LIMNETICA

Asociación Ibérica de Limnología
Associação Ibérica de Limnologia
AIL

Volumen 31 (2)
Diciembre de 2012

Volumen 31. Número 2. 2012

LIMNETICA

Revista de la Asociación Ibérica de Limnología

Asociación Ibérica de Limnología
Associação Ibérica de Limnologia
AIL

Universitat de Barcelona
Publicacions i Edicions

Depósito legal: V-2404-1986
ISSN: 0213-8409
Impresión: Gráficas Rey
Impreso en España/Printed in Spain

Limnetica, 31 (2): i-ii (2012)
 ISSN: 0213-8409

Maria José Lemos Boavida: Limnologist and Teacher, in memoriam

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Maria José Boavida died on the 30th of August, 2012, aged 64.

After graduating in Biology at the University of Lisbon, Portugal, she continued her studies at Kent State University (USA). It was at the end of her first year at Kent that, as she was so fond of mentioning, she became fascinated with a paper published by Ramon Margalef in 1951, relative to the production of phosphatases by *Daphnia*. This fascination led to her Master thesis topic and later to her Ph.D. studies and the demonstration that zooplankters were really producing their own phosphatases and not only releasing those ingested with their algal food (Boavida and Heath, 1984; Boavida, 2010). The role played by phosphorus, phosphorus regeneration and zooplankton interactions in lakes were a fundamental part of her scientific research which led to the development of limnology studies in Portugal. She was the national representative of the International Association of Theoretical and Applied Limnology (SIL), and the Portuguese members of SIL profited from her great effort in keeping us up to date with the latest limnology developments, and organising the bureaucratic aspects of SIL membership. Many of us who were her students, thank her the kindness of translating into Portuguese the book *Limnology* by her friend R.G. Wetzel, which was famously used as syllabus in her course of "Limnology" at the University of Lisbon. Her curiosity and scientific knowledge, further developed in cooperation with researchers both at the University of Lisbon and at several research centres throughout the world, granted her the esteem from co-workers and students alike.

As a teacher, Maria José was well known for her care in preparing her classes and advising students, to whom she imparted her interest in the various phenomena shaping the dynamics of lakes. Many

students and colleagues became interested in aquatic ecology through her influence and guidance. This enthusiasm for science required great dedication and discipline from her part, and often others felt she demanded a similar level of attention and dedication from them. Although the demand for scientific honesty and human decency was a requirement in her dealings with students and co-workers, she was generous with those in need of help, and often brought out the best in them. Allying her drive to help and her characteristic fight against scientific inaccuracy, she recently wrote a "Scientific Glossary of Limnology" in a small format so that "students may use it in the field or poster sessions in conferences, where often doubts arise and there is nobody (...) to ask" (Boavida, 2011). Considering her prolific career, it is fitting that her last book can be carried in the pocket as a protection against embarrassment and error.

Maria José was born in 1948 in Mozambique where she spent her youth, and moved to Portugal in 1968. She always spoke fondly of her free upbringing, the wonderful nature of the land and a time when responsibility for the wellbeing of the fellow human and friendship were all important aspects of the human character. Her passing is a great loss for limnology in Portugal, yet, for those who had the privilege to know her personally, it is the loss of a loyal and generous friend.

REFERENCES

BOAVIDA, M. J. 2010. It all started with Margalef's paper of 1951. *Limnetica Internet* (www.limnetica.es), 1: 1–6. *Limnetica*, 31: 187–192.

BOAVIDA, M. J. 2011. *Scientific Glossary of Limnology*, 63 pp. Escolar Editora, Lisbon.

BOAVIDA, M. J. and R. T. HEATH. 1984. Are the phosphatases released by *Daphnia magna* components of its food? *Limnol. Oceanogr*., 29: 641–645.

MARGALEF, R. 1951. Role des entomostraces dans la régéneration des phosphates. *Verh. Internat. Verein. Limnol*., 11: 246–247.

Limnetica, 31 (2): 187-192 (2012)
 ISSN: 0213-8409

It all started with Margalef's paper of 1951

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AIL's committe has decided to publish this manuscript in this volume in homage to Dr. M. J. Boavida's career. This paper was previously published in 2010 in *Limnetica internet* (www.limnetica.es).

ABSTRACT

It all started with Margalef's paper of 1951

As early as 1951, Margalef speculated on the production of soluble phosphatases by zooplankton; "entomostracans" were producing their own phosphatases and so contributing to phosphate regeneration. After analytical techniques had been considerably improved and introduced into limnology laboratories, it was verified, almost three decades later, that the eminent scientist was right. The role of soluble phosphatase in fresh waters can be investigated either in straight relationship to plankton phosphatase producers or simply in connection with other chemical entities abundant in lake water, with capacity to condition enzyme activity. Such is the case of humic substances which complex with soluble phosphatase; the enzyme activity will be inactivated when making part of the complex (linked to the humic molecule) and reactivated again once the complex is broken down, e.g. by the action of UV light from the sun.

Key words: *Daphnia*, phosphatase, hydrolysis, photolysis.

RESUMEN

Todo empezó con el trabajo de Margalef de 1951

Desde 1951 Margalef especuló sobre la producción de fosfatasas solubles por zooplancton; "entomostracans" produjeron sus propias fosfatasas contribuyendo así a la regeneración de fosfato. Casi tres décadas después se ha confirmado que el eminente cientista tenía razón, después de que las técnicas analíticas hayan mejorado significativamente y se hayan introducido en los laboratorios de limnología. El papel de la fosfatasa soluble en aguas dulces puede ser investigado en estrecha relación con el plancton productor o sencillamente en relación con otras entidades químicas que abundan en el agua de los lagos, con capacidad para condicionar la actividad de enzimas. Es el caso de las sustancias húmicas que forman complejos con fosfatasa soluble; la actividad enzimática será desactivada cuando hace parte del complejo (ligado a la molécula húmica) y reactivada de nuevo cuando el complejo es roto, por ejemplo por la radiación UV solar.

Palabras clave: Daphnia*, fosfatasa, hidrolisis, fotolisis.*

INTRODUCTORY NOTE

This is a brief article, intended to be a tribute paid to Ramon Margalef, five years after his death on the 23rd of May, 2004. It will be written from the point of view of a person who, before meeting him, was inspired by his work to do her Master thesis, her Ph.D. dissertation, and about half of her research thereafter. After meeting him, and similarly to what happened to practically everyone, she would be taken by his natural sympathy and enjoy his company very much.

THE FIRST SUSPITION

I was at the time living in the United States, at Kent, Ohio, teaching and studying at Kent State University. After one year of course work for the Master degree, I needed a topic for my thesis. It was the year of 1980, there was no internet and only a few computers. One night, at the Kent State main library, I was fascinated with a paper published by Margalef, respecting the production of phosphatase activity by *Daphnia* (Margalef, 1951).

Margalef had run experiments in which he was measuring the phosphatase activity of both algae and zooplankton. He attributed the production of phosphatase activity to zooplankton, showing that the levels of the enzyme detected in his experiments could not be accounted for by the low density of algae present in his experimental set up. With an amazing intuition, Margalef suspected that not only phytoplankton, but zooplankton as well, were contributing directly to the production of phosphatase, and therefore indirectly contributing to the regeneration of orthophosphate in lakes.

FROM MARGALEF'S SPECULATION...

The topic was found, and I set up to demonstrate, utilizing equipment and laboratory techniques of almost 30 years later, that zooplankters were really producing their own phosphatases and not only releasing those ingested with their algal food (Boavida and Heath, 1984). In my experiments I did use *Daphnia magna* fed *Chlamydomonas acidophila*; *Daphnia* were grown in small aquaria and *Chlamydomonas* cultures were kept in a light-and-dark cycle of 12 h each and fed to the zooplankton only in exponential phase of growth (more details in Boavida and Heath, 1986).

It was believed by the scientific community of the time that the phosphatase released by *Daphnia*, and other herbivorous zooplankton as well, was the phosphatase produced by their algal food, eventually released into lake water after algal cell disruption in the digestive tracts of the zooplankton. The main purpose of the work was to determine whether the enzyme released by *D. magna* originated from the *Daphnia* itself, from its algal prey, or from both.

By growing one single zooplankter (*D. magna*) on one single, controlled algal food (*C. acidophila*) and by analyzing the phosphatases in the culture medium of *Daphnia* and comparing the eluted enzymes by anion exchange chromatography with those eluting from *Chlamydomonas* treated with a membrane detergent, it was concluded that the phosphatases released from *D. magna* were those of their algal food plus other of their own production; the elution peaks were very well distinct (Boavida and Heath, 1984). The conclusion that *D. magna* were producing their own enzymes corroborated what Margalef had apprehended 30 years earlier, with no technical means to demonstrate it.

PHOSPHATASES IN THE ENVIRONMENT

It was also found that algae were producing several phosphatases each, alkaline and acid, adaptively and constitutively (e.g. Boavida and Heath, 1986). If so many organisms in the phyto- and zooplankton were producing the enzyme, then it would have to be of some relevance to the several communities. It was known that phosphatases would hydrolyze larger phosphorus molecules in lake water (mainly phosphomonoesters, according to Kuenzler and Perras, 1965) and release orthophosphate in the process (Heath and Cooke, 1975).

However, when the importance of phosphatase activity for the whole lake metabolism was inferred, the result was somewhat a deception. In conditions of P-limitation, it seemed that the biological demand for phosphorus was much larger than the orthophosphate supplied for growth by hydrolysis. The main substrate for alkaline phosphatase in natural environments is phosphomonoesters, therefore these molecules will have to be present in lake water simultaneously with the enzyme. In eutrophic East Twin Lake (Ohio, U.S.A.) the phytoplankton was limited by available phosphorus all year around. The significance of hydrolysis by phosphatase was assessed by comparing the orthophosphate release rates with its uptake rates, on a seasonal basis. Although the correlation ob-

tained between alkaline phosphatase and phosphomonoesters in lake water was negative and highly significant ($P < 0.01$ for the significance of r), meaning that this process was important in the regeneration of orthophosphate, the phosphate made available through hydrolysis was but *circa* one percent of the total orthophosphate required for growth (Boavida and Heath, 1988). It was concluded that, although potentially important in the regeneration of orthophosphate, hydrolysis by alkaline phosphatase was insufficient to explain phytoplankton growth in terms of *P*-limitation in East Twin Lake.

The role of enzymatic hydrolysis by alkaline phosphatase as a recycling mechanism remained unclear, since the fraction of phosphorus made available by this mechanism was apparently very small with respect to the total phosphate demand of the seston, in spite of what was indicated by the high phosphatase activity found in lake water. In a mesotrophic lake (Lake Maggiore, Italy) very high levels of alkaline phosphatase activity were found concomitant with incommensurable, below detection levels of phosphomonoesters (Boavida, 1990, 1991). This result suggests that all phosphomonoesters in lake water were being utilized as substrate for phosphatase, and even though the released orthophosphate was not enough to justify all the phytoplankton growth, as evidenced by the situation of *P*-limitation. There were other autochthonous sources of phosphorus in that lake. The need for more research respecting this topic was obvious.

After what was found up to here, one question arose: If phosphatases are unimportant, why is there so much of them and so many organisms spending energy to produce these enzymes?

So far all research had been done in natural lakes. Would the results be similar if the same kind of research was undertaken in artificial lakes? The rare opportunity to study these aspects of phosphorus regeneration on a 35-year old reservoir being emptied for repair came up. Phosphomonoesters seemed to be relatively few during the emptying phase, although they gradually increased to substantial concentrations with the refilling. Alkaline phosphatase, on the other hand, increased with emptying of the reservoir but decreased when refilling began. In this study Marques and Boavida (1993) found that, although the orthophosphate concentrations were relatively high, in some periods alkaline phosphatase seemed to have higher importance in phosphorus dynamics, especially towards the end of the refilling process.

Another study on eutrophic reservoirs produced distinct results (Boavida and Marques, 1995). To assess the potential importance of alkaline phosphatase in orthophosphate regeneration, the activity of the enzyme was determined concomitantly with the determination of phosphomonoester concentrations, among other chemical forms of phosphorus. Contrary to the expectations for such productive waters where algal blooms were frequent, during the study period this process of phosphorus regeneration was not significant, probably because the product of hydrolysis was always abundant. It was concluded that, in spite of what had been repeatedly observed in natural lakes with similar trophic characteristics, the readily available fraction of phosphorus in these reservoirs was large and for that reason alkaline phosphatase activity was low. What seemed intriguing was the low concentration of phosphomonoesters found in the water; with little phosphatase activity this phosphorus fraction should always be high, unless hydrolysis took place as soon as phosphomonoesters were released into the water in the organic matter decomposition process.

CONTRADICTIONS IN THE SCIENTIFIC FINDINGS

As more research was done on the subject, inconsistencies and contradictions gradually appeared. It was sure that plankton organisms were producing phosphatases. The doubts resided on the potential significance of the enzymes to orthophosphate regeneration and on the role of the enzymes as indicators of lake trophic state as well.

On one hand, alkaline phosphatase was found to be produced in large quantities by planktonic algae in response to low orthophosphate concentration in the environment (e.g. Smith and Kalff,

1981). In addition, alkaline phosphatase was included among the good indicators of eutrophication (Istvanovics *et al.*, 1992). On the other hand, when a set of four European lakes and reservoirs of several degrees of trophy were examined (Boavida *et al.*, 1997), inverse correlations were expected between enzyme activity and the substrate and also between phosphatase activity and the product of enzymatic hydrolysis, since it was assumed that the phosphatases were being produced adaptively, i.e. in response to the low concentrations of orthophosphate in the water. Some kind of phosphatase variation was also expected, following the trophic gradient. No significant correlation was found, however, between alkaline phosphatase activity and the concentration of phosphomonoesters, and a highly significant, although positive, correlation between alkaline phosphatase and soluble reactive phosphorus (taken as a measure of orthophosphate) was found. According to the above cited literature alkaline phosphatase should be produced as a response to low orthophosphate in the environment –that did not seem to be the case. Other enzymes, such as 5′-nucleotidase (Cotner and Wetzel, 1991) could be more relevant to phosphorus regeneration in the oligotrophic lake where phytoplankton likely were P-limited and bacteria were limited by organic carbon availability as substrates.

Unlike the overwhelming number of references in the literature for the importance of potential orthophosphate release by alkaline phosphatase, evidence for the "non importance" of alkaline phosphatase in orthophosphate regeneration is hard to find.

ONE EXPLANATION IS OFFERED

After some investigation on phosphorus dynamics in bog lakes, it was thought that orthophosphate would be released from humic substance molecules upon irradiation of these with mild UV light (Francko and Heath, 1979). This would be the UV light from the sun, at the intensities it reaches the earth surface and penetrates lake water only a few centimeters.

Later on it was found that orthophosphate concentrations in lake water would increase, not as a direct consequence of the degradation of complex phosphorus by UV, but, instead, as a result of more complex mechanisms involving phosphatase enzymes (Wetzel, 1991). Humic substances resulting from organic matter decomposition are usually abundant in lake water. These are able to form large complexes with phosphatases, when the two kinds of molecules approach each other in the natural hydrodynamics in the lake. When the phosphatases form complexes with the humic substances, they are inactivated. But, once these large phosphatase/humic complexes are hit by the UV light of the sun, the two original molecules separate and the phosphatase, once free in lake water, becomes active again and capable of performing hydrolysis (Wetzel, 1993).

All this was later tested in laboratory experiments where humic extracts of specific macrophytes were irradiated with low intensity UV light, similar to that of the sun, and the results corroborate what was said in the last paragraph: Phosphatase was able to complex with the humics, and in that condition no phosphatase activity could be measured, showing that the enzymes were inactivated. After irradiation with weak UV light, to break down the humic/phosphatase complexes, phosphatase activity would again be measured, showing that the phosphatase was free and reactivated (Boavida and Wetzel, 1998).

In some relatively recent work (Geraldes and Boavida, 2003) it was seen that none of the factors investigated in two different lakes (water chemistry, reservoir age, and external disturbance) made a difference in phosphatase activity. It appears that much is still to be investigated on the role of phosphatases in freshwater environments (Boavida 2000a). It is necessary to go back to this already old subject and search for the actual function of phosphatases in freshwater environments, utilizing the new techniques available and all the knowledge scientists have

accumulated until now, which they didn't have a few decades ago (Boavida, 2000b).

CONCLUSION

The control of eutrophication may be effected through regulation of phosphatase activity if a means is found to prevent UV photolysis, thus kipping phosphatases complexed to humic substances and, therefore, inactive, unable to perform hydrolysis and make orthophosphate available. It is very important to understand every phenomenon going on in lakes. As Margalef himself said about two decades ago, "The epicontinental (freshwater or limnic) part of the biosphere is not only a section of the global water cycle, but a most important part of it" (Margalef, 1991).

ACKNOWLEDGEMENTS

Great part of what is found in this paper was included in an oral presentation held at the 2005 ASLO summer meeting in Santiago de Compostela, Spain. The oral presentation was included in a special session dedicated to the memory of Ramon Margalef.

REFERENCES

BOAVIDA, M. J. 1990. Natural plankton phosphatases and the recycling of phosphorus. *Verh. Internat. Verein. Limnol.*, 24: 58–259.

BOAVIDA, M. J. 1991. Search for phosphomonoesters in Lake Maggiore (N. Italy) during summer. *Mem. Ist. Ital. Idrobiol.*, 49: 19–27.

BOAVIDA, M. J. 2000a. The obscure role of phosphatases in freshwater lakes. *Verh. Internat. Verein. Limnol.*, 27: 1–3.

