	0.0
22.- Itej	17878.0	0.0	0.0	0.0	2.0	0.0	4.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0	1.0	0.0	0.0	0.0	0.0	488.7	0.3	0.0	2.7
23.- Tejo	1128.0	0.0	11.2	0.0	15.2	10.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	3.2	0.0	0.0	0.8	0.0	39.0	0.0	0.0	0.0
24.- Parra	21.3	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	6.5	0.0	0.0	0.0	0.0	42.7	0.0	0.0	0.0
25.- Llan	462.0	0.0	0.0	0.0	0.0	11.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	137.3	1.3	2.0	0.0
26.- Card	6118.7	0.0	0.0	5.3	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.3	0.3	0.0	3.3	0.3	0.0	0.0
27.- Icar	2016.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0	1792.3	0.0	0.0	0.0

	LECL	LEFL	LEFU	LEHA	LEHO	LEIM	LEQU	LELU	LELS	LENA	LEOH	LEPY	LPTR	LPPA	LOSA	MACO	MONN	MYMU	NOAC	PODO	SYOB	SYPE	TEPA	TRIN	TRSI	TRRA
1.- Ar 1	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0
2.- Ar2-I	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	123.7	0.0	0.0	0.0	0.0	0.0	0.0
3.- Ar2-II	2.0	1.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	28.0	0.0	0.0	0.0	0.0	0.0	0.0
4.- Ar3-II	0.3	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.7	0.0	0.0	0.3	0.0	0.3	0.0	0.0	0.0	0.0	41.7	0.0	0.0	0.0	0.0	0.0	0.0
4'.- Ar 3-I	0.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0
5.- Ar 4	6.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	2.0	0.0	1000.0	2.0	0.0	0.0	0.0	0.0	0.0
6.- Rinc	5.3	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	77.3	0.0	0.0	0.3	0.0	0.0	0.0
7.- Bar 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1040.7	0.0	0.0	0.0	0.0	0.0	0.0
8.- Bar 2	1.0	0.3	0.0	0.0	0.0	0.0	0.0	1.0	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	285.3	0.0	0.0	0.0	0.0	0.0	0.0
9.- Bll 1	0.0	2.0	0.0	0.0	1.0	0.0	0.0	1.5	0.0	1.0	0.0	0.0	0.0	0.0	5.5	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
10.- Bll 2	5.0	0.0	0.0	0.0	13.0	0.0	0.0	35.0	0.0	0.0	0.5	0.0	1.0	8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11.- Bll 3	17.0	0.0	0.0	0.0	23.0	0.0	0.0	5.0	0.0	0.0	13.0	0.0	24.0	52.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
12.- Bll 4	0.0	0.0	0.0	0.0	8.0	0.0	0.0	28.0	0.0	0.0	1.3	0.0	4.7	0.0	0.0	0.0	0.0	0.0	0.0	28.0	0.0	0.0	0.0	0.0	0.0	0.0
13.- Bll 5	13.0	0.7	0.0	0.7	0.0	0.0	0.0	3.7	0.0	13.3	1.0	0.0	1.7	0.0	1.0	0.0	0.0	0.0	0.0	6.0	0.0	0.0	2.7	0.0	0.0	0.0
14.- Bll 6	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	111.7	0.0	0.0	0.0	0.0	0.0	0.0
15.- Fu 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	51.0	0.0	0.0	0.0	0.0	0.0	0.0
16.- Fu 2	0.7	0.0	0.0	0.0	0.7	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	184.7	0.0	418.0	0.0	0.0	0.0	0.0
17.- Fu3-I	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0
18.- Fu3-II	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	2.6	0.3	0.0	0.0	0.0	0.0	0.0
19.- Fu 4	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	69.3	0.0	98.0	0.0	0.0	0.0	0.0
20.- Zoma	2.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	64.0	2.0	0.0	0.0	0.0	0.0	0.0
21.- Cruz	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.2	0.0	0.4	0.4	0.0	0.8	0.0	0.0	0.0	380.2	0.0	3.0	0.0	0.0	285.8	16.4
22.- Itej	12.0	0.0	0.0	0.0	0.0	0.3	4.0	1.7	0.0	0.7	0.0	0.0	5.3	29.0	0.0	0.0	0.0	0.0	0.0	107.0	0.0	0.0	0.0	3.7	0.0	0.0
23.- Tejo	0.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.4	0.0	0.2	0.0	0.0	0.0	3.6	0.0	0.0	0.0	3.2	66.6	0.0
24.- Parra	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	8.8	0.0
25.- Llan	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	1.3	0.7	0.0	0.0	0.0	0.0	0.0	0.0	258.0	0.0	24.0	0.0	0.0	447.3	68.7
26.- Card	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	269.3	0.0	0.0	0.0	0.0	150.7	4.3
27.- Icar	15.7	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.3	0.0	0.0	1.0	15.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0

	TRIC	TRTP	TRTT	ROTI	NAUP	COPP	COPG	CYAB	PAFI	TRPR	CYCM	CERQ	CERR	CHYD	DAPL	DAPM	DIBR	LEYD	ALOR	CHYS	CHAO	CHYR	GAST	NEMA	OLIG	OSTR
1.- Ar 1	0.0	0.0	0.0	0.7	78.3	54.7	0.0	1.7	0.0	41.3	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
2.- Ar2-I	0.0	0.0	0.0	0.0	536.0	44.0	0.0	1.0	0.0	31.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3.- Ar2-II	0.0	0.0	0.0	0.0	268.0	224.0	0.0	1.0	0.0	20.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0
4.- Ar3-II	0.0	0.0	0.0	0.0	1241.0	764.7	0.3	4.3	0.0	140.7	0.7	28.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4'.- Ar 3-I	0.0	0.0	0.0	0.0	428.0	439.0	0.0	0.0	0.0	40.0	0.0	9.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0	0.0	0.0
5.- Ar 4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6.- Rinc	0.0	0.0	0.0	0.0	519.3	194.7	0.7	0.7	0.0	64.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.3	1.0	0.0	0.0	0.0	0.0	0.0
7.- Bar 1	0.0	0.0	0.0	0.0	347.3	208.0	7.3	8.7	0.0	189.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
8.- Bar 2	0.0	0.0	0.0	0.0	416.0	92.0	0.3	0.7	0.0	122.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
9.- Bll 1	0.0	0.0	0.0	0.0	134.0	356.0	0.0	0.0	0.0	26.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0
10.- Bll 2	0.0	0.0	0.0	0.0	23.5	23.5	3.0	0.5	0.0	2.5	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0
11.- Bll 3	0.0	0.0	0.0	0.0	813.0	13.0	23.0	30.0	0.0	1.0	0.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0	0.0	0.0
12.- Bll 4	0.0	0.0	0.0	0.0	362.0	110.7	4.0	14.3	0.0	109.7	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
13.- Bll 5	0.0	0.0	0.0	0.0	1101.7	138.3	3.3	4.3	0.0	157.7	0.0	0.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0
14.- Bll 6	0.0	0.0	0.0	0.0	173.0	75.7	0.0	0.0	0.0	16.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	1.0	0.0	0.0
15.- Fu 1	0.0	0.0	0.0	0.0	283.0	179.3	1.3	9.7	0.0	106.7	0.0	0.0	8.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
16.- Fu 2	0.0	0.0	0.0	0.0	56.3	16.3	0.0	0.0	0.3	11.3	0.0	0.0	0.0	0.0	47.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.3	0.0	0.3
17.- Fu3-I	0.0	0.0	0.0	0.0	12.4	3.5	0.0	0.0	0.0	7.1	0.0	0.0	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18.- Fu3-I	0.0	0.0	0.0	0.0	149.3	83.6	2.7	1.5	0.0	96.9	0.0	0.0	9.4	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
19.- Fu 4	0.0	0.0	0.0	0.0	17.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
20.- Zoma	0.0	0.0	0.0	0.0	276.0	176.0	40.0	5.3	0.0	140.3	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
21.- Cruz	0.0	0.0	0.0	0.0	431.6	51.4	0.0	0.0	0.0	16.2	0.0	2.4	0.0	0.0	15.8	0.0	1.4	0.0	0.0	0.0	2.0	0.0	0.2	0.0	0.0	0.0
22.- ltej	0.0	0.0	0.0	0.0	22.3	5.7	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	6.7	0.0	0.0	0.0	0.0	0.0	20.3	0.0	0.0	0.0	1.3	0.0
23.- Tejo	0.0	0.0	0.0	0.0	330.6	2.2	76.0	1.2	0.0	2.8	0.0	1.2	0.0	0.0	0.2	0.0	29.2	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.0
24.- Parra	0.0	0.0	0.0	0.3	16.8	0.3	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0
25.- Llan	0.0	0.0	0.0	0.0	284.7	158.3	0.0	0.0	0.0	44.0	0.0	0.3	0.0	0.0	0.0	0.0	88.3	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
26.- Card	0.0	0.0	0.0	0.0	1102.0	20.7	0.0	0.0	0.0	7.7	0.0	0.0	0.0	0.0	0.0	0.0	34.3	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0
27.- Icar	0.0	0.0	0.0	0.3	616.7	186.0	0.0	0.0	0.0	77.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	2.0	0.0	0.0	0.0	0.0

V.- RESUMEN GLOBAL DE LOS RESULTADOS Y DISCUSIÓN

RESUMEN GLOBAL DE LOS RESULTADOS Y DE LA DISCUSIÓN

Distribución y características del zooplancton en lagos estratificados

Los grupos mayoritarios que forman el zooplancton lacustre son los crustáceos (representados mayoritariamente por cladóceros y copépodos), rotíferos y ciliados, aunque estos últimos están presentes en menor medida en la zona oxigenada de la columna de agua, además los organismos de este grupo requieren unas técnicas especiales para su fijación y para su clasificación por lo que practicamente no han sido considerados en este trabajo. La mayor parte de lagunas estudiadas en el sistema cárstico de Cuenca tienen una comunidad zooplanctónica dominada en densidad por los rotíferos que son por tanto el grupo sobre el que se centran la mayor parte de los trabajos presentados en este estudio.

Tres de los lagos cuyas comunidades zooplanctónicas han sido estudiadas con mayor detalle (Laguna de La Cruz, Lago del Tobar y Laguna de Arcas 2) presentan como característica común la fuerte estratificación de sus aguas y los marcados gradientes que presentan la mayor parte de los parámetros físico-químicos, entre estos destacan, por su especial relevancia sobre las poblaciones planctónicas, la temperatura y la concentración de oxígeno disuelto en el agua. La temperatura es un parámetro relevante pues afecta en gran medida a la capacidad y velocidad de crecimiento de las poblaciones planctónicas (existen especies cuyos elevados requerimientos térmicos sólo les permiten alcanzar un desarrollo adecuado en verano y en aguas superficiales; otras por contra sólo se desarrollan en invierno, o en verano en capas frías de la columna de agua). La cantidad de oxígeno disuelto en agua también tiene importancia sobre el crecimiento o no de los distintos organismos, pues afecta a distintos aspectos metabólicos y bioenergéticos. Berzins and Pejler en 1989 publicaron varios artículos en los que estudiaron los rangos en que se distribuían una numerosa serie de especies de rotíferos con respecto a estos dos factores y a otros factores, como el grado de eutrofia y el pH. En ellos se muestra como las especies de este grupo, igual que la mayoría de grupos del zooplancton lacustre, se desarrollan de manera óptima bajo unas condiciones determinadas, aunque el rango en el que pueden presentarse es, por lo general, muy amplio. La conductividad es otro parámetro importante en la distribución de las especies del zooplancton y que también puede variar en el perfil vertical. En las lagunas estudiadas, todas de agua dulce aunque mineralizada, presentaba una variabilidad relativamente pequeña, excepto en el lago del Tobar (Capítulo IV.3), que presenta una meromixis de origen crenogénico debida a un influjo de agua salada, por su circulación

en estratos geológicos salados (del Keuper), formando un monimolimnion extremadamente halófilo. En todos estos casos (cap. IV, pág. 84; cap. IV, pág. 101, cap. IV, pág. 94) la estratificación de las aguas se acompaña de la subsiguiente estratificación de las poblaciones del zooplancton que alcanzan densidades muy elevadas, con valores situados entre los más altos registrados en condiciones naturales.

En las figuras se muestran distintos ejemplos de la estratificación que se produce en algunas de las especies que componen el zooplancton. En los estudios realizados siempre hemos encontrado importantes diferencias en cuanto a la distribución vertical de las distintas especies de zooplancton, por lo que se realizó una primera distinción entre especies epilimnéticas y otras meta e hipolimnéticas; esta distinción que fundamentalmente atañe a la distribución a lo largo del perfil vertical está también muy relacionada con la distribución de temperaturas, y por tanto con la estacionalidad de las muestras, ya que especies epilimnéticas en invierno o primavera pueden comportarse como hipolimnéticas en verano. Durante el invierno debido a la uniformización de las temperaturas de las distintas profundidades se produce la mezcla vertical y no existe estratificación térmica, manteniéndose la estratificación sólo en los lagos meromícticos a causa de los permanentes gradientes de densidad de sus aguas (La Cruz y El Tobar). En los capítulos IV.2 y IV.4 se muestra la estratificación de las especies más representativas de cada lago. En ambos casos se puede observar la marcada estratificación de las densidades de rotíferos en estas capas y como con una variación en profundidad de sólo unos centímetros la población puede aumentar en varios órdenes de magnitud. En el caso del Tobar (cap. IV.3), en el que por lo general dominan los crustáceos en número, también encontramos una diferenciación vertical, pero no alcanza la magnitud de las otras lagunas.

Las especies consideradas epilimnéticas no suelen descender por debajo de la termoclina y algo similar (pero a la inversa) sucede con las especies consideradas hipolimnéticas, que no suelen ascender atravesando la termoclina; únicamente especies que hemos denominado hipolimnéticas facultativas son capaces de ocupar el epilimnion pero también desarrollarse y ocupar las zonas hipolimnéticas, entre éstas destaca el rotífero *Anuraeopsis fissa,* que mostró una gran capacidad para colonizar toda la columna de agua (con excepción de las capas anóxicas).