BOAVIDA, M. J. 2000b. Phosphatases in phosphorus cycling: A new direction for research on an old subject. In *Limnology and Lake Management 2000* + (ed. T. Berman, K. D. Hambright, J. Gat, S. Gafny & M. Tylzer), pp. 433–440. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

BOAVIDA, M. J., W. HAMZA, D. RUGGIU & R. T. MARQUES. 1997. Eutrophication: Alkaline phosphatase revisited. *Mem. Ist. Ital. Idrobiol.*, 56: 15–21.

BOAVIDA, M. J. & R. T. HEATH. 1984. Are the phosphatases released by *Daphnia magna* components of its food? *Limnol. Oceanogr.*, 29: 641–645.

BOAVIDA, M. J. & R. T. HEATH. 1986. Phosphatase activity of *Chlamydomonas acidophila* Negoro (Volvocales, Chlorophyceae). *Phycologia*, 25: 400–404.

BOAVIDA, M. J. & R. T. HEATH. 1988. Is alkaline phosphatase always important in phosphate regeneration? *Arch. Hydrobiol.*, 111: 507–518.

BOAVIDA, M. J. & R. T. MARQUES. 1995. Low activity of alkaline phosphatase in two eutrophic reservoirs. *Hydrobiologia*, 297: 11–16.

BOAVIDA, M. J. & R. G. WETZEL. 1998. Inhibition of phosphatase activity by dissolved humic substances and hydrolytic reactivation by natural ultraviolet light. *Freshwat. Biol.*, 40: 285–293.

COTNER, J. B. & R. G. WETZEL. 1991. 5′nucleotidase activity in a eutrophic lake and in an oligotrophic lake. *Appl. Environm. Microbiol.*, 57: 1306–1312.

FRANCKO, D. & R. T. HEATH. 1979. Functionally distinct classes of complex phosphorus compounds in lake water. *Limnol. Oceanogr.*, 24: 463–473.

GERALDES, A. M. & M. J. BOAVIDA. 2003. Do distinct water chemistry, reservoir age and disturbance make any difference on phosphatase activity? *J. Limnology*, 62: 163–171.

HEATH, R. T. & G. D. COOKE. 1975. The significance of alkaline phosphatase in a eutrophic lake. *Verh. Internat. Verein. Limnol.*, 19: 959–965.

ISTVANOVICS, V., K. PETTERSSON, D. PIERSON & R. BELL. 1992. Evaluation of phosphorus deficiency indicators for summer phytoplankton in Lake Erken. *Limnol. Oceanogr.*, 37: 890–900.

KUENZLER, E. J. & J. P. PREPAS. 1965. Phosphatases of marine algae. *Biol. Bull.*, 128: 271–248.

MARGALEF, R. 1951. Role des entomostraces dans la régéneration des phosphates. *Verh. Internat. Verein. Limnol.*, 11: 246–247.

MARGALEF, R. 1991. Comments on rivers and models. *Limnética*, 7: 185–190.

MARQUES, R. T. & M. J. BOAVIDA. 1993. Effects of the water level fluctuations on the forms of phosphorus in mesotrophic Maranhão Reservoir. *Verh. Internat. Verein. Limnol.*, 25: 1207–1209.

SMITH, R. E. H. & J. KALFF. 1981. The effect of

phosphorus limitation on algal growth rates: evidence from alkaline phosphatase. *Can. J. Fish. Aquat. Sci.*, 38: 1421–1427.

WETZEL, R. G. 1991. Extracellular enzyme interactions: Storage, redistribution, and interspecific communication. In *Microbial Enzymes in Aquatic Environments* (ed. R. J. Chróst), pp. 6–28. Springer-Verlag, Berlin.

WETZEL, R. G. 1993. Humic compounds from wetlands: Complexation, inactivation, and reactivation of surface-bound and extra-cellular enzymes. *Verh. Internat. Verein. Limnol.*, 25: 122–128.

Limnetica, 31 (2): 193-204 (2012)

Influencia de los procesos naturales y antrópicos sobre la calidad del agua en cuatro embalses cubanos

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Received: 19/3/2010 Accepted: 23/1/2012

ABSTRACT

Influence of natural and antropic processes on the water quality in four cuban reservoirs

The waters of the reservoirs Paso Bonito, Avilés, Abreus and El Salto, located at south-center of Cuba, are used in agriculture, fishing, industries and human consumption. The aim of this research was to identify the physicochemical characteristics of the water of these reservoirs and the influential processes. Application of Gibbs and Piper diagrams to the major ions of the water, measured during the period 1986-2005, identified weathering as the natural process with greater influence on chemical composition of the water. The concentrations of major ions were only significantly different between periods (dry and wet) in Abreus reservoir, in relationship to its position within basin. Significant similarities according to ANOVA were frequent between Abreus and El Salto, where the alkalinity was also higher by silicates weathering in correspondence with its geology. The influence of anthropogenic activities on water quality was revealed by mean of Cl^- : $Na^+ + K^+$, $Ca^{2+} + Mg^{2+}$: $Na^+ + K^+$ ratios and trophic state index determined by measurements of transparency, nutrients and chlorophyll *a*. Eutrophy was predominant in reservoirs, where the basins are more antropized. The application of a graphical method revealed that values of *Chlorophyll a* were the cause of turbidity of water in Aviles, Abreus and El Salto and that nitrogen was the limiting nutrient for phytoplankton growth.

Key words: Major ions, rock weathering, reservoir, eutrophication.

RESUMEN

Influencia de los procesos naturales y antrópicos sobre la calidad del agua en cuatro embalses cubanos

Las aguas de los embalses Paso Bonito, Avilés, Abreus y El Salto, situados en el centro-sur de Cuba, son usadas en la agricultura, la pesca, la industria y para el consumo humano. El objetivo de esta investigación fue identificar las características físicas y químicas de las aguas de estos embalses y los procesos influyentes. La aplicación de los diagramas de Gibbs y trilineal, sobre los componentes mayoritarios del agua medidos durante la etapa 1986-2005, permitió identificar la meteorización como el proceso natural de mayor influencia sobre la composición química de las aguas. Las concentraciones de los iones mayoritarios solo registraron diferencias significativas entre periodos (seco y lluvioso) en el embalse Abreus, lo cual se relacionó con su posición dentro de la cuenca. Las similitudes significativas según el ANOVA, fueron frecuentes entre los embalses Abreus y El Salto, donde también fue mayor la alcalinidad por la disolución de los silicatos, en concordancia con su geología. La influencia de las actividades antrópicas sobre la calidad del agua se reveló mediante la razones Cl^- : $Na^+ + K^+$, $Ca^{2+} + Mg^{2+}$: $Na^+ + K^+$ y el índice del estado trófico, determinado mediante mediciones de la transparencia y la concentración de nutrientes y Clorofila a. *La eutrofia fue mayor en los embalses donde las cuencas estaban más antropizadas. La aplicación de un método gráfico reveló que la turbiedad del agua en los embalses Avilés, Abreus y El Salto se debió a los valores de Chlorophyll* a *y que el nitrógeno fue el nutriente que limitó el desarrollo fitoplanctónico.*

Palabras clave: *Iones mayoritarios, meteorización, embalses, eutrofización.*

INTRODUCCIÓN

Los embalses son considerados centinelas, integradores y reguladores del cambio climático (Williamson *et al*., 2009). Sin embargo, es necesario disponer de un conocimiento básico sobre la calidad de las aguas embalsadas que permita distinguir el efecto del cambio climático de otros procesos naturales o antrópicos influyentes.

El estudio de los componentes mayoritarios del agua permite reconocer procesos de interacción entre la roca y el agua que son responsables de su composición química (Li *et al*., 2009). El proceso de meteorización se puede identificar mediante el modelo de Gibbs (1970), el diagrama de Piper (1944) y mediante el uso de relaciones iónicas (Chung *et al*., 2009). Este proceso es dependiente de la temperatura, de las precipitaciones y de las actividades humanas desarrolladas en las cuencas (Subramanian *et al*., 2006).

Las actividades antrópicas generadoras de altas cargas de nutrientes estimulan procesos de eutrofización de las aguas. Las aguas eutróficas generan altos costes de tratamiento (Dodds, 2007), así como alteraciones en el olor y el sabor del agua (Peter, 2008) con peligros potenciales para la salud, debido a la presencia de toxinas producidas por algunas especies de cianobacterias (Sömek *et al*., 2008).

Esta investigación está dirigida a identificar las características físicas y químicas de las aguas de los embalses Paso Bonito, Avilés, Abreus y El Salto situados en cuatro cuencas de la región central cubana, y los procesos que las determinan, a partir del trabajo de campo y del análisis de los datos recogidos en un periodo de 20 años.

Estos resultados constituyen una referencia para la observación de cambios en los procesos geoquímicos influyentes en la calidad química de las aguas en esta región, y representan una herramienta para la gestión del recurso.

MATERIALES Y MÉTODOS

Área de estudio

Los embalses Paso Bonito, Avilés, Abreus y El Salto se localizan en la provincia de Cienfuegos, en el centro-sur de Cuba (Fig. 1). Entre los principales usos de sus aguas destacan la agricultura,

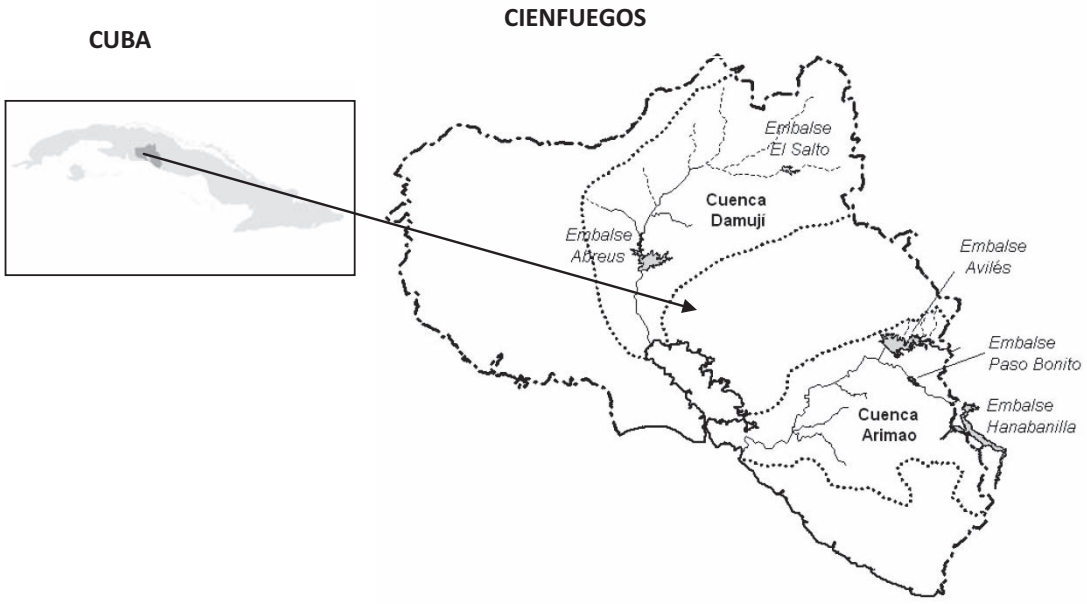

Figura 1. Área de estudio. Se muestran las cuencas de los ríos Arimao y Damují y los embalses Paso Bonito, Avilés, Abreus y El Salto. *Study area. The map shows the watershed of Arimao and Damují rivers and the reservoirs Paso Bonito, Avilés, Abreus and El Salto.*

la pesca y el consumo industrial y humano. Estos embalses son impactados por industrias azucareras y residuos humanos y agrícolas. En las cuencas de los embalses Abreus y El Salto se localiza un mayor número de fuentes de contaminación.

Avilés y Paso Bonito fueron construidos en la parte alta de la cuenca del río Arimao, caracterizado por una topografía variable y una geología compleja, compuesta fundamentalmente por rocas ígneas y metamórficas. En Avilés predominan las llanuras y las rocas anfibolitas, granito, cuarzodioritas con algunas rocas sedimentarias como las calizas, margas y tobas. Paso Bonito tiene su cuenca en la zona montañosa, donde predominan los esquistos.

Los embalses El Salto y Abreus ocupan una llanura en la cuenca del río Damují (en la cabecera y final de la cuenca, respectivamente). Yacen principalmente sobre rocas sedimentarias (margas, calizas, aleurolitas, brechas, conglomerados, areniscas). Las rocas ígneas, en menor cuantía, están representadas por basaltos. Algunas características de los embalses se muestran en la Tabla 1.

Características físicas y químicas

La base de datos para el estudio de los componentes mayoritarios del agua procede de la Empresa de Aprovechamiento Hidráulico de Cienfuegos. Incluye la conductividad eléctrica (CE), la dureza total (D_T) y la concentración de los iones $(HCO_3)^-$, $(Cl)^-$, $(SO_4)^{2-}$, Ca^{2+}, Mg^{2+} y $(Na^+ + K^+)$, medidos durante la etapa 1986-2005. Las sales solubles totales (SST) se calcularon mediante la suma de las concentraciones (mg/L) de los iones antes mencionados.

Para evaluar el estado trófico de los embalses Avilés, Abreus y El Salto se muestreó la superficie del punto de toma durante los meses de abril, agosto, octubre y diciembre de 2008 y marzo de 2009. Se determinó la concentración de fósforo total (TP) por reducción con ácido ascórbico (APHA, 1998), la transparencia del agua como profundidad de visión de un disco de Secchi (SD) de 20 cm de diámetro, la concentración de clorofila *a* (CHL *a*) por el método de fluorescencia APHA (1998) y la concentración de nitrógeno inorgánico total (Ni_T) mediante la suma de las concentraciones de nitrógeno amoniacal ($N–NH_4$), nitrógeno en forma de nitrito ($N–NO_2$) y nitrógeno en forma de nitrato ($N–NO_3$). Las concentraciones de ($N–NH_4$) se determinaron por formación de indofenol azul, el ($N–NO_2$) por diazotación con sulfanilamida y el ($N–NO_3$) por reducción con hidracina APHA (1998). Estos ensayos se realizaron en el laboratorio del Centro de Estudios Ambientales de Cienfuegos. Los detalles del estado trófico del embalse Paso Bonito fueron evaluados por Betancourt (2009).

Tratamiento de datos

Para la clasificación del agua según los valores de la CE se usó el criterio de González (2000). Este autor considera que el agua es "ligeramente salina" cuando los valores de la conductividad eléctrica se encuentran en el intervalo 210-400 µS/cm y "medianamente salina" para el intervalo 410-600 µS/cm. La clasificación del agua según su contenido de dureza se realizó de acuerdo con el criterio de Durfor y Becker (1964). Estos autores plantean que cuando la

Tabla 1. Características morfométricas de los embalses. *Morphometric characteristics of the reservoirs.*

Características*	Paso Bonito	Avilés	Abreus	El Salto
Puesta en funcionamiento	1975	1980	1986	1975
Altitud del embalse (msnm)	86.3	77	10	52
Altitud media de la cuenca (msnm)	187	165	50	76
Área de la cuenca (km^2)	65	310	1075	80.0
Área del embalse (km^2)	1.25	77.0	5.40	2.46
Área de la cuenca: Área del embalse (Ac:Ae)	52	4	199	32.5
Volumen de almacenamiento (hm^3)	8	190	50	9.5
Profundidad máxima del embalse (m)	19.5	36.6	12.5	17

* Datos tomados del archivo de la Delegación de Recursos Hidráulicos en Cienfuegos.

dureza total está dentro del intervalo 121-180 mg/L el agua se considera "dura". Para valores superiores se clasifica como "muy dura".

Para identificar los mecanismos que intervinieron en la química del agua de los cuatro embalses en estudio se aplicaron las relaciones iónicas y los diagramas de Gibbs (1970) y de Piper (1944), también conocido como diagrama trilineal.

Se aplicó ANOVA de un factor para comparar la calidad del agua referida a los componentes mayoritarios, en los cuatro embalses estudiados. La prueba *T* para dos muestras independientes se usó para comparar los valores de las razones iónicas y los componentes mayoritarios del agua durante los periodos seco y lluvioso, en los cuatro embalses. Se usó el coeficiente de Spearman para determinar las relaciones entre los índices de estado trófico calculados.

La clasificación trófica se hizo mediante un índice de estado trófico (TSI) sugerido por Carlson (1977) y modificado por Toledo *et al.* (1983) para zonas tropicales. Las ecuaciones usadas en el cálculo de los índices para las variables diagnóstico (transparencia SD, TP, PO_4 y CHL *a*) así como el índice de estado trófico medio que combina los índices de cada una de las variables mencionadas se expresan:

$$TSI_{\text{Modificado}}(SD) = 10 * \left[6 - \left(\frac{0.64 + \ln(SD)}{\ln 2}\right)\right]$$

$$TSI_{\text{Modificado}}(TP) = 10 * \left[6 - \frac{\ln\left(\frac{80.32}{TP}\right)}{\ln 2}\right]$$

$$TSI_{\text{Modificado}}(PO_4) = 10 * \left[6 - \left(\frac{\ln\left(\frac{21.67}{PO_4}\right)}{\ln 2}\right)\right]$$

$$TSI_{\text{Modificado}}(CHL\ a) = 10 * \left[6 - \left(\frac{2.04 - 0.695 \ln CHL\ a}{\ln 2}\right)\right]$$

$$TSI_{\text{Modificado}}\ (\text{medio}) = \frac{TSI(SD) + 2\,[TSI(TP) + TSI(PO_4) + TSI(CHL\ a)]}{7}$$

Con el resultado del cálculo del $TSI_{\text{Modificado}}$ (medio) se clasificó el estado trófico de las aguas según el siguiente intervalo: Oligotrofia ≤ 44; Mesotrofia $44 < \text{TSI} < 54$ y Eutrofia ≥ 54.