Aunque la fenología de estas importantes concentraciones de organismos depende de la especie, suele ser al final del verano cuando se producen máximos destacados ya que se verifica la acumulación de importantes cantidades de materia orgánica provenientes de la producción biológica de la columna superior de agua, en estas capas que poseen un marcado gradiente de densidad (picnoclina). El agotamiento de oxígeno asciende en la columna de agua y, la profundidad a la que se forma la

oxiclina, con los consiguientes cambios de temperatura, puede determinar cambios en las especies dominantes en esta interfase. Si la oxiclina llega a coincidir con la parte alta o media del metalimnion especies como la mencionada *A. fissa* resultan favorecidas.

Como ejemplo de especie epilimnética destaca *Hexarthra mira* bastante abundante y bien representada en ambas lagunas (cap. IV.2, pág. 85; cap. IV.5, pág. 119). En La Cruz (pág. 85) este ciclo parece repetirse en los dos veranos, la población presenta máximos en superficie cuando las temperaturas son altas, con el avance de la estación la poblacion tiende a formar picos secundarios en la zona de la termoclina probablemente capaces de aprovechar las acumulaciones de fitoplancton en el gradiente de densidades que se forma en esta capa. En Arcas 2 (pág. 119), sólo en el primero de los años se muestreó la población en su apogeo, en el segundo año no se recogieron muestras a mediados de verano por lo que no se encontraron grandes densidades de esta especie.

Sucesión de especies a lo largo del ciclo anual, aplicación del Análisis de Componentes Principales a un ciclo anual en la laguna Arcas 2

Los ciclos anuales de las principales especies de rotíferos que componen la comunidad planctónica han sido estudiados en la laguna de La Cruz y en Arcas 2 (cap. IV.2, IV.4 y IV.5), esta última en dos ciclos anuales, 1987-1988 y 1990-1991, del estudio de estos ciclos se desprende que los principales parámetros responsables de estas variaciones fueron la temperatura y el oxígeno (capítulos IV.2, 4 y 5). Destaca la especie hipolimnética facultativa *Anuraeopsis fissa*, en la laguna de La Cruz se muestra el ciclo anual 1987-88 (pág. 84), y de la misma especie en Arcas 2, el ciclo 1987-88 (pág. 120) y 1990-91 (pág. 101). Se observan en estos casos los importantes crecimientos registrados en la oxiclina y la ocupación de estas capas y de las superiores, en el ciclo 1987-88 se da la circunstancia que esta especie sólo fue abundante en uno de los dos años estudiados (1988), siendo muy escasa en el año anterior, esto se atribuyó a la competencia en las capas de la oxiclina con otra especie congenérica *A. miraclei*, muy abundante en el 87, y a las diferentes condiciones climatológicas en los dos periodos, siendo el año 1987 seco en primavera mientras que el 1988 presentó abundantes lluvias en la primavera-verano, estas lluvias repercutieron con un aumento del nivel freático de la zona en cuestión lo que se reflejó en un aumento de nivel de la laguna de la Cruz y el llenado de lagunas temporales. Además el invierno de 1987 fue más frío que el de 1988 con el consiguiente efecto en la circulación y mezcla vertical de las aguas. Estas diferencias de precipitaciones y temperaturas entre ambos años determinaron en parte las diferencias en los crecimientos poblacionales mostrados por ambas especies.

El zooplancton de la laguna de Arcas 2 también mostró considerables diferencias entre los distintos años aunque no fueron tan acusadas como en La Cruz, al igual que ocurría en La Cruz se observaron masivos crecimientos en la oxiclina, que se agudizaron en especial al final del verano.

El estudio de las Componentes Principales (capítulo IV.5), nos muestra la posición relativa de las distintas especies de rotíferos y de los principales parámetros físico-químicos medidos "in situ" durante los muestreos (pág. 125 y 126), así como la posición relativa de las especies de rotíferos en otro análisis realizado en ausencia de la físico-química (pág. 124). En esta figura se observa que el resultado del análisis realizado con sólo las abundancias de las especies se corresponde con el resultado del análisis con los parámetros físico-químicos. Esto confirma que los factores que mayor porcentaje de la varianza de los datos de distribución de las especies de zooplancton nos explican están directamente relacionados con la temperatura y el oxígeno, o lo que es lo mismo, con la variación que presentan las aguas a través del perfil vertical y en las distintas estaciones del año. Este Análisis de la Componentes Principales también pone de manifiesto la separación de nichos que se verifica entre las diferentes especies de rotíferos.

Estudio de la relación zooplancton-fitoplancton mediante la Correlación Canónica. Ejemplo del estudio realizado en el lago del Tobar

Las especies más abundantes de fitoplancton y zooplancton de las muestras de septiembre y abril del lago del Tobar (Capítulo IV.3) han sido representadas según la posición que ocupan en un plano formado por las dos primeras variables canónicas obtenidas mediante un Análisis de Correlación Canónica (pág. 95), la comparación entre ambas figuras, fitoplancton (izquierda) y zooplancton (derecha), nos proporciona información sobre la forma en que se distribuyen las distintas especies con relación a estas dos variables. La primera de las variables canónicas separa entre las dos épocas de muestreo lo que, como suele ser habitual, explica la mayor varianza entre los datos, el segundo eje separa las muestras en profundidad, lo que en el caso del Tobar separa las muestras de la haloclina de las muestras de superficie. Las especies zooplanctónicas y fitoplanctónicas que se presentan próximas en el plano formado por estas dos variables son especies que, por lo general, comparten una misma zona del perfil vertical de la laguna y una misma distribución estacional. De esta comparación podemos inferir que existe alguna relación ecológica probablemente de coincidencia en los factores ambientales o estadio de la sucesión que se inicia en primavera y finaliza antes de la mezcla de otoño. Sin embargo se puede observar alguna relación de carácter trófico, por

ejemplo entre los nauplios *Arctodiaptomus.salinus* y todos los estadios de *Tropocyclops prasinus,* y la especie de fitoplancton *Chlamidomonas sp2*, organismos típicos de septiembre y con centro de gravedad cercano a la haloclina. Otras relaciónes tróficas descritas en la literatura como las que se establecen entre el dinoflagelado *Ceratium hirundinella* y el rotífero *Ascomorpha ovalis*, y las *Cryptomonas* y el rotífero *Polyarthra* se observan también en este análisis por la coincidencia de los pares de especies en su posición respecto de las variables canónicas.

Junto con los rotíferos se han ubicado los huevos de las especies más abundantes para ver cual era su situación en el plano, es decir si estaban próximos o no al centro de gravedad de la especie, en dos de los casos (*Keratella* y *Synchaeta*) esto fue así pero en el tercero, huevos de *Polyarthra spp.*, se encontraron grandes diferencia entre la ubicación de los huevos y los adultos sin huevo, pero sin duda esto fue debido a la presencia de dos especies de *Polyarthra* una en superficie con gran cantidad de huevos y otra de distribución más profunda y con menor tasa reproductiva.