Se siguió el criterio propuesto por Morris y Lewis (1988) para evaluar la relación Ni_T:TP (nitrógeno inorgánico total: fósforo total), como indicador del nutriente que limita la productividad del sistema. Estos autores consideran limitaciones de nitrógeno cuando la relación es menor que 0.5, para el intervalo 0.5-4.0, ambos limitan y para valores superiores a 4 es el fósforo el nutriente limitante.

RESULTADOS

Composición de las aguas y procesos químicos

Los estadísticos descriptivos de los iones mayoritarios, CE y D_T se muestran en la Tabla 2. Los embalses en la cuenca del río Damují (El Salto y Abreus) registraron los valores más altos de la CE, iones mayoritarios y D_T. En estos embalses el agua fue muy dura según la clasificación de Durfor y Becker (1964), y medianamente salina de acuerdo con la clasificación de González (2000). Según estas clasificaciones, el agua de los embalses construidos en la cuenca del río Arimao (Paso Bonito y Avilés) fue dura y ligeramente salina. En los cuatro embalses las concentraciones de los iones mayoritarios (mg/L) se pudo ordenar de la siguiente manera: $Ca^{2+} > Na^+ + K^+ > Mg^{2+}$ y $(HCO_3)^- > Cl^- > SO_4^{2-}$ y el agua resultó bicarbonatada cálcica.

La mayor cantidad de similitudes (ANOVA, $p > 0.05$) se encontró entre las concentraciones de los iones mayoritarios de los embalses El Salto y Abreus.

De acuerdo con el diagrama de Gibbs (1970), la composición química de las aguas en los cuatro embalses estuvo controlada por procesos de meteorización. En los embalses construidos en el río Damují las observaciones se localizaron más pró-

Tabla 2. Estadísticos descriptivos de la conductividad eléctrica, la dureza total y los iones mayoritarios. *Descriptive statistics of conductivity, total hardness and major ions.*

		CE µS/cm	$(HCO_3)^-$ mg/L	Cl^- mg/L	$(SO_4)^{2-}$ mg/L	Ca^{2+} mg/L	Mg^{2+} mg/L	Na^++K^+ mg/L	D_T mg/L
Paso Bonito	Media	257	139	12	7	39	6	7	125
	Máx.	358	266	25	22	59	19	15	230
	Mín.	160	70	6	1	13	1	3	65
	DS	35.8	20.1	2.5	2.7	7.6	2.8	1.9	20.2
	n	240	240	240	240	240	240	240	240
Avilés	Media	306	147	17	10	29	12	15	125
	Máx.	377	183	23	17	40	18	21	155
	Mín.	240	119	12	5	17	7	9	95
	DS	30.6	13.7	2.1	2.4	4.4	2.8	2.6	12.3
	n	105	105	105	105	105	105	105	105
Abreus	Media	556	236	41	33	64	13	35	216
	Máx.	745	327	63	53	94	22	49	318
	Mín.	380	152	10	19	32	6	16	130
	DS	72.6	36.9	7.0	5.5	12.0	2.7	5.5	37.0
	n	233	233	233	233	233	233	233	233
El Salto	Media	479	223	27	23	47	15	32	186
	Máx.	680	451	46	43	74	31	56	452
	Mín.	310	147	14	9	21	5	11	90
	DS	69.0	39.5	6.1	7.0	11.2	4.9	9.1	44.1
	n	94	94	94	94	94	94	94	94

ximas al área de evaporación-cristalización que en los casos de los embalses construidos en el río Arimao, originado por los valores más altos de concentración de SST (Fig. 2). Este resultado es compatible con el obtenido por la aplicación del ANOVA, el cual mostró diferencias significativas ($F = 1307$; $p < 0.0001$) en las mediciones de la CE entre estos embalses. La prueba de comparación múltiple de Tukey reveló que hay diferencias significativas ($p = 0.000$, en todos los casos) al comparar dos a dos.

En el diagrama trilineal los puntos se ubicaron próximos a los vértices que corresponde a los iones Ca^{2+} y $(HCO_3)^-$ en los cuatro embalses (Fig. 3). En los embalses Abreus y El Salto las observaciones se acercaron al área del gráfico que corresponde a las mayores proporciones de (Na^++K^+). Este resultado se corroboró con las similitudes (ANOVA, $p > 0.05$) obtenidas para las concentraciones de (Na^++K^+) entre dichos embalses y las diferencias ($p < 0.05$) con los embalses Paso Bonito y Avilés.

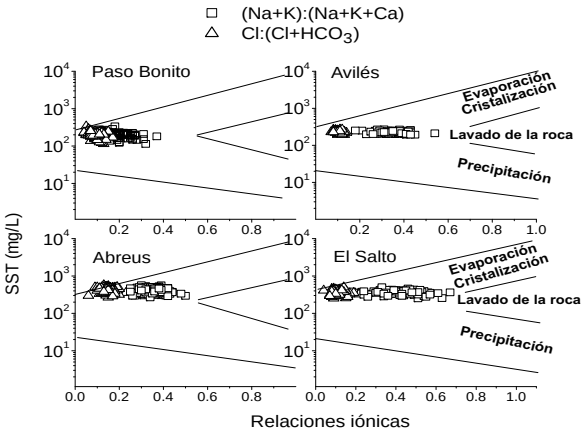

Figura 2. Representación gráfica de la dependencia entre las sales solubles totales y las relaciones iónicas del agua en los cuatro embalses estudiados, según el modelo de Gibbs (1970). La relación SST *vs* Cl^-:[Cl^-+$(HCO_3)^-$] se simbolizó con un cuadrado sin relleno y la relación SST *vs* (Na^++K^+):(Na^++K^++Ca^{2+}) con un triángulo sin relleno. *Dependence between total soluble salts and ionic relations of the water for the studied reservoirs: TSS vs Cl^-:[Cl^-+$(HCO_3)^-$] and TSS vs (Na^+ + K^+):(Na^+ + K^++Ca^{2+}) following Gibbs (1970). SST vs Cl^-:[Cl^-+$(HCO_3)^-$] is showed by empty square and TSS vs (Na^+ + K^+):(Na^+ + K^++Ca^{2+}) by empty triangle.*

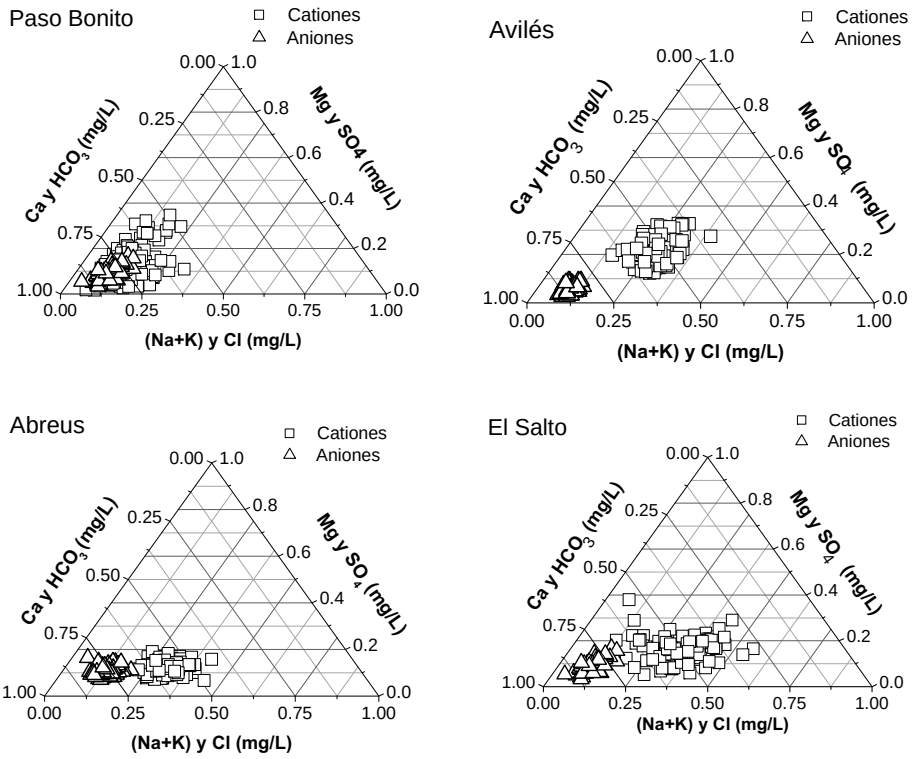

Figura 3. Representación de la composición relativa de aniones (triángulo) y cationes (cuadrado) mediante el diagrama triangular. Muestra la composición relativa de las concentraciones de aniones y cationes expresados en mg/L en los embalses situados en la cuenca del río Arimao (Paso Bonito y Avilés) y en la cuenca del río Damují (Abreus y El Salto). *Ternary plots for mean concentrations expressed in mg/L of anions (triangle) and cations (square) in Paso Bonito and Avilés reservoirs (Arimao watershed) and Abreus y El Salto reservoirs (Damují watershed).*

En el embalse Abreus hubo diferencia significativa ($t = -4.425$ y $p < 0.0001$) para las razones $(Ca^{2+}+Mg^{2+})$: $(Na^{+}+K^{+})$, Ca^{2+}: $(SO_4)^{2-}$ y para las concentraciones de los iones mayoritarios ($p < 0.0001$) al comparar sus valores en ambos periodos. En la figura 4 (C y E) se puede observar que en este embalse las observaciones correspondientes a las razones del periodo seco registraron los mayores valores.

En el embalse El Salto la razón $(Ca^{2+}+Mg^{2+})$: $(HCO_3)^{-}$ fue inferior a la unidad (0.99; Fig. 4A), en el resto de los embalses fue superior (entre 1.03 y 1.12) e indicó el predominio de la dureza permanente en sus aguas y la asociación del Ca^{2+}y Mg^{2+} a aniones diferentes al $(HCO_3)^{-}$.

La elevada contribución del $Ca^{2+}+Mg^{2+}$ al total de cationes (TC) en los cuatro embalses se manifestó en los altos valores de la razón $(Ca^{2+}+Mg^{2+})$: TC (Fig. 4B). La mayor contribución se verificó en los embalses Paso Bonito (0.89) y Avilés (0.79).

Las razones $(Ca^{2+}+Mg^{2+})$: $(Na^{+}+K^{+})$ alcanzaron cifras superiores a la unidad en todos los embalses (en el intervalo 2.85-8.78; Fig. 4C). Los valores más altos corresponden a los embalses situados en la cuenca del río Arimao.

Los valores medios de la razón Cl^{-}: $Na^{+}+K^{+}$ fueron inferiores a la unidad (en el intervalo; 0.59-0.77), con una distribución de las observaciones por debajo de la línea 1:1, excepto en el embalse Paso Bonito, donde la razón fue 1.21 (Fig. 4D).

En la figura 4E se muestra la poca relación existente entre los iones Ca^{2+} y $(SO_4)^{2-}$ con valores de la razón $r = Ca^{2+}$: $(SO_4)^{2-}$ mayores que la unidad.

La alcalinidad producida por la disolución de carbonato ($Alcalinidad_{disolución\ de\ carbonato} = 0.74\ Ca_{total} + 0.4\ Mg_{total}$) y la producida por la diso-

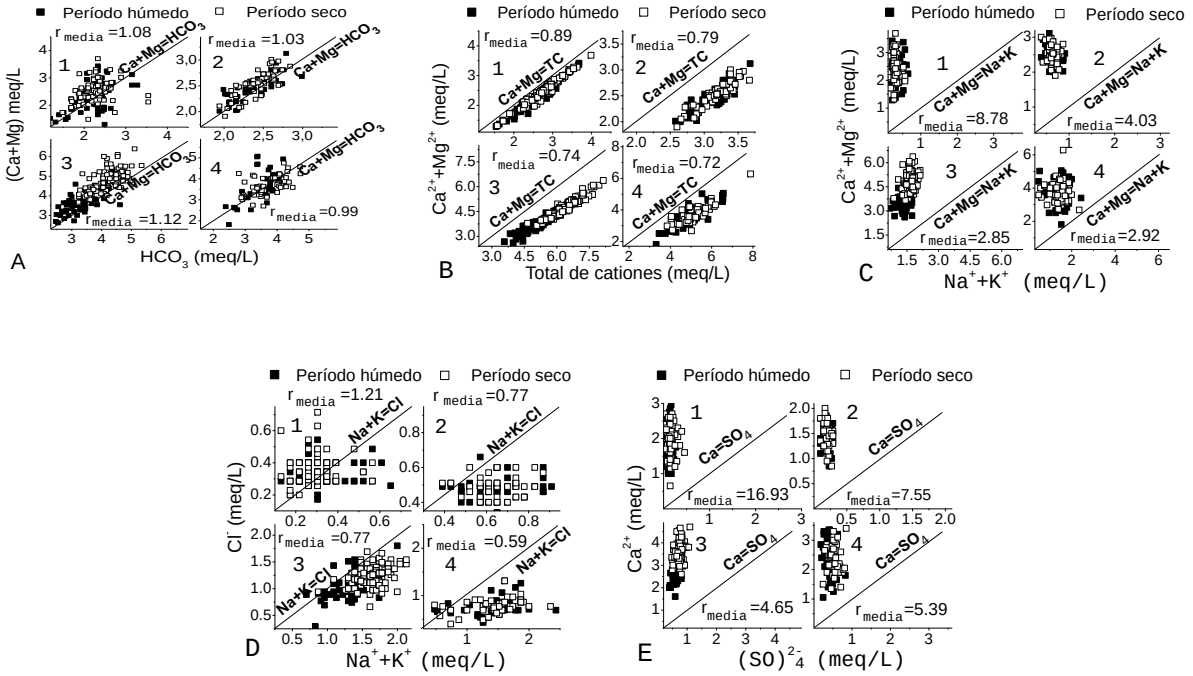

Figura 4. Relación entre las concentraciones iónicas (meq/L) en los cuatro embalses estudiados. Cada embalse se identificó con un número: Paso Bonito (1), Avilés (2), Abreus (3) y El Salto (4). La figura 4A expresa la relación entre el $Ca^{2+}+Mg^{2+}$ y el $(HCO_3)^-$; 4B, la relación entre el $Ca^{2+}+Mg^{2+}$ y los iones totales; 4C, la relación entre el $Ca^{2+}+Mg^{2+}$ y el Na^++K^+; 4D, la relación entre el Cl^- y el Na^++K^+, y 4E, la relación entre Ca^{2+} y $(SO_4)^{2-}$. Las razones entre las especies iónicas se identificaron por "*r*" y representan el promedio de las razones durante los periodos seco y húmedo. *Relationship between ionic concentrations (meq/L) in the studied reservoirs. They were identified by numbers: Paso Bonito (1), Avilés (2), Abreus (3) and El Salto (4). Figure 4A, 4B, 4C and 4D shows, respectively, the relationship between* $Ca^{2+}+Mg^{2+}$ *and:* $(HCO_3)^-$*, total ions and* Na^++K^+ *while 4D represents the relationship between* Ca^{2+} *and* $(SO_4)^{2-}$*. The ratios between the ionic specie were labeled as "*r*" and they represent the mean ratio during the dry and wet periods.*

lución de silicato ($Alcalinidad_{disolución\ de\ silicato}$ = $Alc._{total}$ − $Alc._{disolución\ de\ carbonato}$) se exponen en la figura 5. Los valores más altos en ambos casos corresponden a los embalses localizados en la cuenca del río Damují.

Estado trófico y nutrientes

Concentraciones de Ca^{2+} cercanas a 40 mg/L limitan fuertemente las concentraciones de fósforo soluble (Margalef, 1982). Estrada (1978) propuso que la precipitación del fosfato con el $CaCO_3$ es el principal mecanismo que controla su solubilidad en aguas duras previniendo la eutrofización. Sin embargo, los altos valores de Ca^{2+} en los embalses estudiados (Tabla 2) no limitaron las concentraciones de TP, lo cual se demostró en los altos valores del TSI_{medio} calculado para

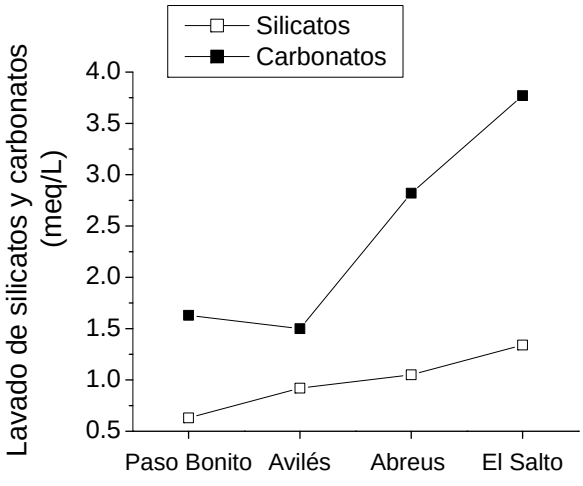

Figura 5. Contribución de la disolución de carbonatos y silicatos a la alcalinidad del agua en los cuatros embalses. *The contribution of weathering of carbonates and silicates to total alkalinity in the four considered reservoirs.*

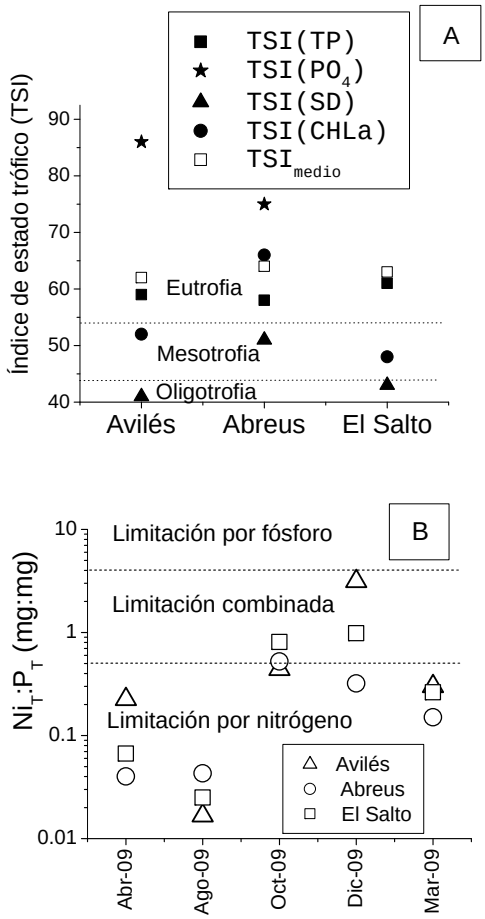

Figura 6. A: Índice del estado trófico medio de las variables TP, $(PO_4)^{3-}$, SD y CHL *a*, calculado según el criterio de Carlson (1977), modificado por Toledo *et al.* (1983) para zonas tropicales. Se representan los índices de estado trófico calculados con las concentraciones promedio de fósforo total: TSI (TP); ortofosfato: TSI(PO_4); clorofila *a*: TSI(CHL) y de las mediciones promedio de la transparencia: TSI(SD), así como el índice de estado trófico calculado con el promedio de los TSI de cada variable: TSI_{medio}. Las líneas de puntos separan los límites del estado trófico. En 6B se representan las relaciones entre el nitrógeno inorgánico y el fósforo total. Las líneas horizontales indican niveles de la razón de Ni_T y TP sugeridos por Morris y Lewis (1988) para identificar el nutriente limitante. *A: Mean trophic state index for TP, $(PO_4)^{3-}$, transparency and chlorophyll* a*, computed according to the criterion of Carlson (1977) modified by Toledo* et al. *(1983) for tropical zones. Trophic State Index calculated by means of the average concentrations of: total phosphorus: TSI(TP); orthophosphate: TSI(PO_4); chlorophyll* a*: TSI(CHL) and the average measurements of transparency: TSI(SD). Additionally, the Trophic State Index calculated with the average of the TSI of each variable: TSI_{medio} is presented. The dotted line shows the limits between the different trophic states. B: relationships between inorganic nitrogen and total phosphorus. The horizontal lines indicate DIN:TP ratios suggested by Morris and Lewis (1988) to identify the limiting nutrient for phytoplankton.*

las concentraciones de TP y PO_4 en los embalses Abreus, Avilés y El Salto (Fig. 6A). Estos resultados demostraron que la precipitación del fósforo es un proceso complejo y que en aguas duras también se verifican procesos de eutrofia.

El uso del TSI de Carlson (1977) modificado por Toledo y colaboradores (1983) reveló un predominio de aguas eutróficas en los cuatro embalses. De acuerdo con el TSI calculado para la CHL *a* como variable diagnóstico, los embalses Avilés y El Salto fueron mesotróficos y Abreus fue eutrófico, mientras que el TSI calculado con los valores de la transparencia clasificó a los embalses El Salto y Avilés como oligotróficos y al embalse Abreus como mesotrófico. El TSI resultado de la aplicación de la ecuación que usa el valor medio de todos los índices ($TSI_{modificado}$ medio) clasificó a estos tres embalses como eutróficos (Fig. 6A).

Las correlaciones entre los TSI de las tres variables diagnóstico fueron positivas. Solo resultó significativa ($p < 0.01$) la correlación TSI(CHL) *vs* TSI(SD).

Los resultados de las diferencias entre los TSI para las variables diagnóstico en los tres embalses estudiados se muestran en la figura 7B. En el eje de las abscisas se representaron las diferencias entre los TSI(CHL) y TSI(SD) y en las ordenadas las diferencias entre TSI(CHL) y TSI(TP). Cuando se comparan las figuras 7A y 7B se advierte que la mayoría de las observaciones se ubicaron en el área donde predominan las partículas grandes y la herbivoría del zooplancton. Todos los puntos se ubicaron por debajo de la diagonal y separado del origen (con un intercepto en $y = -21.07$).

El 80 % de los valores de la razón Ni_T: TP fue menor que 0.5, lo que mostró al nitrógeno como el nutriente limitante del desarrollo fitoplanctónico en los embalses Avilés, Abreus y El Salto, según la aplicación del criterio de Morris y Lewis (1988). El 20 % de los valores reveló limitación por ambos nutrientes ($0.5 < NiT : TP < 4$) (Fig. 6B).

DISCUSIÓN

Las relaciones iónicas y los diagramas de Gibbs (1970) y trilineal permiten establecer cómo han

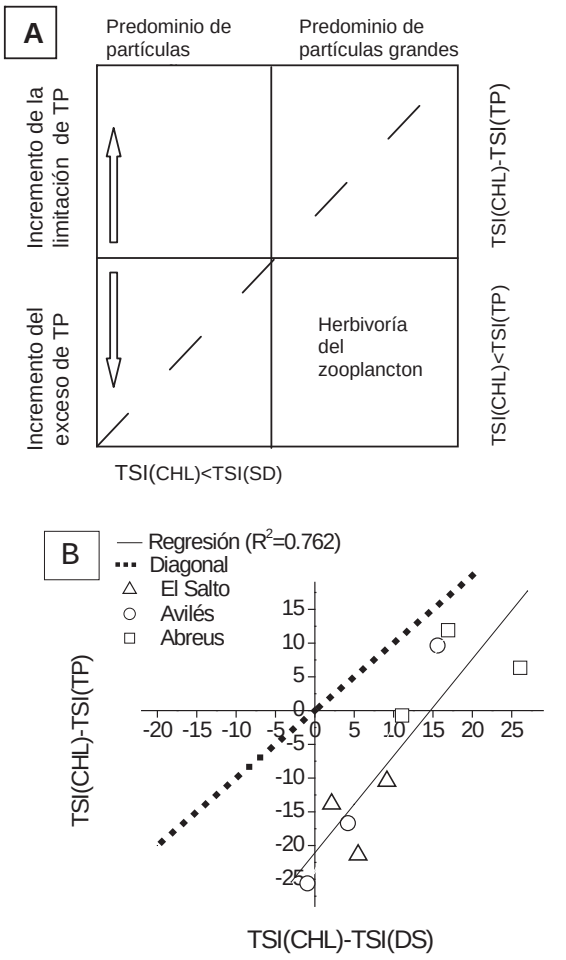

Figura 7. A: Posibles interpretaciones de las desviaciones del índice de estado trófico, según Carlson y Havens (2005). B: diferencias de los Índices de Estado Trófico para los tres embalses estudiados. La mayor cantidad de observaciones se localizaron en el cuadrante que corresponde con el predominio de partículas grandes y la herbivoría del zooplancton. *A: Possible interpretations of deviations of Trophic State Index (TSI) values of Carlson 1977, according to Carlson and Havens (2005). B: differences between the trophic state index for the three studied reservoirs are showed in 7B. Most of the observations were located in the quadrant of the predominance of big particles and zooplankton's herbivory.*

sido los procesos geoquímicos en una cuenca determinada (Fernández & Miretzky, 2004; Pehlivan & Yilmaz, 2005; Rajmohan & Elango, 2007). Este estudio, realizado a partir de una base de datos de 20 años en dos cuencas con diferente localización geográfica, representa una referencia que servirá para comparar la composición química del agua y los procesos vinculados. Esta técnica demuestra que la meteorización de la roca es el proceso natural más influyente en la química del agua de los cuatro embalses estudiados.

Los valores más elevados de la salinidad en los embalses Abreus y El Salto están relacionados con la génesis de las rocas donde yacen las cuencas que alimentan dichos embalses, en las cuales predominan las rocas sedimentarias, que son más vulnerables a los procesos de meteorización (Bruhns & Ramdohr, 1968). En las cuencas de Avilés y Paso Bonito, predominan las rocas ígneas que por su dureza son más resistentes a los procesos de meteorización.

La elevada proporción de Ca^{2+} encontrada en el embalse Paso Bonito también guarda relación con su geología. Según un estudio realizado por IGT (2008), en esta cuenca se localiza una zona cárstica, con abundantes surgencias.

La ubicación de las observaciones próximas al vértice en el diagrama trilineal (Fig. 3) y los resultados de las razones iónicas corroboraron el aporte de la disolución de carbonatos a la mineralización del agua en los cuatro embalses (Baca y Threlkeld, 2000). Para la cuenca del río Damují la disolución de los silicatos fue mayor (Fig. 5) en correspondencia con su geología. Jha *et al.* (2009) obtuvieron resultados similares en una cuenca caracterizada por la presencia de basaltos (silicatos) y carbonatos.

El CO_2 necesario para la disolución de silicatos proviene de la atmósfera y es el doble del que se necesita para el de los carbonatos (Raymahashay, 1986; Subramanian *et al*., 2006). Sin embargo, la fuente para este último puede ser, además de la atmósfera, la descomposición de la biomasa presente en el suelo. Por esta razón, la disolución de los silicatos representa un importante sumidero del CO_2 atmosférico y es de especial interés en el control de sus concentraciones en la atmósfera y el océano a escala de tiempo geológico (Berner *et al*., 1983; Brady & Carrol, 1994). Los resultados obtenidos significaron que los embalses Abreus y El Salto contribuyeron en mayor medida en la disolución de silicatos y por tanto en la retención del CO_2 atmosférico que el resto de los embalses estudiados.

Los valores de la razón Cl^-: Na^++K inferiores a la unidad sugieren la ocurrencia de la diso-

lución de silicatos de Na^+ y K^+ y de aporte de Na^+ por actividades antrópicas (Das *et al.*, 2005; Krishnaswami & Singh, 2005). En la cuenca de estos embalses se localizan fuentes de contaminación como son los asentamientos humanos y la cría de ganado vacuno y porcino (en mayor cuantía en los embalses Abreus y El Salto). La influencia de las actividades antrópicas sobre la calidad del agua también se reveló en los TSI obtenidos.

La localización del embalse Abreus al final de la cuenca del río Damují justifica las concentraciones significativamente inferiores de los iones mayoritarios durante el periodo húmedo. En esta etapa ocurre la dilución del agua embalsada producto de los volúmenes de agua de escorrentías que se incorporan desde la cuenca. En este embalse el área de la cuenca es 199 veces superior al área del embalse (Ac:Ae; Tabla 1), mientras que para el resto de los embalses estudiados las razones Ac:Ae son menores.

La correlación significativa entre los TSI (CHL) y TSI(SD) sugiere que la turbiedad del agua en estos embalses se debe a la CHL *a* del fitoplancton. En los mismos se detectó un florecimiento de *Microcystis* spp, cianobacteria colonial (Comas *et al*., 2010), cuya presencia justifica la ubicación de la mayoría de las observaciones en el área correspondiente a partículas grandes y valores de TSI(CHL)-TSI(SD)> 0.

El uso de este método gráfico también reveló que en estos embalses hay menos CHL *a* que la predicha por las concentraciones de TP (observaciones por debajo de la línea y = 0). Cuando esto ocurre significa que factores como la limitación de nitrógeno o la herbivoría del zooplancton están limitando el desarrollo del fitoplancton (Carlson & Havens, 2005). La limitación de nitrógeno en estas aguas también fue observada al aplicar el criterio de Morris y Lewis (1988).

La mineralización de la roca determina la composición química del agua en los embalses estudiados, pero la actividad del hombre está cambiando estos sistemas. Se recomienda establecer planes de remediación encaminados a reducir los vertidos de compuestos orgánicos en las cuencas de estos embalses, con el fin de mitigar los procesos de eutrofización.

BIBLIOGRAFÍA

APHA-AWWA-WPCF. 1998. *Standard methods for the examination of water and wastewater*. 20.ª ed. Washington, DC. 1100 pp.

BACA, R. M. & S. T. THRELKELD. 2000. Inland dissolved salt chemistry: statistical evaluation of bivariate and ternary diagram models for surface and subsurface waters. *Journal of Limnology*, 59(2): 156–166.

BERNER, R. A., A. C. LASAGA & R. M. GARRELS. 1983. The carbonate-silicate geochemical cycle and its effect on atmospheric carbon dioxide over the past 100 million years. *American Journal of Science*, 283: 641–683.

BETANCOURT, C., R. SUÁREZ & L. TOLEDO. 2009. Ciclo anual del nitrógeno y el fósforo en el embalse Paso Bonito, Cienfuegos, Cuba. *Limnetica*, 28: 79–90.

BRADY, P. V., & S. A. CARROL. 1994. Direct effects of CO2 and temperature on silicate weathering: Possible implications for climate control. *Geochimica et Cosmochimica Acta*, 58: 1853–1856.

BRUHNS, W., & P. RANDOHR. 1968. *Petrografía*, 1.ª ed. Edición Revolucionaria. La Habana, 125 pp.

CARLSON, R. E. 1977. A Trophic State Index for Lakes. *Limnology and Oceanography*, 22: 363–369.

CARLSON, R. E., & K. E. HAVENS. 2005. Simple Graphical Methods for the Interpretation of Relationships Between Trophic State Variables. *Lake and Reservoir Management*, 21 (1): 107–118.

CHUNG, C. H., C. F. YOU & H. Y. CHU. 2009. Weathering sources in the Gaoping (Kaoping) river catchments, southwestern Taiwan: Insights from major elements, Sr isotopes, and rare earth elements. *Journal of Marine Systems*, 76(4): 433–443.

COMAS, A., A. MOREIRA, C. BETANCOURT & F. JORGE. 2010. Cyanobacteria blooms in freshwater reservoir of Central Cuba. *Harmful Algae News*, 43: 18–19.

DAS, A., S. KRISHNASWAMI, M. M. SARIN & K. PANDE. 2005. Chemical weathering in the Krishna Basin and Western Ghats of the Deccan Traps, India: Rates of basalt weathering and their controls. *Geochimica et Cosmochimica Acta*, 69(8): 2067–2084.

DODDS, W. K. 2007. Trophic state, eutrophication and nutrient criteria in streams. *Trends in Ecology and Evolution*, 22(12): 669–676.

DURFOR, C. N., & E. BECKER. 1964. *Public water supplies of the 100 largest cities in the United States, 1962*. U.S. Geological Survey Water-Supply Paper 1812. 364 pp.

ESTRADA, M. 1978. Relationship among biological and physicochemical parameters in Spanish reservoirs. *Verhandlungen des Internationalen Verein Limnologie*, 20: 1642–1646.

FERNÁNDEZ, A., & P. MIRETZKY. 2004. Ionic relations: a tool for studying hydrogeochemical processes in Pampean shallow lakes (Argentina). *Quarternary International*, 114(1): 113–121.

GIBBS, R. J. 1970. Mechanisms controlling world water chemistry. *Science*, 170: 1088–1090.

GONZÁLEZ, J. 2000. *Guía Metodológica para el estudio integral de cuencas hidrológicas de cuencas superficiales con proyección de manejo*. Grupo de Hidroclimatología y Manejo de Cuencas. Facultad de Geografía. Universidad de la Habana. 32 pp.

INSTITUTO DE GEOGRAFÍA TROPICAL (IGT). 2008. *Estudio de los recursos hídricos en la cuenca del río Arimao*. Proyecto Ramal, Ministerio de Ciencia Tecnología y Medio Ambiente, La Habana, Cuba. 146 pp.

JHA, P. K., J. TIWARI, U. K. SINGH, M. KUMAR & V. SUBRAMANIAN. 2009. Chemical weathering and associated CO_2 consumption in the Godavari river basin, India. *Chemical Geology*, 264(1-4): 364–374.

KRISHNASWAMI, S. & S. K. SINGH. 2005. Chemical weathering in the river basins of the Himalaya, India. *Current Science*, 89(5): 841–849.

LI, S., Z. XU, H. A. WANG, J. WANG & Q. ZHANG. 2009. Geochemistry of the upper Han River basin, China: 3: Anthropogenic inputs and chemical weathering to the dissolved load. *Chemical Geology*, 264(1-4): 89–95.

MARGALEF, R. 1983. *Limnología*. Editorial Omega, Barcelona. 1010 pp.

PETER, A. 2008. *Taste and Odor in Drinking Water: Sources and Mitigation Strategies.* Tesis doctoral. Swiss Federal Institute of Technology Zurich. 143 pp.

PEHLIVAN, R. & O. YILMAZ. 2005. Water quality and hydrogeochemical characteristics of the River Buyukmelen, Duzce. Turkey. *Hydrological Processes*, 19: 3947–3971.

PIPER, A. M. 1944. A graphic procedure the geochemical interpretation of water analysis. *Eos. Transactions of the American Geophysical Union*, 25: 914–923.

RAJMOHAN, N. & L. ELANGO. 2007. Hydrogeochemistry and its relation to groundwater level fluctuation in the Palar and Cheyyar river basins, southern India. *Hydrological Processes*, 20, 2415–2427.

RAYMAHASHAY, B. C. 1986. Geochemistry of bicarbonate in river water. *Journal of the Geological Society of India*, 27: 114–118.