Relaciones tróficas del rotífero depredador *Asplanchna girodi*, estudio de los contenidos estomacales

Del estudio del contenido estomacal de *Asplanchna* se desprendió que esta especie utilizaba en el lago del Tobar individuos de la especie *Keratella quadrata* como fuente nutritiva siempre que se presentaban juntos (Capítulo IV.3). Aunque *Asplanchna girodi* no fue incluida en el análisis descrito en el párrafo anterior debido a su escasa densidad en las fechas correspondientes a los datos incluidos en el análisis si que podemos destacar que cuando coincidía en el tiempo con *Keratella quadrata,* sus centros de gravedad estaban muy próximos. Otros estudios similares confirmaron esta observación en la laguna de La Cruz (Capítulos IV.2 y IV.6), aunque aquí el mayor número de restos encontrados en el interior de *A. girodi* correspondieron a la especie *Anuraeopsis fissa.* En la laguna Arcas-2 un nuevo estudio de los contenidos estomacales de *A. girodi* realizado con las muestras del ciclo anual 1987-88, dió como resultado que la principal presa ingerida por *Asplanchna* fue *A. fissa* seguido de *F. hofmanni* y fitoplancton de tamaño grande, entre los ejemplares estudiados no se encontraron restos de *Keratella*, pero hay que señalar el escaso grado de coincidencia temporal que presentaron ambas especies (Capítulo IV.5).

Fecundidad, densidad relativa de hembras portadoras de huevos en el ciclo anual y en el perfil vertical

La permanencia de los huevos adosados al cuerpo de las hembras hasta la eclosión de los mismos es una característica de la mayoría de rotíferos planctónicos, esto nos permite evaluar el porcentaje de hembras ovígeras en la población y por tanto tener un conocimiento del potencial de crecimiento de estas especies; a su vez la presencia de huevos mícticos (de resistencia) nos permite identificar los periodos en que se verifica la reproducción sexual. En la laguna de Arcas-2 (Capítulo IV.4) se realizó un estudio de la tasa de fecundidad en poblaciones de rotíferos hipolimnéticas *sensu stricto* (*F. hofmanni*) e hipolimnéticas facultativas (*A. fissa*), de este estudio se desprende que en el caso de la especie hipolimnética facultativa -*A. fissa*- las hembras ovígeras se distribuyeron por casi todo el perfil vertical de la laguna durante gran parte del ciclo anual, la producción de huevos de resistencia en este caso tuvo lugar al final de su presencia, después del periodo de máximo desarrollo de la población -otoño- coincidiendo, la producción de machos, con los últimos picos de densidad poblacional. En *F. hofmanni* por contra el periodo sexual tiene lugar enseguida del establecimiento de la población, encontrándose huevos de resistencia y de machos desde las primeras fases del desarrollo de la población. La cantidad de huevos de resistencia también estableció diferencias entre ambas especies, encontrando un número mayor de estos en la población de *F. hofmanni* que en la de *A. fissa.*

En el caso de *A. fissa*, la nueva población que se desarrolla tras el periodo invernal, podría regenerarse a partir de algunos individuos que han permanecido durante el invierno o a partir de huevos depositados en las orillas de la laguna; por contra en el caso de *F. hofmanni*, la población parece desarrollarse a partir de huevos durables que eclosionan en los inicios de la estratificación tras la mezcla invernal, procedentes del sedimento del fondo de la laguna.

Durante la experiencia de migración vertical (Capítulo IV.6) también se contabilizaron los huevos de las distintas especies para conocer si existían movimientos migratorios diferenciales en las hembras ovígeras, lo más interesante de los resultados obtenidos en este punto viene dado por la comparación realizada entre la distribución de los huevos en el perfil vertical -que además en ambos casos se mantuvo constante a lo largo del ciclo diario- en dos especies: *A. fissa* (especie hipolimnética facultativa) y *Polyarthra dolichoptera* (de distribución hipolimnética *sensu stricto* en esta época). Se observaron importantes diferencias pues en el caso de *P. dolichoptera* los huevos, al igual que el resto de la población, tienen su centro de gravedad en aguas del hipolimnion; *A. fissa* por contra presenta el centro de gravedad poblacional desplazado

al hipolimnion (casi coincide con el de *P. dolichoptera*), pero el centro de gravedad de sus huevos se encuentra bastantes metros por encima, en el epilimnion, a una temperatura considerablemente superior. Esta es una de las principales razones que refuerzan la consideración de esta especie como hipolimnética facultativa, con crecimiento en aguas más calientes, mientras que *P. dolichoptera* es característica de aguas más frías.

Estudio de los movimientos verticales del zooplancton en la laguna de La Cruz

Constituyen el Capítulo IV.6 de la tesis, el estudio se abordó desde dos puntos de vista: el primero la realización de muestreos en el perfil vertical a distintas horas de un ciclo diario y segundo, la colocación de una serie de trampas destinadas a capturar individuos en trayectoria ascendente y descendente que nos ayudasen a interpretar los resultados obtenidos en los perfiles del ciclo diario. Estos resultados muestran la existencia de importantes movimientos migratorios en el epilimnion, estos movimientos que se ajustan al denominado patrón "normal" de migración vertical (ascenso al atardecer y descenso al amanecer), son casi generales para todas las especies, observándose un cierto desfase en el inicio del movimiento ascensional dependiendo de la profundidad de partida, más restrasado en la zona más superficial. Sólo se ha encontrado un caso de migración "inversa" (ascenso al mediodía) que fue el de *T. similis*.

En el hipolimnion este fenómeno está muy amortiguado y las especies de rotíferos que lo habitan presentan ligeras variaciones en sus centros de gravedad durante el ciclo diario, sin embargo en estas profundidades las capturas en las trampas fueron importantes constituyendo esto una clara indicación de la gran actividad de los organismos en estas capas con concentraciones de oxígeno bajas, sirviendo esto como comprobación de que las importantes densidades que se dan en ellas no se deben a la acumulación de organismos moribundos. Esta última afirmación viene también apoyada por la observación de muestras vivas procedentes de estas capas.

Los resultados de las trampas también nos permiten dar algún índice sobre la intensidad de la migración para las distintas especies y nos informan sobre los periodos de tiempo en los que ésta es más acusada, complementando de este modo la información obtenida de los muestreos del ciclo diario. Del mismo modo las diferencias obtenidas entre las trampas que capturaban individuos en descenso y aquellas que capturaban individuos en ascenso sugieren un descenso pasivo en la mayoría de especies lo que les es bioenergéticamente positivo. Sólo en el caso de *P. dolichoptera* este descenso por razones morfológicas probablemente, se realiza principalmente de manera activa. Las diferentes reacciones de escape de las distintas especies también nos ayudan a explicar

los resultados obtenidos en las trampas, aquellas especies que en la literatura están descritas como capaces de reacciones de escape más eficaces -*Hexarthra, Polyarthra*- presentaron, por lo general, tasas menores de captura en las trampas.

Las diferencias observadas en la distribución de los huevos de *A. fissa*, comentada en el apartado anterior, unida a los importantes movimientos que tienen lugar en el hipolimnion podrían apoyar la afirmación de que los cambios de temperatura pueden aumentar las tasas de producción de huevos en determinadas especies.

Las causas que provocan la migración vertical en los rotíferos pueden ser variadas; una adaptación para reducir la depredación visual puede ser importante en el caso de los rotíferos de mayor talla, o quizás también el escapar de Chaoborus (abundante en esta laguna) que procedente del fondo puede capturar primero a los individuos más restrasados. Sin embargo nuestros resultados podrían interpretarse también como que algunos de estos movimientos verticales podrían estar acoplados a los ritmos de actividad (alimentación) y reposo, puesto que estos organismos tienen acopladas la función motriz y alimenticia mediante la actividad de la corona de cilios, de manera que la actividad filtradora causaría movimientos ascensionales y el reposo un descenso pasivo, tal como sugiere la escasez de capturas en las trampas situadas boca arriba.

Estudio de la diversidad del zooplancton en las lagunas del sistema cárstico de Cuenca

La diversidad es uno de los principales descriptores biológicos de las comunidades, son destacables en este trabajo las referencias a la diversidad realizadas en los capítulos IV.5 y IV.7. En el primer caso se estudió la diversidad de los rotíferos en la laguna de Arcas-2 durante el ciclo anual 1987-88(cap. IV.5); durante todo este ciclo la diversidad de rotíferos planctónicos fue baja, en particular en la zona de la oxiclina. Las principales razones que explican esta situación son; por un lado, las altas densidades que una o dos especies alcanzan en estas capas y que producen importantes descensos de diversidad, por otra parte las peculiaridades morfométricas de esta laguna -en particular su pequeño tamaño, gran profundidad relativa y las pronunciadas pendientes de sus orillas- que dificultan la colonización por macrófitos y favorecen la estratificación, de esta forma la columna de agua se simplifica al quedar muy próximos oxiclina y metalimnion desde mitad del verano. Este efecto contrasta con las altas diversidades encontradas en las comunidades de ciliados de la zona anóxica de esta misma laguna.

En el capítulo IV.7 se ha estudiado la diversidad de varias lagunas del sistema cárstico de Cuenca en dos épocas. En primer lugar se observaron diversidades más altas

en otoño que las obtenidas en la primavera y una correlación negativa entre la diversidad y la densidad zooplanctónica. Al representar la relación entre la diversidad y el tamaño de las lagunas, en las distintas estaciones se observaron, mediante los coeficientes de correlación obtenidos, diferentes situaciones: (1) en primavera existía una correlación positiva y significativa de la diversidad con el tamaño (tanto con el diámetro medio como con la profundidad máxima), (2) por el contrario en otoño los coeficientes de correlación obtenidos entre las mismas variables no fueron significativos y además mostraron correlaciones negativas. Aunque en general lagos más grandes presentan mayores diversidades pues ofrecen más tipos de hábitats a los organismos; en estas lagunas, que poseen una marcada estratificación de la columna de agua, al final del verano y principios del otoño se producen importantes acúmulos de determinados organismos en estas capas profundas, estas elevadas densidades zooplanctónicas debidas auna o pocas especies disminuyen la diversidad integrada de la columna de agua lo que explica el efecto observado, puesto que el número de especies planctónicas es mayor.

Estudio de los principales factores físico-químicos responsables de la estructura de la comunidad zooplanctónica en 27 dolinas de tres zonas cársticas de Cuenca

Para investigar cuales son los principales factores físico-químicos que explican las diferencias entre las comunidades de organismos zooplanctónicos de un conjunto de lagunas situadas próximas en el espacio, se muestrearon un total de 28 lagunas o cubetas (ya que alguna de estas lagunas estaban formadas por 2 dolinas conectadas) de tres zonas cársticas próximas a la ciudad de Cuenca. Los datos físico-químicos obtenidos, así como los recuentos de zooplancton fueron analizados mediante: Correlación, PCA y TWINSPAN (cap. IV.7).

Se encontraron correlaciones significativas entre algunos descriptores de las comunidades biológicas por ejemplo la diversidad, equitatividad, IFO, proporción de organismos litorales, etc. y las características morfométricas de las lagunas. Se realizaron 4 Análisis de Componentes Principales; dos sobre datos físico-químicos (PCA-1 y PCA-2), uno sobre el conjunto de las especies de primavera y otoño (PCA-3) y otro únicamente con las especies de primavera (PCA-4). Los resultados mostraron que para los análisis realizados con datos físico-químicos la fuente de variación más importante estaba relacionada con la composición mineralógica del substrato, principalmente separaba las lagunas de aguas carbonatadas de las de aguas silico-sulfatadas; en segundo término los parámetros relativos al estado trófico también jugaban un papel importante para explicar las agrupaciones u ordenaciones de las lagunas (pág. 177). Cuando se realizó el análisis sobre las densidades del zooplancton

en primavera y otoño (PCA-3) estos dos factores se invirtieron, estando el primer factor relacionado principalmente con el grado trófico y con algún otro factor, ya que separó las lagunas que presentaban surgencia de agua y las someras; y el segundo con la composición mineralógica del sustrato y con la morfometría (pág. 178). Esto se confirmó con un análisis de correlación entre las componentes principales y los parámetros físicos y químicos.

Los datos de composición específica del zooplancton de primavera fueron tratados mediante dos métodos; en el primero (PCA-4) se utilizaron densidades de especies planctónicas, en el segundo sólo se utilizaron datos de presencia-ausencia pero incluyendo todas las especies planctónicas y las semiplanctónicas o litorales que se encontraban en las muestras. Los resultados obtenidos por ambas metodologías fueron muy similares obteniéndose los mismos grupos de lagunas en ambos casos (pág. 180).

Estos resultados indican que la ordenación de las distintas lagunas, en base a la composición del zooplancton en general va pareja a la ordenación que se obtiene con los parámetros físico-químicos; destacan entre estos la composición mineralógica y el estado trófico del lago. Sin embargo, los resultados derivados del estudio realizado en base a la composición del zooplancton, ponen de manifiesto otros factores como los relacionados con la presencia de surgencias (turbidez, estabilidad térmica...) que afectan a la comunidad y no siempre son detectados en los análisis físico-químicos más comunes.

VI.- CONCLUSIONES

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1. Las especies del zooplancton de las diferentes lagunas del sistema cárstico de Cuenca ((55 especies de rotíferos, 6 de copépodos y 10 cladóceros) son en su mayor parte o de amplia distribución o las mismas que se encuentran en otros lagos europeos de alcalinidad alta. Sin embargo, se han econtrado dos especies de ecología particular, *F. lhofmanni* y *A. miraclei* que son dominantes en las capas profundas de la oxiclina. Esta última es una nueva especie que fue descubierta en estas lagunas.

2. En la oxiclina de lagos fuertemente estratificados, las poblaciones de rotíferos presentan una marcada microestratificación vertical, produciéndose variaciones de las densidades de rotíferos de varios órdenes de magnitud en pocos centímetros, por lo que es necesario utilizar técnicas de muestreo de pequeña escala para su estudio.