SÖMEK, H., M. R. USTAOĞLU & M. YAĞCI. 2008. A Case Report: Algal Bloom of *Microcystis aeruginosa* in a Drinking-Water Body, Eğirdir Lake, Turkey. *Turkish Journal of Fisheries and Aquatic Sciences*, 8: 177–179.

SUBRAMANIAN, V. V., D. U. ITTEKKOT & N. MADHAVAN. 2006. Silicate weathering in South Asian Tropical River Basins. In: *Role of silica in Land-Sea Interactions*. V. Ittekkot, D. Unger, C. Humborg, and N. Tac An (eds.): 3–13. Scope Washington D.C. USA.

TOLEDO, A. P., M. TALARICO, S. J. CHINEZ & E. G. AGUDO. 1983. A aplicação de modelos simplificados para a avaliação de processo da eutrofização em lagos e reservatórios tropicais. XIX Congresso Interamericano de Engenharia Sanitária e Ambiental. Camboriú, 1983, 57 pp.

WILLIAMSON, C. E., J. E. SAROS, W. F. C. VINCENT & J. P. SMOL. 2009. Lakes and reservoirs as sentinels, integrators, and regulators of climate change. *Limnol. Oceanogr.*, 54: 2273–2282.

Limnetica, 31 (2): 205-212 (2012)

On the biology of two high mountain populations of stoneflies (Plecoptera, Perlodidae) in the southern Iberian Peninsula

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Received: 20/6/11 Accepted: 27/12/11

ABSTRACT

On the biology of two high mountain populations of stoneflies (Plecoptera, Perlodidae) in the southern Iberian Peninsula

The life history of two species of Perlodidae stoneflies, *Perlodes microcephalus* (Pictet, 1833) and *Isoperla nevada* Aubert, 1952, are studied in a high mountain stream of the Sierra Nevada (Granada, Spain). Both species show a univoltine life cycle. The nymphal development of *P. microcephalus* occurs mainly in summer and autumn, and adults emerge at the end of spring. The embryonic development period is short, taking only two months. *I. nevada* develops and grows mainly during the summer, but the embryonic development period is even shorter. Despite both species having a relatively similar nymphal development period, *P. microcephalus* reaches a considerably larger size than *I. nevada*. The two taxa behave as predators, but *P. microcephalus* exhibits a wider prey spectrum. Thus, although *I. nevada* is more abundant in the studied stream, *P. microcephalus* appears to play a more important role as top predator.

Key words: *Perlodes microcephalus*, *Isoperla nevada*, life cycle, nymphal feeding, Sierra Nevada, Spain.

RESUMEN

Sobre la biología de dos poblaciones de plecópteros de alta montaña (Plecoptera, Perlodidae) en el sur de la Península Ibérica

Se estudian las estrategias vitales de dos especies de plecópteros Perlodidae, Perlodes microcephalus *(Pictet, 1833) e* Isoperla nevada *Aubert, 1952, en un arroyo de alta montaña de Sierra Nevada (Granada, España). Ambas muestran un ciclo de vida univoltino. El desarrollo de las ninfas de* P. microcephalus *tiene lugar principalmente en verano y otoño, y los adultos emergen al final de la primavera. El período de desarrollo embrionario es corto, de solo dos meses. También* I. nevada *se desarrolla y crece principalmente durante el verano, pero el período de desarrollo embrionario es incluso más corto. A pesar de que ambas especies tienen un período de desarrollo de las ninfas relativamente similar,* P. microcephalus *alcanza un tamaño considerablemente mayor que* I. nevada*. Los dos taxones se comportan como depredadores, pero* P. microcephalus *exhibe un espectro de presas más amplio. Así pues, a pesar de que* I. nevada *es más abundante en el arroyo estudiado,* P. microcephalus *parece jugar un papel más importante como depredador en esta comunidad fluvial.*

Palabras clave: Perlodes microcephalus, Isoperla nevada, *ciclo de vida, alimentación de las ninfas, Sierra Nevada, España.*

INTRODUCTION

High mountain streams are systems with particular characteristics, such as low water temperature (generally lower than 10 °C, even in the summer), fast flow, high turbulence and oxygen content, and an almost complete absence of plankton and macrophytes (Stoch, 2008). These pressures favour the development of particular strategies to cope with low temperatures and the relative scarcity of resources, mainly in those streams above the tree line. Some aquatic insects find in these environments an "island" of proper conditions to grow and are closely linked to these ecosystems. This is the case of some stoneflies, whose temperature optimum is low compared with other aquatic insects. In our study, we focus on two species of Plecoptera that inhabit a high mountain stream in the Sierra Nevada (Granada, Spain): *Perlodes microcephalus* (Pictet, 1833) and *Isoperla nevada* Aubert, 1952.

Perlodes microcephalus is a widely distributed species in a large part of Europe (Fochetti & Tierno de Figueroa, 2004). Nevertheless, its presence in the southern Iberian Peninsula is highly punctual and is reduced to few populations in the high mountains of the Sierra Nevada (Southern Spain) (Tierno de Figueroa *et al.*, 2003). In more meridional mountains, such as the Pyrenees, this species is found at lower altitudes (300-1400 m.a.s.l.) than the congeneric *P. intricatus* (1000-2200 m.a.s.l.), which replaces *P. microcephalus* at higher altitudes (Berthélemy, 1966). In fact, the population in Sierra Nevada is one of the highest-altitude populations of *P. microcephalus* in Europe. For stoneflies, these mountains act more as a refuge for northern species, such as *P. microcephalus*, than as a speciation centre (Tierno & Sánchez-Ortega, 1996).

In contrast, *I. nevada* Aubert, 1952, is endemic to the Iberian Peninsula and is widely distributed within it, with an altitudinal range of 800 to 2900 m.a.s.l. (Tierno de Figueroa *et al.*, 2003).

The aim of this work is to deepen the understanding of the biology of these species under low-temperature conditions by studying their life cycle and nymphal feeding and to compare these results with those previously reported in nearby areas and in other parts of Europe.

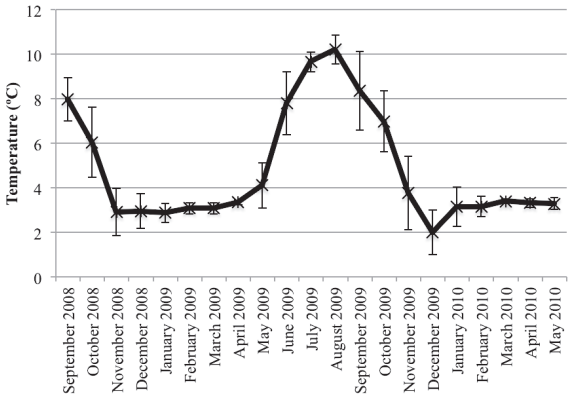

Figure 1. Mean daily temperature recorded during the study period. *Temperatura media diaria registrada durante el período de estudio.*

MATERIAL AND METHODS

The study was performed in the Puerto de Jeres stream (Sierra Nevada, Granada, Spain. 30S X: 479419, Y: 4104892) at 2500 m.a.s.l. Samplings were performed at monthly intervals over two years (from June 2008 to May 2010) except for some winter months, when snow made it impossible to reach the sampling site. In fact, the stream was covered with snow for 6 months during the first year of study and for 5 months during the second. Nymphs were collected with a Surber sampler (0.16 m^2 and 250 μm mesh size) and preserved in 4 % formalin. Six Surbers were collected on each date. Because these samples provided few nymphs, other samples were captured using a *kick* net (250 μm mesh size). Nymphs from both samples were used to represent the life cycle and to study feeding, but only nymphs from the Surber sampler were used to estimate the densities. At the same time, some physicochemical parameters were recorded (Table 1). Temperature was recorded hourly with a HOBO® U22 Water Temp Pro V2 Data Logger (Fig. 1). Adults were searched for in the stones of both shores and in the riparian vegetation. Adult collection was conducted with tweezers, and the material was preserved in 70 % ethanol. The total length of the nymphs of both species was measured under a stereomicroscope with an ocular micrometre. The nymphs were grouped

Table 1. Mean ± SD of the physicochemical parameters in the study site for each year. *Media ± DS de parámetros físicos medidos en el punto de muestreo para cada año.*

Discharge (l/s)		pH		Conductivity (µS/cm)		$\%O_2$		O_2 (mg/l)	
1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd
114.6±101.5	138.5±109.5	7.3±0.2	7.7±0.7	14.0±1.4	17.8±4.2	83.9±11.4	85.1±11.0	8.0±0.5	9.1±1.2

into intervals to represent the life cycle using FiSAT II software (Gayanilo *et al.*, 2002). Although no data were available for some months, nymphal development and growth were inferred for these months, as in Silveri *et al.* (2008).

Some of the *P. microcephalus* nymphs (the largest) were dissected ($N = 12$), while others (the smallest) were clarified ($N = 24$) with Hertwigs' liquid to study their gut content, as in other studies on nymphal feeding (e.g., López-Rodríguez *et al*., 2009). All the studied nymphs of *I. nevada* were clarified ($N = 54$) using this method. Only the presence of each non-animal component of the diet was considered, without analysing its abundance.

RESULTS

Due to the adverse conditions of this high mountain environment, but mainly because of the scarcity of this relict species in the area, only 59 nymphs of *P. microcephalus* were collected during the two years (18 in the first and 41 in the second). However, these nymphs provide a clear representation of the life cycle of *P. microcephalus*, particularly in the second year. Despite an intensive search, only one adult (a male) of this species was captured in June 2009. However, a total of 187 nymphs (73 the first year and 114 the second) and 21 adults (9 the first year and 12 the second) of *I. nevada* were collected at the sampling site.

The life cycle of *P. microcephalus* was univoltine at the study site, with nymphs hatching at the end of July (after approximately two months of embryonic development) and mature nymphs present at the end of May (Fig. 2). Although only one adult was collected, its flight period is probably short, approximately one month, because no nymphs are present in the stream after May. Nymphal growth is rapid from July to the end of November. Although no data are available from December to April, the presence of nymphs of the same size before and after this period in the second year suggests that little or no growth occurs during these colder months, although in the first year, nymphal growth seems to occur. The only adult collected the first year was found in June.

I. nevada has a univoltine life cycle at this site (Fig. 3). The hatching of nymphs occurs mainly in August, although a longer recruitment period

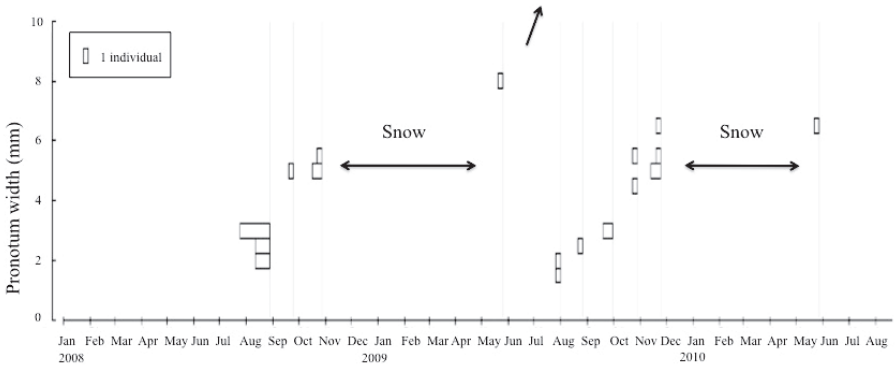

Figure 2. Size-frequency graph showing the life cycle of *Perlodes microcephalus*. The presence of adults on the sampling dates is marked with an arrow. *Representación gráfica de la frecuencia de tamaños a lo largo del ciclo de vida de* Perlodes microcephalus. *Se han capturado adultos en las fechas de muestreo marcadas con una flecha.*

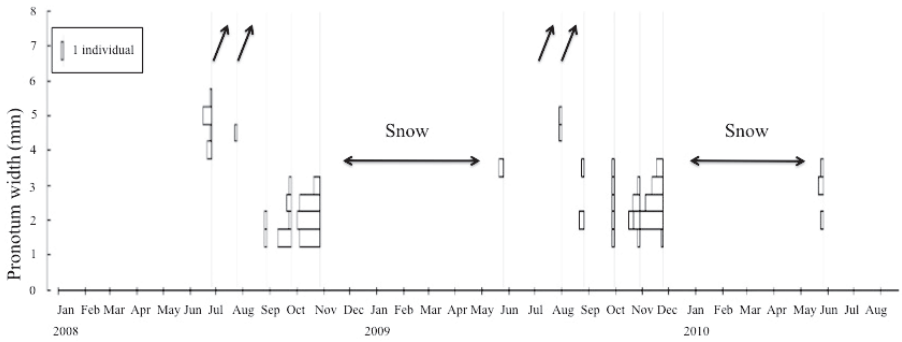

Figure 3. Size-frequency graph showing the life cycle of *Isoperla nevada*. The presence of adults on the sampling dates is marked with an arrow. *Representación gráfica de la frecuencia de tamaños a lo largo del ciclo de vida de* Isoperla nevada. *Se han capturado adultos en las fechas de muestreo marcadas con una flecha.*

seems to exist. Adults emerge in the summer. No data are available for the winter and spring months, but little growth seems to occur during this period because after this period, we could still find some small nymphs. The embryonic development is rapid, lasting scarcely one month. Adults were collected in June and July of the first year and in July and August of the second year.

The mean monthly density of individuals during the months when nymphs were present in the stream was 4.29 ind/m^2 for *P. microcephalus* and 15.27 ind/m^2 for *I. nevada*.

Ten of the 50 studied nymphs of *P. microcephalus* had empty guts. Of the remaining 40, 34 contained some animal matter (85.0 %) and only six had ingested exclusively non-animal matter. The diet study showed that the nymphs fed mainly on Diptera Chironomidae (75.0 % of the nymphs), but also on Ephemeroptera Baetidae (7.5 %), Plecoptera Nemouroidea (2.5 %), Trichoptera Hydropsychidae (2.5 %), Glossosomatidae (2.5 %), and Nematomorpha (2.5 %) (Table 2). The 5 % of the gut contents studied included unidentifiable Trichoptera larvae and Ephemeroptera nymphs. Some nymphs ingested detritus, algae (mainly diatoms), coarse particulate organic matter (CPOM), hyphae and pollen (Table 2). Sand grains were found in four nymphs.

The gut contents of 54 *I. nevada* nymphs were analysed. Twenty-six nymphs had empty guts. The remaining 28 had eaten some animal prey, though many of them also contained detritus (21.4 %), algae (14.3 %) and sand grains (7.1 %). Diptera Chironomidae was the prey this species ingested most, although unidentifiable Plecoptera and Ephemeroptera were also consumed by this species (Table 2).

Regarding number of prey found in the gut of each species, the nymphs of *P. microcephalus*

Table 2. Presence of different food items in the gut contents of the studied species. *N* = the number of individuals that contain a food item; % = the percentage of individuals that fed on each food item with respect to the total number of individuals with full guts. *Tipos de alimento presentes en el contenido digestivo de las especies estudiadas.* N = *número de individuos que contienen un recurso concreto; % = porcentaje de individuos que han comido un recurso en relación al número total de individuos que tienen el digestivo lleno.*

	Perlodes microcephalus		*Isoperla nevada*	
	N	%	N	%
Detritus	21	52.5	6	21.4
Sand	4	10.0	2	7.1
Algae	17	42.5	4	14.3
Hyphae	1	2.5	0	0.0
CPOM	5	12.5	0	0.0
Pollen	1	2.5	0	0.0
Non-identifiable animals	4	10.0	4	14.3
Chironomidae	30	75.0	21	75.0
Plecoptera undet.	0	0.0	1	3.6
Plecoptera Nemouroidea	1	2.5	0	0.0
Ephemeroptera undet.	2	5.0	1	3.6
Baetidae	3	7.5	0	0.0
Nematomorpha	1	2.5	0	0.0
Hydropsychidae	1	2.5	0	0.0
Glossosomatidae	1	2.5	0	0.0
Trichoptera undet.	2	5.0	0	0.0
Ind. with gut contents	34	85.0	26	92.9

ingested up to 54 larvae of Chironomidae, while the maximum number of prey recorded in the nymphs of *I. nevada* was five Chironomidae (Fig. 4).