3. Las especies planctónicas de la laguna de La Cruz y Arcas 2 presentan una estructurada distribución vertical, habiéndose propuesto para ellas las categorías de epilimnéticas, metalimnéticas, hipolimnéticas e hipolimnéticas facultativas, según su distribución en la columna de agua a lo largo del año.

4. Hay una competencia entre las especies dominantes de rotíferos por ocupar la zona de la oxiclina, los factores principales que decantan la ventaja en favor de una u otra especie parecen ser los derivados de las condiciones climáticas de los periodos anteriores, al influir sobre los aportes hídricos y la circulación vertical de las aguas. En La Cruz esta competencia se observó entre 2 especies congenéricas *A. miraclei* y *A. fissa*, mientras en Arcas 2 la competencia se produce entre *A. fissa* y *Filinia hofmanni*, observándose en los dos casos un reparto de los nichos cuando ambas coexistieron.

5. Del Análisis de las Componentes Principales efectuado con los datos obtenidos al estudiar el ciclo anual y la distribución vertical del zooplancton de Arcas-2 se puede concluir que la temperatura y la cantidad de oxígeno disuelto, íntimamente relacionadas con la sucesión estacional y la distribución a lo largo del perfil vertical, son los factores que explican la mayor cantidad de varianza en dichos datos.

6. Del estudio realizado mediante Correlación Canónica de la relación entre zooplancton y fitoplancton, se desprende que en la Laguna del Tobar se dan varias de las relaciones tróficas descritas en otros sistemas, destacando la que se verifica entre *Ascomorpha*

ovalis y *Ceratium hirundinella*, *Polyarthra* y *Cryptomonas,* y también se pueden deducir cuales son los principales recursos alimenticios utilizados por los copépodos dominantes.

7. En las lagunas estudiadas, la principal fuente de alimentación de *Asplanchna girodi* son rotíferos de la especie *A. fissa* seguidos de *Keratella quadrata* y *F. hofmanni*, y especies de fitoplancton de tamaño grande, no se han encontrado restos de otras especies de rotíferos en los contenidos estomacales aunque en ocasiones dominasen en las comunidades, especialmente las dotadas de reacciones de escape.

8. Las dos especies dominantes (*A. fissa* y *F. hofmanni*) de la laguna Arcas 2, muestran diferentes estrategias reproductivas. Los periodos de reproducción sexual no se solapan, lo que puede estar relacionado con la estrategia de recolonización del lago tras la estación desfavorable. *F. hofmanni* empieza su desarrollo a finales de invierno-primavera a partir de huevos durables depositados en el fondo de la laguna, presentando enseguida reproducción sexual. *A. fissa* se originaría en aguas más superficiales a partir de huevos de resistencia en las orillas, o bien, a partir de un escaso número de individuos que se han mantenido durante toda la estación desfavorable y no produce huevos durables hasta finales de verano-otoño.

Las tasas de fecundidad de huevos amícticos fueron superiores en *A. fissa* y estuvieron distribuidas por todo el perfil vertical. Por contra, *F. hofmanni* presentó tasas más bajas y restringidas a la zona de la oxiclina. En cuanto a los huevos mícticos *F. hofmanni* presentó tasas superiores a las de *A. fissa*, que fueron muy bajas.

9. *A. fissa* presenta notables diferencias entre la situación del centro de gravedad de los huevos y el centro de gravedad de la población a finales de verano cuando ocupa la oxiclina, a todas las horas del día estudiadas en el experimento de migración vertical. Esto refuerza la consideración de esta especie como hipolimnética facultativa y de desarrollo muy dependiente de la temperatura. En cambio, las especies más carcterísticas de la oxiclina están adaptadas a temperaturas bajas. En el experimento de migración vertical *Polyarthra dolichoptera*, se comportaba como hipolimnética *sensu stricto* y la distribución vertical de los huevos coincidía con la de la población.

10. En el epilimnion, casi todas las especies de rotíferos planctónicos presentan migraciones verticales ajustadas al patrón "normal" (permanencia en aguas superficiales durante la noche y en aguas más profundas por el día); solamente una especie, *Trichocerca similis*, presentó migración "inversa" aunque con escasa magnitud.

11. Estos movimientos migratorios conectados con el ciclo diario, no se verifican en la zona de la oxiclina; pero sí que se producen importantes capturas en las trampas destinadas a la observación de desplazamientos verticales, con lo que se puede concluir que la ingente cantidad de organismos que en ocasiones se acumulan en esta zona, son animales activos y no poblaciones residuales.

12. La utilización de trampas para el estudio de la migración vertical ha sido de gran ayuda para interpretar las variaciones en distribución vertical del zooplancton durante un ciclo diario y nos han permitido confeccionar un índice que permite cuantificar de forma relativa la importancia de la migración vertical diurna de cada una de las especies. Una de las conclusiones más interesantes de los resultados del experimento con trampas es que apoyan la idea de una subida activa frente a un descenso pasivo de los organismos, lo que se deduce de las enormes diferencias entre las capturas obtenidas en las trampas que cogían individuos en ascenso y las que los cogían en descenso. Sólo una especie no se ajustó a esta observación, tal fué el caso de *P. dolichoptera* abundante en las trampas de captura de animales en desenso lo.que indica un descenso activo

13. La migración en otros grupos del zooplancton distintos de los rotíferos fue especialmente acentuada en *Daphnia longispina*, mientras que en el caso de los copépodos no se observaron grandes movimientos migratorios. Se observó migración en el díptero *Chaoborus* sp. aunque las técnicas de muestreo empleadas no son las adecuadas para dicho organismo.

14. Los resultados del experimento de migración vertical indican que no hay un importante trasiego de organismos entre epi e hipolimnion durante el ciclo diario.

15. La diversidad de la comunidad de rotíferos estudiada durante un ciclo anual de la laguna de Arcas 2 es muy baja, entre las causas más aparentes de esto podemos citar las siguientes: grandes concentraciones de organismos de una sola especie en la oxiclina, características morfométricas que favorecen la ausencia de macrófitos y una marcada estratificación y, la proximidad de la oxiclina a la parte alta del metalimnion en el periodo estival.

16.- Las características batimétricas y morfométricas de las dolinas cársticas tienen gran interés para la caracterización del zooplancton de estas lagunas, por su estrecha relación con algunos descriptores tales como la diversidad, equitatividad o la cantidad de

rotíferos litorales. En primavera encontramos una correlación positiva entre la diversidad y el tamaño (superficie y profundidad máxima) de las lagunas, en otoño esta correlación no fue significativa. Esto se explica porque las lagunas más grandes, que por lo general eran más profundas, al final del verano y principios de otoño están marcadamente estratificadas, y las elevadas densidades monoespecíficas de la oxiclina producen notables descensos de la diversidad.

17. La diversidad integrada de la columna de agua en estas lagunas fue mayor a principios de otoño (antes de la circulación vertical de las aguas) que en primavera, tal como predice la teoría de la sucesión ecológica.

18.- La ordenación de las lagunas por métodos de estadística multivariada (PCA, TWINSPAN) en función de las características físico-químicas y la que se realizó en función de las densidades de zooplancton se asemejan bastante. Los factores abióticos relacionados con el gradiente trófico, con la composición mineralógica y la morfometría parecen explicar la mayor cantidad de varianza en la distribución de las comunidades zooplánctónicas en las diferentes lagunas. Sin embargo la ordenación en base a las abundancias de las especies puso de manifiesto la importancia de otros factores no incluidos en el análisis de la físico-química, como los derivados de las condiciones hidrológicas (flujo de agua y evaporación en lagunas muy someras).

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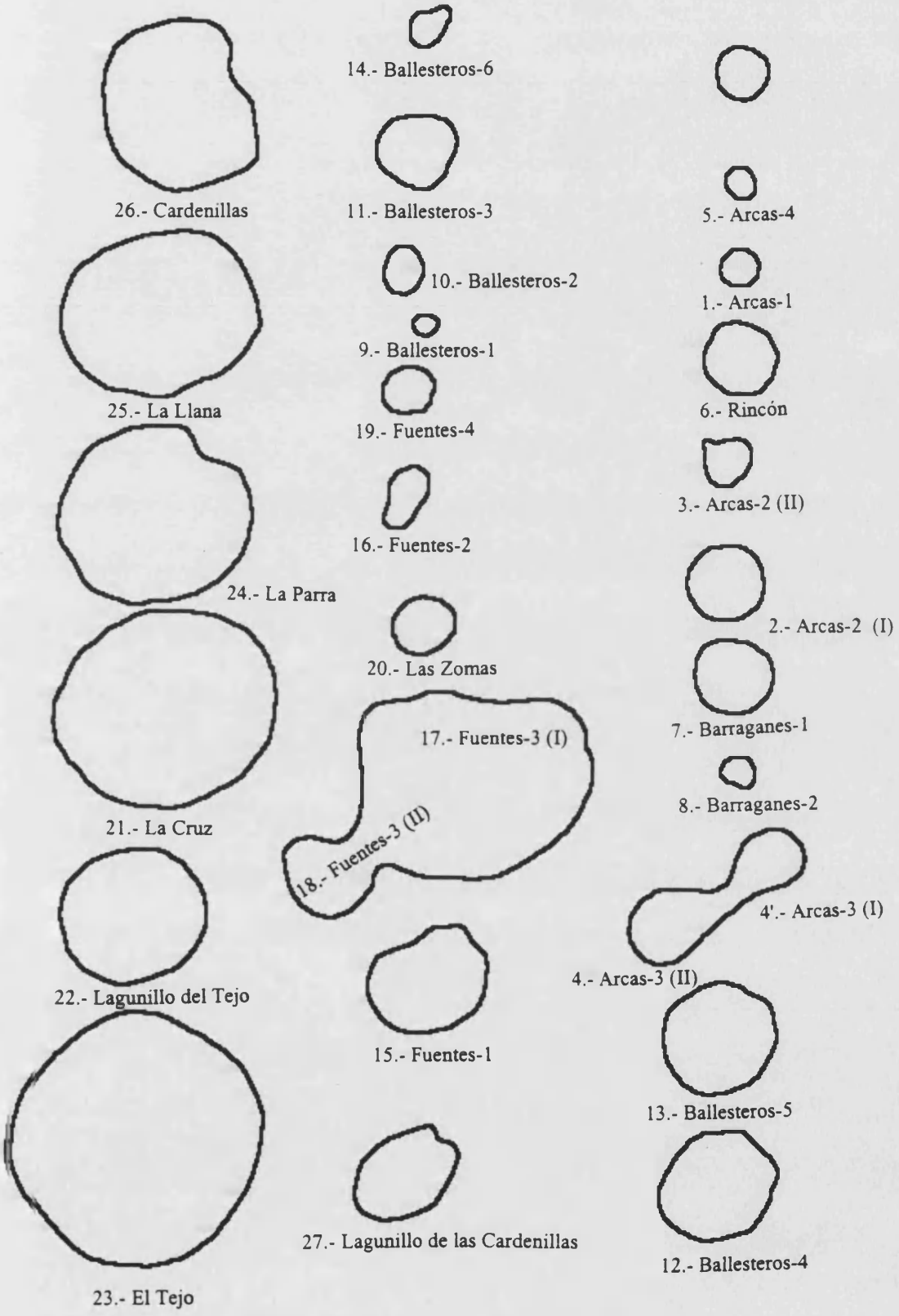
Apéndice