DISCUSSION

Studies in other European areas show a univoltine life cycle for *P. microcephalus* [e.g., in Great Britain (Hynes, 1941, 1961; Elliott, 1967, 1992, 2000) and in Fennoscandia (Lillehammer, 1988)]. Elliott (2000) in particular mentioned that this species has very rapid growth, attaining a size similar to that of large perlids in only one year, while the latter require approximately two or three years to complete their development in cold waters. The embryonic development of approximately two months in the Puerto de Jeres stream coincides with that found in several studies in similar temperatures. For example, Marten (1991) found that in experimental studies in Germany, egg development at approximately 10-11 °C (the temperature of the Puerto de Jeres stream during the months in which the eggs are present, Fig. 1) lasted 50-60 days, while Elliott (1992), in a experimental study in Great Britain, found that the maximum hatching period occurs approximately 2-2.5 months after oviposition at temperatures of approximately 11 °C. These results are very similar to those previously found by Schwarz (1970) for this species, who noted an embryonic development period from 56 to 70 days depending on temperature (5-16 °C). Nevertheless, Berthélemy (1979) mentioned that the

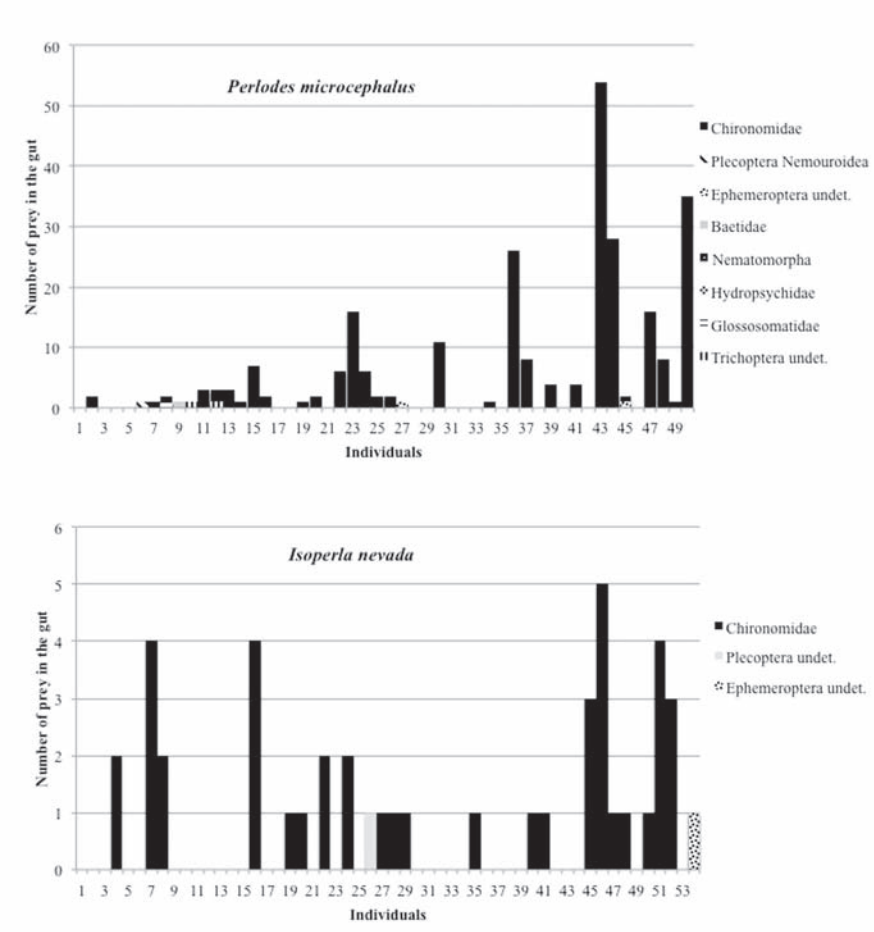

Figure 4. Number of each prey found in the gut contents of the studied nymphs. *Número de individuos de cada tipo de presa encontrados en el digestivo de las ninfas estudiadas.*

eggs of this species could hatch at 2-5 months after oviposition or one year later. Under this hypothesis, which has not been confirmed by experimental data, if nymphal development occurs in approximately one year, the life cycle would be semivoltine for some individuals.

Regarding nymphal growth, Elliott (1967) noted, in a study in Great Britain, that *P. microcephalus* was the only species that did not slow down growth in the winter months. The data in the Puerto de Jeres stream from the second year do not seem to support this conclusion, though in the first year, some growth seems to occur.

Although only one adult was captured, the flight period can be inferred to occur in the spring, based on the presence of mature nymphs in June.

Thus, the general life cycle pattern of *P. microcephalus* in the southern Iberian Peninsula is very similar to that found at higher latitudes. The flight period appears to be delayed in comparison with some of these areas: Hynes (1961) cited that emergence occurs in April, and Graf *et al*. (2009) suggested that it occurs mainly in the spring. This period is advanced in other places, such as in the Pyrenees, where adults are collected up to August (Sánchez-Ortega *et al.*, 2002).

Additionally, for *I. nevada*, a univoltine life cycle has already been noted by Sánchez-Ortega & Alba-Tercedor (1990) in the nearby Dílar stream, Sierra Nevada [but was identified as *I. grammatica* (Poda, 1761), see Tierno & Sánchez-Ortega (1994)]. In this stream, the population had a similar pattern: mature nymphs were recorded in July, and hatching began in September; they also found a short period of embryonic development.

The flight period of this species is summer, but it was slightly delayed in the second year of the study. A similar flight period has been recorded in other areas at altitudes between 1510 and 1900 m.a.s.l. (Tierno de Figueroa *et al.*, 2001, 2003), although this period was longer at these altitudes than in the Puerto de Jeres stream, probably because of the higher altitudes. At our study site, the short time with relatively favourable conditions for the adults would have reduced the emergence and flight period.

Regarding feeding, the nymphs of both *P. microcephalus* and *I. nevada* are clearly predators, although some of them also fed on non-animal matter and others behaved solely as detritivorous-herbivorous (ingesting only detritus, algae and/or CPOM). The presence of sand grains in several nymphs is probably anecdotic and could be related to the feeding behaviour of this species, as field observations made by the authors show that nymphs ingest non-animal matter together with prey when feeding on soft substrates (e.g., mud, sand). Nonetheless, these grains could proceed from the case of ingested caddisflies, as at least in one of the nymphs, Trichoptera were found together with the sand grains.

Nymphal feeding in other streams has been studied only in *P. microcephalus*. Our study is in agreement with these previous studies with respect to the prey eaten. For example, Fenoglio *et al*. (2005) found that Chironomidae were the most frequent prey found in the gut of a northwestern Italian population of this species and that some families of Trichoptera (Glossosomatidae, for instance) were also positively selected among the entire community of potential prey. Additionally, Berthélemy & Lahoud (1981), in a study performed in the Pyrenees, found that Chironomidae (60-85 %), followed by *Baetis* sp. (30 %) were the main prey consumed by this species, and they also recorded non-animal contents in the gut.

Comparing the feeding habits of *P. microcephalus* and *I. nevada*, it is noteworthy that the first species has a wider prey spectrum than the latter, and *P. microcephalus* ingested a quantitatively higher number of prey than *I. nevada*. Thus, despite being less abundant in the study site, *P. microcephalus* exerts greater predatory pressure and, thus, a higher control on other aquatic insects than *I. nevada*. This higher ingestion rate would be essential in an insect that must achieve a large size in a very short period and under very low temperatures.

ACKNOWLEDGEMENTS

The authors wish to thank to two anonymous referees for their helpful comments, which greatly improved the original version of the manuscript. This research has been supported by the Span-

ish project “Programa de seguimiento de los efectos del cambio global en el Parque Nacional y Natural de Sierra Nevada, Consejería de Medio Ambiente, Junta de Andalucía” and by the project “CGL2008-02221” (Ministerio de Ciencia e Innovación, Spain).

REFERENCES

BERTHÉLEMY, C. 1966. Recherches écologiques et biogéographiques sur les Plécoptères et Coléoptères d’eau courante (Hydraena et Elminthidae) des Pyrénées. *Annales de Limnologie*, 1: 227–458.

BERTHÉLEMY, C. 1979. Accouplement, période d’incubation et premiers stades larvaires de *Brachyptera braueri* et de *Perlodes microcephalus* (Plecoptera). *Annales de Limnologie*, 15: 317–335.

BERTHÉLEMY, C. & M. LAHOUD. 1981. Régimes alimentaireset pièces buccales de quelques Perlodidae et Perlidae des Pyrénées (Plecoptera). *Annales de Limnologie*, 17: 1–24.

ELLIOTT, J. M. 1967. The life histories and drifting of the Plecoptera and Ephemeroptera in a Dartmoor stream. *Journal of Animal Ecology*, 36: 243–262.

ELLIOTT, J. M. 1992. The effect of temperature on egg hatching for three populations of *Perlodes microcephala* (Pictet) and three populations of *Diura bicaudata* (Limnaeus) (Plecoptera: Perlodidae). *Entomologist’s Gazette,* 43: 115–123.

ELLIOTT, J. M. 2000. Contrasting diel activity and feeding patterns of four species of carnivorous stoneflies. *Ecological Entomology*, 25: 26–34.

FENOGLIO, S., T. BO & M. CUCCO. 2005. Winter prey preference of *Perlodes microcephalus* (Pictet, 1833)(Plecoptera, Perlodidae) nymphs in an Apenninic creek, northwestern Italy. *Entomological News*, 116: 245–252.

FOCHETTI, R. & J. M. TIERNO DE FIGUEROA. 2004. Plecoptera. Fauna Europaea Web service. www.faunaeur.org (*Fauna Europaea* Project Ref. EVR1-CT-1999-2001).

GAYANILO, F. C. JR., P. SPARRE & D. PAULY. 2002. FiSAT II (ver. 1.2.0.). Food and Agriculture Organization of the United Nations (FAO) (www.fao.org/fi/statist/fisoft/fisat/index.htm).

GRAF, W., A. LORENZ, J. M. TIERNO DE FIGUEROA, S. LÜCKE, M. J. LÓPEZ-RODRÍGUEZ & C. DAVIES. 2009. Plecoptera. In: *Distribution and Ecological Preferences of European Freshwater Organisms.* A. Schmidt-Kloiber & D. Hering (eds.): 207–223. Pensoft Publishers. Sofia. Bulgaria.

HYNES, H. B. N. 1941. The taxonomy and ecology of the nymphs of British Plecoptera, with notes on the adults and eggs. *Transactions of the Entomological Society of London*, 91: 459–557.

HYNES, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. *Archiv für Hydrobiologie*, 57: 344–388.

LILLEHAMMER, A. 1988. *Stoneflies (Plecoptera) of Fennoscandia and Denmark*. Fauna Entomologica Scandinava. Vol. 21. E. J. Brill, Scandinavian Science Press LTD. 165 pp.

LÓPEZ-RODRÍGUEZ, M. J., J. M. TIERNO DE FIGUEROA, S. FENOGLIO, T. BO & J. ALBA-TERCEDOR. 2009. Life strategies of 3 Perlodidae species (Plecoptera) in a Mediterranean seasonal stream in southern Europe. *Journal of the North American Benthological Society*, 28: 611–625.

MARTEN, M. 1991. The effect of temperature on the egg incubation period of *P. microcephalus*, *P. dispar* (Pl.: Perlod.) and *Perla burmeisteriana* (Pl.: Perlid.). In: *Overview and strategies of Ephemeroptera and Plecoptera*. J. Alba-Tercedor & A. Sánchez-Ortega (eds.): 387–401. The Sandhill Crane Press. Inc. Florida. USA.

SÁNCHEZ-ORTEGA, A. & J. ALBA-TERCEDOR. 1990. Life cycles of some species of Plecoptera in Sierra Nevada (South of Spain). In: *Mayflies and Stoneflies: Life history and Biology*. I. C. Campbell (ed.): 43–52. Kluwer Academic Publishers. Dordrech. Holland.

SÁNCHEZ-ORTEGA, A., J. ALBA-TERCEDOR & J. M. TIERNO DE FIGUEROA. 2002. *Lista faunística y bibliográfica de los plecópteros (Insecta, Plecoptera) de la Península Ibérica e Islas Baleares*. Publicaciones de la Asociación española de Limnología. Madrid. España. 198 pp.

SCHWARZ, P. 1970. Autokologische untersuchungen zum Lebenszyklus von setipalpia-arten (Plecoptera). *Archiv für Hydrobiologie*, 67(1): 103–140.

SILVERI, L., J. M. TIERNO DE FIGUEROA & B. MAIOLINI. 2008. Notes on the nymphal biology of *Nemoura mortoni* Ris 1902 (Plecoptera, Nemouridae) in a high altitude stream (Trentino, Italian Alps). *Zoologica Baetica*, 19: 51–56.

STOCH, F. 2008. Ecologia dei torrenti montani. In: *Torrenti montani. La vita nelle acque correnti.* F. Stoch (ed.): 101–119. Ministero dell’Ambiente e

della Tutela del Territorio e del Mare-Museo Friulano do Storia Naturale. Udine. Italy.

TIERNO, J. M. & A. SÁNCHEZ-ORTEGA. 1994. Sobre la distribución espacial y temporal de *Isoperla nevada* Aubert, 1952 (Insecta: Plecoptera). *Zoologica Baetica*, 5: 107–112.

TIERNO, J. M. & A. SÁNCHEZ-ORTEGA. 1996. Revisión de la distribución y el estado de conservación de la fauna de Plecópteros (Insecta: Plecoptera) de los sistemas montañosos andaluces, con especial referencia a S. Nevada. *Proceedings of 1ª Conferencia Internacional Sierra Nevada. Conservación y Desarrollo Sostenible*, 3: 69–74.

TIERNO DE FIGUEROA, J. M., J. M. LUZÓN-ORTEGA & A. SÁNCHEZ-ORTEGA. 2001. Fenología de los plecópteros (Insecta, Plecoptera) de Sierra Nevada (Granada, España). *Zoologica Baetica*, 12: 49–70.

TIERNO DE FIGUEROA, J. M., A. SÁNCHEZ-ORTEGA, P. MEMBIELA-IGLESIA & J. M. LUZÓN-ORTEGA. 2003. Plecoptera. In: *Fauna Ibérica, vol. 22*, M. A. Ramos *et al*. (eds.): 66–72. Museo Nacional de Ciencias Naturales. CSIC. Madrid. España.

Limnetica, 31 (2): 213-230 (2012)

Estimación de los costes de la invasión del mejillón cebra en la cuenca del Ebro (periodo 2005-2009)

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Received: 10/11/2011 Accepted: 19/3/2012

ABSTRACT

Estimation of costs of zebra mussel invasion in the Ebro basin (2005-2009 period)

This study presents the monetary costs that the zebra mussel invasion has involved in the Ebro basin since 2005 to 2009 for the sectors which use water in their activities. The economic impact associated with this invasion is derived from the operation problems in affected facilities and the costs added due to the cleaning and control treatments. The work methodology is based on the analysis of the survey address to energetic, industrial, agricultural, recreational, public administrations and supplies sensitive to be affected by the zebra mussel invasion. In total, 1329 surveys were sent by post and email to different agents of several sectors. The response rate was 28.4 %, allowing a detection of 103 affected users in the basin. The results indicate that costs associated to the zebra mussel expansion in the Ebro basin have not stopped to increase in the last years, reaching 11.6 millions of Euros in the period of study. The most implicated sectors are public administrations, with a 55.1 % of the total costs followed by energetic companies, with a 26.4 %. Geographically, it is in the High Ebro where more money has been invested in the fight against this alien species during the five years of study.

Key words: Ebro basin, alien species, economic impact, zebra mussel.

RESUMEN

Estimación de los costes de la invasión del mejillón cebra en la cuenca del Ebro (periodo 2005-2009)

Este estudio presenta los costes monetarios que ha supuesto la invasión del mejillón cebra en la cuenca del Ebro desde el año 2005 al 2009 para los sectores que utilizan el agua en sus actividades. El impacto económico asociado a esta invasión se deriva tanto de los problemas de funcionamiento de las instalaciones afectadas como de los gastos añadidos por la limpieza y tratamientos de control de las mismas. La metodología de trabajo se basó en el análisis de una encuesta dirigida a los sectores energético, industrial, agrícola, lúdico-deportivo, administraciones públicas y abastecimientos, susceptibles de estar afectados por la invasión del mejillón cebra. En total se enviaron por vía postal y electrónica 1329 cuestionarios a distintos agentes de los diversos sectores. La tasa de respuesta fue del 28.4 %, permitiendo detectar 103 afectados en la cuenca. Los resultados indican que los costes asociados a la expansión del mejillón cebra en la cuenca del Ebro no han cesado de crecer en los últimos años, llegando a alcanzar los 11.6 millones de euros en el periodo de estudio. Los sectores más implicados son las administraciones públicas, con un 55.1 % del total de costes contabilizados seguidas de las empresas energéticas, con un 26.4 %. Geográficamente, es en el Alto Ebro donde más dinero se ha invertido en la lucha contra esta especie invasora durante los cinco años de estudio.

Palabras clave: *Cuenca Ebro, especie invasora, impacto económico, mejillón cebra.*

INTRODUCCIÓN

El mejillón cebra (*Dreissena polymorpha*) se instaló en el río Ebro hace ya una década (Altaba *et al*., 2001; Álvarez, 2001; Navarro *et al*., 2006). Desde entonces, este bivalvo ha provocado y provoca importantes impactos ecológicos y económicos (Hunter & Bailey, 1992; Karatayev *et al*., 1997; Strayer, 1999; Araujo & Álvarez, 2001; Bobat, 2004; Connelly *et al*., 2007; Higgins *et al*., 2008; Strayer, 2009; Sousa *et al*., 2011). Las implicaciones económicas de esta invasión han resultado imprescindibles a la hora de poner en marcha políticas de prevención y control sobre los ecosistemas indemnes y afectados.

Los costes se originan a partir de la afección a obras e infraestructuras hidráulicas, donde su presencia masiva causa la obturación de captaciones y conducciones de agua al fijarse sin dificultad en paredes y fondos de depósitos, rejas, tuberías, etc. De esta afección se derivan problemas de funcionamiento en instalaciones de abastecimientos, industrias, infraestructuras de riegos y de centrales hidroeléctricas o en sistemas de refrigeración de centrales térmicas y nucleares, además de gastos adicionales de mantenimiento por actuaciones de limpieza y aplicación de métodos de control para su mitigación; en ciertos casos, incluso es necesario introducir cambios en el proceso productivo. En ausencia de un tratamiento adecuado, la experiencia muestra que la mayoría de las conducciones, a medio o largo plazo, acaban parcial o totalmente obturadas.