En la figura de la siguiente página se muestran los contornos digitalizados para el análisis de imagen de las diferentes cubetas estudiadas.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25.- La Llana
19.- Fuentes-4
6.- Rincón
3.- Arcas-2 (II)
16.- Fuentes-2
24.- La Parra
2.- Arcas-2 (I)
20.- Las Zomas
17.- Fuentes-3 (I)
7.- Barraganes-1
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18.- Fuentes-3 (II)
21.- La Cruz
4'.- Arcas-3 (I)
22.- Lagunillo del Tejo
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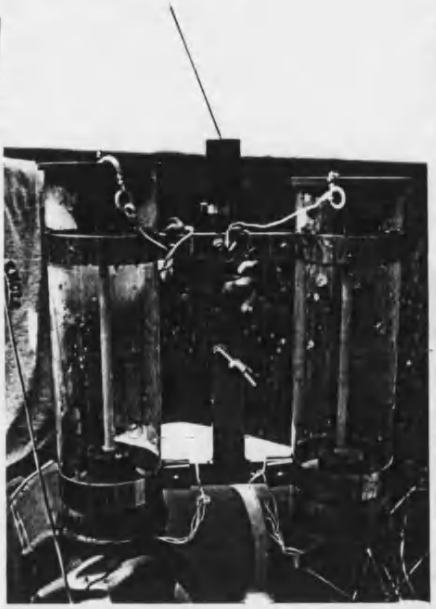
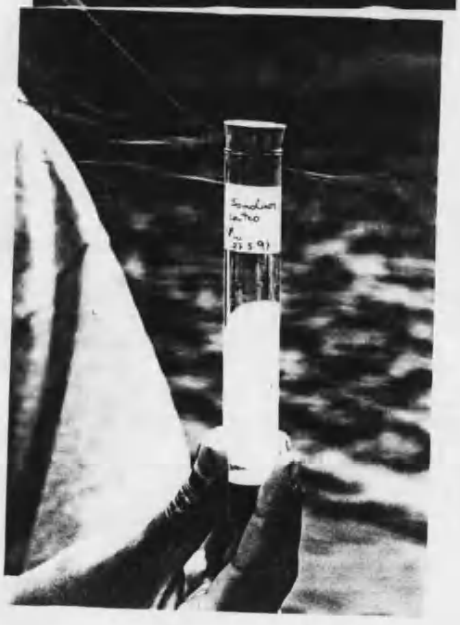
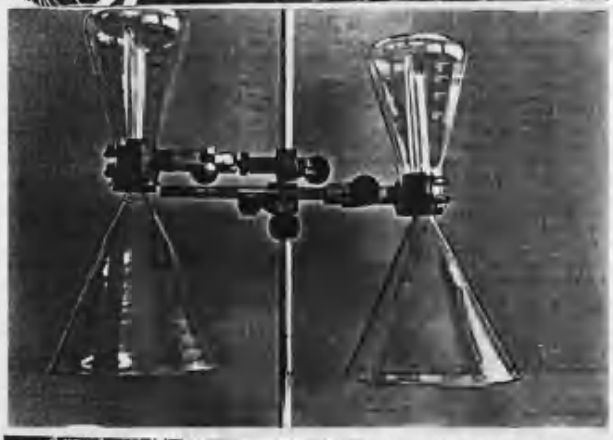
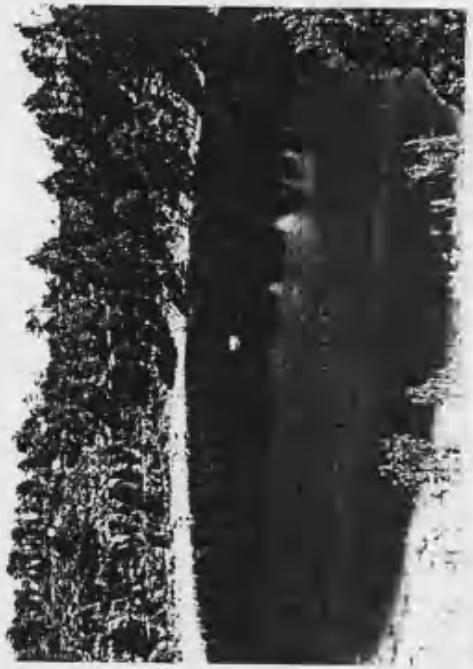
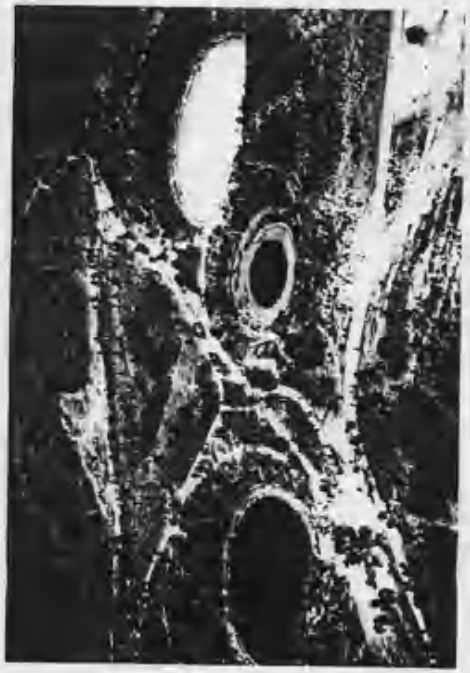
23.- El Tejo

Láminas

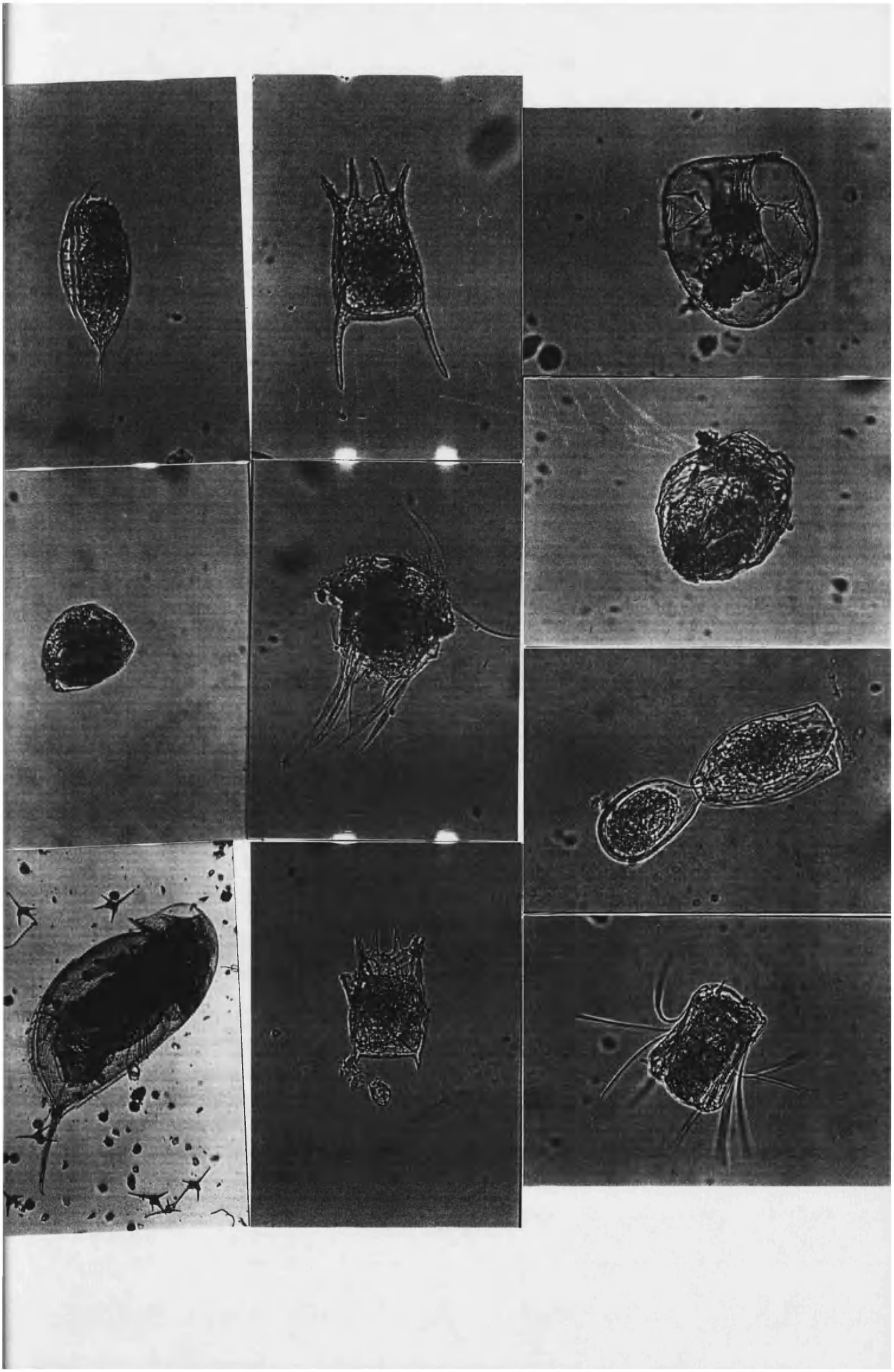








UNIVERSIDAD DE VALENCIA FACULTAD DE CIENCIAS BIOLOGICAS

Reunido el Tribunal que suscribe, en el día de la fecha, acordó otorgar, por unanimidad, a esta Tesis doctoral de D. Javier Armengol Díaz

la calificación de APTO "Cum laude" por unanimidad

Valencia, a 12 de Septiembre de 1997

El Secretario,

El Presidente

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