Gozlan (2010) recopiló recientemente los trabajos científicos existentes sobre especies exóticas invasoras en España con el fin de establecer la proporción de especies acuáticas exóticas introducidas en el país que son responsables de impactos ecológicos y económicos. A pesar de la gravedad de las consecuencias que pueden llegar a tener estas invasiones, las valoraciones de los costes económicos de las especies invasoras son escasas y aún menor, el número de estudios disponibles en la literatura económica especializada (US-OTA, 1993; Perrings *et al*., 2000; Pimentel *et al*., 2000; McLeod, 2004; Born *et al*., 2005; Pimentel *et al*., 2005; Collautti *et al*., 2006; Lovell *et al*., 2006; Olson, 2006; Binimelis *et al*., 2007; Vilà *et al*., 2010).

Cuando se desciende en el análisis a escala de una especie concreta, no solo el número de estudios en la literatura económica se reduce aún más drásticamente, sino que también se constatan divergencias entre las estimaciones de los costes que provocan estas invasiones. A este respecto y para el caso de los Estados Unidos el estudio de Pimentel (2000, 2005), basados en O'Neill (1997) y U.S. Army (2002) y el estudio de Connelly (2007); en Canadá, Canadian Biodiversity Information Network (2004) y en España, Pérez y Pérez & Chica (2006).

El área de estudio en este trabajo abarca la cuenca del Ebro, localizada en el cuadrante noreste de la península ibérica. La cuenca ocupa una superficie total de 85 362 km^2, siendo la más extensa de España. Engloba territorios de nueve Comunidades Autónomas y está surcada por 347 ríos, con 152 embalses construidos.

El principal objetivo de esta investigación radica en calcular los costes económicos asumidos por los distintos usuarios afectados por la plaga en la cuenca del Ebro desde 2005 hasta 2009, con el objeto de evaluar la tipología de estos costes, localización y su evolución durante el periodo de estudio.

METODOLOGÍA

Con el objeto de cuantificar estos costes se diseña una encuesta dirigida a seis sectores socioeconómicos, cuyas características generales se detallan en la Tabla 1. La información solicitada a través de un cuestionario elaborado de forma *ad hoc* para este estudio se organiza en dos partes diferenciadas. La primera recoge información sobre el tipo de actividad desarrollada, localización de la empresa y datos técnicos de las instalaciones. En la segunda, se solicitan datos sobre la tipología de costes derivados de la afección de la plaga y cuantía anual de los mismos durante el periodo de estudio, que abarca desde 2005 hasta 2009. No son obligatorios los campos destinados a la identificación del entrevistado con la finalidad de ganar amplitud y veracidad en el estudio (ver cuestionario completo en anexo I).

Los cuestionarios se envían en formato papel y formato electrónico, en función de cada sec-

Tabla 1. Características de los sectores analizados. *Characteristics of the sectors analyzed.*

Sector	Características
Energético	Empresas energéticas de origen hidráulico, térmico o nuclear.
Administraciones públicas	Administraciones públicas estatales y autonómicas.
Abastecimientos urbanos	Captaciones de agua de las poblaciones a partir de aguas superficiales y/o subterráneas.
Lúdico-deportivo	Empresas que gestionan los descensos por el río en piraguas, kayaks, embarcaciones a motor en los embalses, inmersiones submarinistas, material para la práctica de la pesca deportiva y otras actividades acuáticas. Estaciones de desinfección y limpieza de embarcaciones y material.
Agrícola	Comunidades de regantes con tomas de agua tanto en ríos como embalses.
Industrial	Empresas no energéticas que se abastecen de ríos y embalses de la zona para uso industrial en sus procesos productivos.

tor, con la finalidad de favorecer el alcance del envío. Esta primera fase del estudio se complementa con apoyo telefónico. La recogida de datos dura de julio a diciembre de 2009. En los envíos de cuestionarios por correo postal se incluye un sobre con la dirección de envío y el sello incluido, facilitando así el cumplimento y posterior remisión del mismo.

Desde un punto de vista geográfico, la encuesta se lleva a cabo en las 16 provincias que conforman la cuenca del Ebro, por lo que se cubre la totalidad del territorio afectado por la invasión. En la figura 1 se representa la distribución de usuarios consultados en la cuenca por provincias, destacando los ríos afectados por la plaga en el momento del inicio del estudio. El número total de envíos es inferior (Tabla 2), pues hay entidades que albergan varias empresas en la cuenca o existen entidades con varios usos, por lo que en el mismo envío se pueden llegar a incluir varios tipos de cuestionarios.

A la hora de planificar estos envíos se tienen en cuenta las especificidades de algunos de los sectores de estudio. Los cuestionarios destinados a abastecimientos se envían a poblaciones con captaciones de aguas superficiales, derivadas

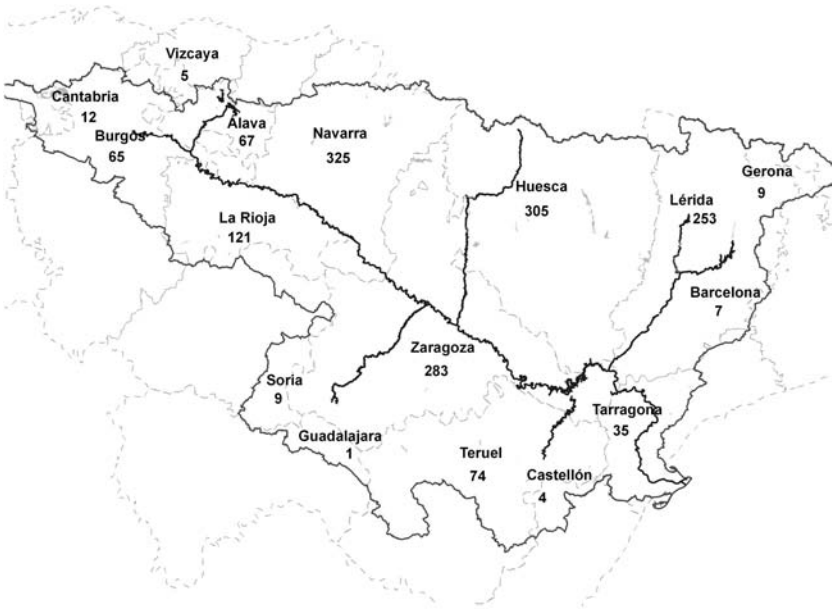

Figura 1. Mapa de distribución provincial del muestreo. *Map of provincial sampling distribution.*

Tabla 2. Resultados de la encuesta. *Results of the survey.*

Sectores	Correo postal	Correo electrónico	Total envíos	Respuestas totales	Respuestas por carta	Afectados por MC
Energía	351	5	356	79	58	22
Administraciones	0	15	15	10	0	9
Abastecimientos	45	201	246	41	31	8
Lúdicos	69	1	70	25	24	17
Regadío	76	82	158	139	37	37
Industrias	482	2	484	84	84	10
TOTAL	1023	306	1329	378	234	103

de los cauces fluviales del río Ebro. En un primer análisis se comprueba que los abastecimientos con aguas subterráneas suelen corresponder a pequeños núcleos de población y, además, en este tipo de abastecimientos, el suelo y el subsuelo actúan de filtro natural impidiendo el paso de larvas, por lo que no resulta de interés incluirlos en el estudio. Por otra parte, se tienen en cuenta los abastecimientos derivados de canales de uso múltiple, ya que la detección del mejillón cebra en alguna toma dependiente de un canal significa la afección potencial a los restantes usuarios.

En el sector lúdico, además de analizar las empresas de deporte acuático, también se analizan mediante seguimiento telefónico los gastos de las estaciones de limpieza y desinfección de embarcaciones y material que se han ido instalando por la cuenca, generalmente aprovechando instalaciones existentes como campings, gasolineras, embarcaderos, etc. Se han considerado los gastos de inversión de adecuación de las instalaciones para convertirlas en estaciones de limpieza sin tener en cuenta las ayudas prestadas por las distintas administraciones, para evitar una doble contabilización. A estos gastos se añaden los de material y mantenimiento asumidos por las propias empresas que las gestionan.

La encuesta dirigida al sector agrario se lleva a cabo entre la mayoría de los regantes de la cuenca, agrupados en comunidades de regantes. Se distinguen en función de la superficie de riego, del caudal de la toma o según la tecnología de riego (superficial a manta, por aspersión o por goteo), para caracterizar la parte de las instalaciones afectadas y sus correspondientes costes.

En el sector industrial se desestiman para el estudio aquellas empresas que se abastecen directamente de aguas subterráneas mediante pozos, aunque sí se consideran las que están conectadas a canales de varios usos. Finalmente, tampoco se consideran las empresas industriales dependientes de redes municipales o de abastecimiento, dado que éstas se incluyen en el apartado de análisis de los abastecimientos.

Respecto a la representación de la muestra, diferenciada por sectores, resultan unos porcentajes específicos del 92 % de la potencia eléctrica instalada en la cuenca del Ebro para el sector energético; del 100 % de los Organismos estatales y autonómicos implicados en medio ambiente, para las administraciones públicas; del 90 % del agua consumida en abastecimientos de origen fluvial, para el sector abastecimientos; del 85 % de las empresas ligadas a deportes fluviales y estaciones de limpieza y desinfección, para el sector lúdico; del 80 % de la superficie de regadío con aportaciones de cauces fluviales, para el sector agrícola y del 100 % de las empresas no energéticas censadas en la Confederación Hidrográfica del Ebro con tomas fluviales, para el sector industrial.

Debido a que el cuestionario puede ser anónimo y resulta de interés saber en qué localización geográfica de la cuenca se producen gastos, se solicita la localización por áreas predefinidas de la cuenca del Ebro. Para ello, la cuenca se divide en tres tramos siguiendo el curso del río. Así se establece el Alto Ebro (desde la cabecera del Ebro hasta la desembocadura del río Aragón en la ciudad de Alfaro), Ebro Medio (desde la desembocadura del río Aragón hasta la desembocadura

del río Segre en la ciudad de Mequinenza) y Bajo Ebro (desde la desembocadura del río Segre hasta el mar), distinguiendo además entre margen derecha e izquierda del río.

Una vez recibidos los cuestionarios, los datos recogidos se tratan informáticamente para permitir su contraste e integración y análisis de los resultados de los distintos sectores, por áreas geográficas y tipologías de costes.

RESULTADOS Y DISCUSIÓN

La Tabla 2 muestra, por sectores, los principales resultados de envíos, respuestas y número de afectados recogidos por las encuestas. En total se enviaron 1329 cuestionarios, de los cuales el 77 % se remitieron por correo postal y, el resto, por correo electrónico. En el marco de los sectores socioeconómicos, el 66.2 % se dirigieron a empresas, tanto industriales no energéticas (36.4 %) como energéticas (26.8 %); el 18.5 % se enviaron a empresas y organismos responsables del abastecimiento urbano; el 11.9 % de los cuestionarios se mandaron a comunidades de regantes; el 5.2 % de los cuestionarios, a empresas de usos lúdicos y ocio relacionadas con el agua y, por último, el 1.1 % de las encuestas, a organismos de las administraciones públicas relacionados con la gestión del agua.

Se recibieron 378 contestaciones (61.9 % por carta y 38.1 % por correo electrónico), lo que supone una tasa de respuesta del 28.4 %. Entre las respuestas recibidas, 103 usuarios (el 27.2 % de las contestaciones) indicaron estar afectados por la invasión del mejillón cebra en sus instalaciones o estar trabajando en evitar su dispersión y distribución a masas de agua no afectadas.

Del análisis sectorial cabe destacar que la tasa de respuesta del sector energético fue del 22.2 %, como se deduce de la Tabla 2. Esta tasa puede ser calificada de bastante alta, ya que sólo el 6.2 % de las industrias energéticas, 22, declararon estar afectadas por la invasión y, por tanto, la mayoría de los que recibieron el cuestionario tenían pocos incentivos para responder cuestiones sobre un problema que, en principio, no les afectaba. Además, la mayor parte de las centrales hidroeléctricas corresponden a grandes grupos empresariales que respondieron de manera agrupada por ríos y no individualizada por el gran número de centrales que aglutinan. No obstante, en términos de potencia hidroeléctrica instalada, la tasa de respuesta obtenida alcanzó el 95 % del total, puesto que solo tres empresas concentran el 90 % de este tipo de potencia (grandes centrales). En el subsector nuclear la tasa de respuesta fue del 100 % de la potencia instalada, mientras que en el térmico alcanzó el 80 %.

La integración de los costes por sectores se refleja en la figura 2, donde se representan los costes económicos anuales durante el periodo de estudio. Con respecto al sector energético, a excepción de 2006, se observa una tendencia lige-

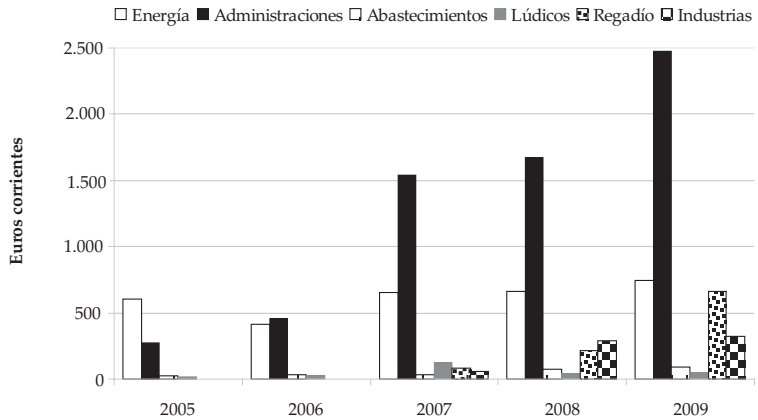

Figura 2. Costes económicos anuales (× 1000 euros) por sector socioeconómico en la cuenca del Ebro, periodo 2005-2009. *Annual economic costs (× 1000 Euros) by socioeconomical sector in the Ebro basin, 2005-2009 period.*

Tabla 3. Distribución temporal de los costes en las empresas energéticas por tecnología de producción (€ corrientes, 2005-2009). *Temporal distribution of the costs in the energetic companies according to the production technology (2005-2009, current Euros).*

Tipo de producción energética	2005	2006	2007	2008	2009	2005-2009
Hidroeléctrica	489 636	268 834	225 439	416 130	280 500	1 680 539
Nuclear	117 250	144 500	426 500	235 500	345 500	1 269 250
Térmica	0	0	0	7500	118 500	126 000

ramente creciente, al pasar de 606 886 euros en 2005 hasta alcanzar los 744 500 en 2009, situándose como media en 615 000 euros/año. El tipo de producción energética que más costes económicos ha soportado, Tabla 3, ha sido la hidroeléctrica con 1 680 539 euros en los cinco años analizados, seguida de la nuclear con 1 269 250 euros y, en menor grado, la térmica con 126 000 euros. De hecho, las centrales térmicas no comienzan a generar costes hasta 2008. Respecto a la tipología de los costes en este sector, las centrales hidroeléctricas han visto incrementados sus gastos al invertir en mano de obra de limpieza y mantenimiento de las captaciones de agua y filtros localizados en cauces afectados. En las centrales térmicas, dado el pequeño caudal de derivación que necesitan, los gastos se centran principalmente en la construcción de filtros y rejas e investigación en métodos de control de la plaga. En las centrales nucleares se contabilizan costes de I+D, gastos en productos químicos de control e importantes pérdidas económicas por disminución de la potencia generada.

El grado de respuesta de las administraciones públicas estatales y autonómicas de la cuenca fue del 60 %, Tabla 2, contando con nueve organismos que participaron en tareas de prevención y control de la invasión. Los costes para las distintas administraciones públicas involucradas se han disparado en los últimos años. Se ha pasado de un coste en la lucha contra el mejillón cebra de 271 857 euros en el primer año de estudio a otro de 2 472 796 euros en el 2009 (Fig. 2). En este sector, los costes han ido dirigidos a estudios para el conocimiento de la biología del invasor y para el desarrollo de métodos de control, seminarios, labores de información y concienciación, campañas de monitorización larvaria y de adultos para una detección precoz de la plaga en las masas de agua de la cuenca, construcción y mantenimiento de estaciones de desinfección de embarcaciones y material en embalses y otras actuaciones de gestión.

En el sector de abastecimientos, la tasa de respuesta fue del 16.6 %, con 8 ayuntamientos afectados al final del periodo de estudio, Tabla 2. Este sector ha estado afectado desde el comienzo de la invasión en 2001 y, desde entonces, las afecciones han estado siempre presentes sin dejar de crecer su coste, aunque ligeramente con respecto a otros sectores (Pérez y Pérez & Chica, 2006). Los efectos de la invasión en los sistemas hidráulicos de abastecimientos se localizan en los tramos de conducciones comprendidos entre la captación y la entrada al proceso de potabilización, ya que, a partir de este punto, las larvas son eliminadas en las distintas etapas de la línea de tratamiento de aguas. Por ello, los costes derivados de este sector son menores. Como se observa en la figura 2, y a pesar del incremento de los costes observados durante el periodo de estudio, la participación relativa de los mismos es, junto con la del sector lúdico-deportivo, la de menor magnitud. Sin embargo, sería conveniente un mayor estudio de las repercusiones económico-sociales en este sector por su importancia y afección a la ciudadanía, pudiendo repercutir en las tarifas del agua.

En el sector lúdico-deportivo, 17 de las 25 empresas que respondieron han incurrido en costes económicos en la lucha contra esta especie, Tabla 2. En el estudio realizado en el periodo 2001-2005 (Pérez y Pérez & Chica, 2006) no se detectaron costes asociados a este sector. Los resultados actuales constatan que ha habido un número creciente de usuarios lúdico-deportivos afectados por la invasión, figura 2, cuyos costes se han materializado fundamentalmente en inversiones en limpieza y desinfección del material que utilizan, pues es obligatorio desinfectar las embarcaciones que navegan en embalses afectados por mejillón cebra y protegidos en la cuen-

ca del Ebro (Resolución de 24 de septiembre de 2002 y Resolución de 15 de mayo de 2007 de la Confederación Hidrográfica del Ebro). Hay un incremento puntual de gastos en 2007 localizado en Zaragoza capital con motivo de la Expo 2008, en respuesta a inversiones y gastos en material de limpieza y desinfección. Exceptuando lo acontecido en 2007, los costes se han duplicado en el periodo de análisis al pasar de 20 550 euros en 2005 a 50 471 en 2009, pero la participación relativa de los mismos en el total de costes, como se ha indicado previamente, es baja.

El sector agrícola fue el sector más participativo, debido en parte a la organización de los usuarios bajo la figura de comunidades generales de regantes, facilitando la distribución de la información a todos los usuarios y su posterior seguimiento. Se obtuvo contestación de 139 usuarios, lo que representa una tasa de respuesta del 88 % (Tabla 2). Treinta y siete comunidades declararon estar afectadas por la invasión y 24 de ellas incurrieron en gastos en alguno de los años del periodo de estudio. Existe una tipificación de las afecciones en función del método de riego, ya sea a manta, aspersión o goteo. Independientemente del método, se detectan problemas en rejas, compuertas y bombas en la zona de captación. Donde predomina la aspersión o el goteo los problemas más importantes se traducen en obstrucciones de tuberías de distribución de pequeño diámetro, desgaste de válvulas y bombas de elevación, colapso de filtros y aspersores. En los riegos superficiales a manta predomina la afección a acequias y tajaderas, aunque es el tipo de riego que menos problemas genera a los agricultores, pues el riesgo de obstrucción es mínimo. La limpieza anual de balsas interiores de regulación implica un coste que empieza a considerarse en los sistemas de riego, pues estas balsas actúan de reservorios importantes de larvas de mejillón cebra. La tipología de costes correspondientes a las afecciones indicadas se traduce fundamentalmente en un incremento del coste de la mano de obra en mantenimiento y explotación, así como costes asociados a limpieza y extracción de conchas acumuladas en filtros. El incremento de costes en este sector ha sido importante, pasando de un valor de 2000 euros en 2005 a 664 907 en el último año de estudio, como muestra la Figura 2. De hecho, en este último año el regadío casi ha igualado los costes generados por el sector energético, contrastando con la poca incidencia de sus costes hasta 2005 (Pérez y Pérez & Chica, 2006).

Finalmente, la tasa de respuesta del sector industrial no energético fue del 17 %. Sólo 10 de las 84 empresas que cumplimentaron el cuestionario afirmaron haber incurrido en costes monetarios, que empiezan en 2007 (Tabla 2). Como se puede apreciar en la Figura 2, a pesar de la tardía aparición de afecciones en este sector, en los tres últimos años del periodo de análisis su cuantía se ha multiplicado por seis, al pasar de 53 000 euros en 2007 a 321 450 en 2009. También se ha duplicado el número de empresas afectadas, pasando de 3 a 6, así como se ha incrementado la participación relativa de estos costes en el total de costes derivados de la invasión en la cuenca del Ebro, al pasar de representar apenas el 2 % en 2007 al 7.5 % en 2009. Las afecciones en este sector se localizan en las partes de la industria en contacto con el cauce afectado, es decir, rejas y compuertas, tuberías, válvulas, filtros y depósitos de almacenamiento de agua interiores. Especial atención merecen los sistemas de refrigeración presentes en algunos tipos de industrias (CHE & KEMA, 2011). La tipología de costes correspondientes a estas afecciones se centra en costes de mano de obra para trabajos de mantenimiento y limpieza, así como en gastos asociados a productos químicos de control para eliminar las poblaciones de mejillón cebra instaladas en las infraestructuras afectadas. En el anterior estudio realizado por Pérez y Pérez & Chica (2006) no se detectaron afecciones en este sector.

Atendiendo a la localización geográfica de los costes, la figura 3 muestra los costes asumidos por cada sector analizado en función de las áreas establecidas en la cuenca del Ebro. No se ha tenido en cuenta en esta parte del análisis los costes asociados a las administraciones públicas, pues no pueden ser referenciados geográficamente, ya que en el caso de la Confederación Hidrográfica del Ebro, todas las provincias de la cuenca se benefician de los mismos.

En la figura 4 se muestran los costes anuales por tramos del río Ebro. Aunque las prime-

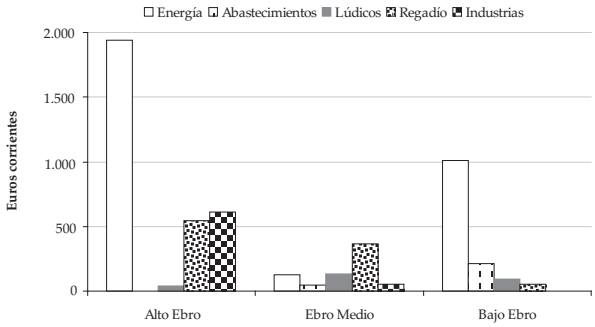

Figura 3. Costes económicos totales (× 1000 euros) de los distintos sectores por tramo de río en la cuenca del Ebro, 2005-2009. *Total economic costs (× 1000 Euros) of different sectors by stretch of river in the Ebro basin, 2005-2009.*

ras afecciones se detectaron en el Bajo Ebro, y por tanto, las inversiones iniciales se centraron en esa zona de la cuenca (Pérez y Pérez & Chica, 2006), se puede observar en las figuras 3 y 4 que los costes generados en el Alto Ebro están adquiriendo un mayor protagonismo en los últimos cinco años, en coherencia con su expansión paulatina en contracorriente, con unos costes totales de 3 133 856 euros. En la figura 3 se observa que los costes asumidos por los sectores energéticos, industrial y agrícola son los más relevantes en esta zona, superando de manera significativa la inversión asumida por estos mismos sectores en otras zonas. El sector energético alcanzó, en todo el periodo de análisis, un coste total de 1 938 552 euros, asumido por diversas centrales hidroeléctricas de Iberdrola y Endesa y la central nuclear de Garoña. En las redes de abastecimiento del Alto Ebro no se han constatado afecciones que conlleven costes económicos. Sin embargo, en los regadíos ubicados en este tramo se incurrieron en 2008 en los primeros costes en la lucha contra el mejillón cebra por parte de comunidades de regantes del tramo del Ebro lindante con Navarra y La Rioja, con aguas derivadas del propio río Ebro. En 2009 este sector tuvo un gasto puntual debido a la construcción de un sistema de filtrado en una comunidad de regantes que utiliza riego por goteo. No se presentan casos de costes en regadíos con aguas de sus afluentes, ni por su margen izquierda ni por su derecha en este tramo del Ebro, aunque se han empezado a tomar medidas en alguna de las comunidades de regantes del Canal de Lodosa, en la margen derecha. El foco con mayores repercusiones económicas en el sector industrial se produjo inicialmente en el Alto Ebro con aguas del embalse de Sobrón y de las derivaciones de caudales ubicadas a lo largo del cauce principal.

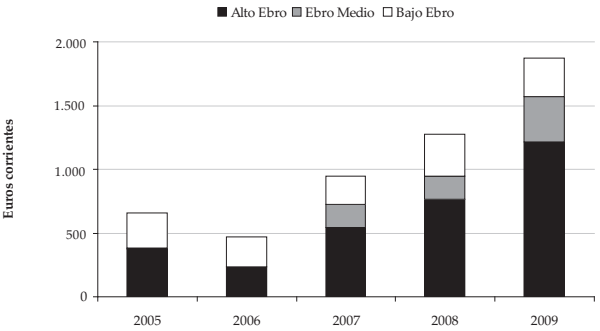

Figura 4. Costes económicos anuales (× 1000 euros) por tramo de río Ebro, 2005-2009. *Annual economic costs (× 1000 Euros) by stretch of Ebro river, 2005-2009.*

Analizando los resultados mostrados en la figura 4 sobre el Bajo Ebro, se puede observar que los costes derivados de la invasión se mantienen constantes a lo largo de los cinco años de estudio, situándose como media en 237 135 euros/año. Los principales costes asociados al sector energético se localizan en la Central Nuclear de Ascó y las centrales hidroeléctricas de Ribarroja y Flix, que supusieron una cuantía total de 1 365 000 euros para el periodo de estudio. Los costes del regadío en esta zona se inician en 2007, fundamentalmente en las tomas de riegos en el eje del río aguas abajo del embalse de Flix y en la margen derecha, en el río Guadalope, con una cuantía de 53 000 euros. No se ha constatado la presencia de mejillón cebra en las instalaciones industriales que toman agua en esta parte de la cuenca del Ebro, mientras que dos abastecimientos con toma directa del embalse de Ribarroja han indicado afecciones por valor de 210 051 euros.

En el tramo del Ebro Medio no se contabilizan costes para el control del mejillón cebra hasta 2007, pero a partir de este año estos tienen una tendencia al alza (Fig. 4). La inversión total ha sido de 729 848 euros. En esta zona de la cuenca, como se puede observar en

la figura 3, el sector que incurre en más costes es el sector agrícola, con un montante total de 362 466 euros en el periodo de estudio. La mayor parte de las comunidades de regantes afectadas tienen sistemas de riego por goteo y por aspersión. Se localizan en el eje del Ebro (Canal de Lodosa y Canal Imperial, riegos de ribera con toma directa del río en Zaragoza y las elevaciones desde el embalse de Mequinenza).

Las empresas lúdico-deportivas afectadas por la invasión del mejillón cebra se distribuyen por el Alto, Medio y Bajo Ebro tanto en el eje del río (empresas de pesca deportiva y navegación) como en afluentes de su margen derecha e izquierda (empresas de rafting).

La figura 5 muestra los costes totales en orden creciente de cada sector durante los cinco años analizados. Los organismos públicos ocupaban el segundo lugar en importancia tras las empresas energéticas hasta 2005. En el periodo 2005-2009 pasan a ocupar el primer puesto, multiplicándose por 9 y alcanzando un total de 6.4 millones de euros. Representan un 55.1 % del total de costes de la lucha contra la expansión del bivalvo. En el estudio anterior citado, las administraciones representaban un 22 % del total. La cuantía total asumida por el sector energético superó los 3 millones de euros en el periodo 2005-2009. Esta cantidad representa el 26.4 % de los costes totales en dicho periodo. El protagonismo de este sector ha disminuido con respecto al 74 % de los costes totales que asumió durante el periodo 2001-2005 (Pérez y Pérez & Chica, 2006). En cuanto a abastecimientos y empresas dedicadas a usos deportivos y lúdicos, a pesar del incremento de los costes observados, apenas alcanzan cada sector el 2.2 % de los costes totales del periodo considerado (259 491 y 262 824 euros, respectivamente), contando con una participación similar a la del citado estudio. En el mismo, los costes motivados por el mejillón cebra en regadíos e industrias fueron prácticamente despreciables, mientras que en el presente análisis la participación del sector agrícola asciende a un 8.2 % de los costes totales, 963 403 euros, mientras que el sector industrial, 667 870 euros, representa un 5.7 % del total. Estos resultados suponen la inclusión de regadíos e industrias en el grupo de sectores económicos afectados en el periodo 2005-2009.

La suma de los costes totales generados por todas las categorías de usuarios del agua se agrupan por años en la figura 6, donde se constata que los costes originados por la expansión de la invasión del mejillón cebra en la cuenca del Ebro no han cesado de crecer en los últimos años. Durante los dos primeros años los costes se mantuvieron estables, no llegando al millón de euros. Sin embargo, en 2007 y 2008, la cuantía alcanzó 2.5 y 3 millones de euros, respectivamente. En 2009, coincidiendo con el plan de generación de empleo en España, esa cifra alcanza los 4 347 373 de euros. Los costes económicos se multiplicaron por 4.7 entre 2005 y 2009 y supusieron un total de 11 641 997 euros en dicho periodo para el más del centenar de usuarios del agua que se vieron afectados a lo largo de la cuenca del Ebro.

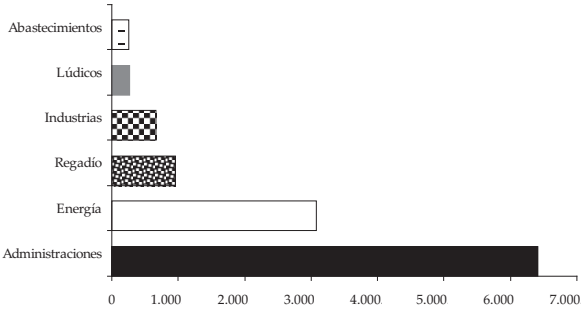

Figura 5. Costes totales (× 1000 euros) por sectores socioeconómicos. Periodo 2005-2009. *Annual costs (× 1000 Euros) by socioeconomical sectors. 2005-2009 Period.*

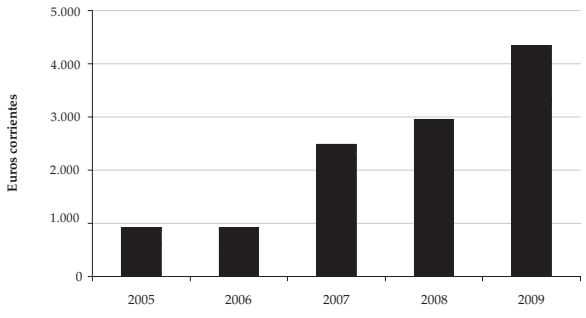

Figura 6. Costes económicos anuales (× 1000 euros) de la lucha contra el mejillón cebra de todos los sectores socioeconómicos encuestados. *Annual economic costs (× 1000 Euros) from the fight against the zebra mussel of all socioeconomic sectors polled.*

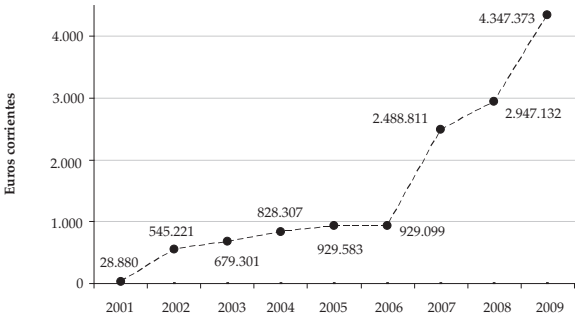

Figura 7. Evolución del coste total anual (× 1000 euros) de la invasión del mejillón cebra para todos los usuarios de la cuenca del Ebro (2001-2009). *Evolution of the annual total cost (× 1000 Euros) of the zebra mussel invasion for all the users of the Ebro basin (2001-2009).*

O'Neill (1997) establece que los gastos totales anuales de la lucha contra el mejillón cebra en el noreste de los Estados Unidos pasaron de 234 140 dólares en 1989 a 17 millones de dólares en 1995. En esos siete años se estima que el coste total alcanzó los 69 millones de dólares, siendo las centrales eléctricas y los sistemas de abastecimiento de agua las infraestructuras que soportaron más del 80 % de los costes. Según los datos recogidos por U.S. Army (2002), los costes provocados por este invasor durante el periodo 1993-1999 superaron los 5000 millones de dólares, de los que más del 60 % fueron soportados por la industria eléctrica. La dimensión de estos resultados se aleja en gran medida de los datos recogidos en la cuenca del Ebro, en parte debido a que el avance del molusco en España ha sido más lento que en el continente americano.

Por otra parte, también se han estimado los costes de las medidas de control aplicadas por el sector eléctrico canadiense, estableciéndose una inversión de más de 20 millones de dólares con unos costes variables anuales que superan el millón de dólares (Canadian Biodiversity Information Network, 2004).

Las cifras obtenidas en este estudio han dejado bastante atrás las previsiones que se barajaban en 2005 (Pérez y Pérez & Chica, 2006). En el periodo 2001-2005, los costes totales estimados en la lucha contra *Dreissena polymorpha* fueron de 2 081 709 euros, por lo que en los nueve años transcurridos desde que se detectó el mejillón cebra, los costes en defensa, control y prevención de los distintos sectores económicos y administraciones afectadas se ha multiplicado prácticamente por 150, alcanzando una suma total de 13.7 millones de euros, observándose un ritmo de crecimiento más elevado en el periodo 2005-2009 que en el anterior 2001-2005 (Fig. 7).

CONCLUSIONES

La expansión de la invasión del mejillón cebra en la cuenca del Ebro no ha cesado de aumentar en los últimos años y se confirma el hecho de que en su propagación concurren actividades antrópicas, pues la colonización de la cuenca del Ebro se efectúa a contracorriente en sentido de la desembocadura al nacimiento. Geográficamente es en el Alto Ebro donde más recursos económicos se han invertido, como corresponde a la zona de más reciente colonización.

Para analizar la afección se determinaron seis sectores implicados: energético, industrial, agrícola, lúdico-deportivo, administraciones públicas y abastecimientos, lo que, por una parte, incrementó el trabajo de elaboración de encuestas diferenciadas, pero, por otra, ha permitido analizar más en profundidad los datos y la problemática de dichos sectores, aunque este trabajo se focaliza hacia los aspectos económicos, quedando establecida una base de datos para desarrollar posteriores estudios de otra índole. También la división permitió delimitar la muestra y centrarla en usuarios de los recursos hídricos susceptibles de estar afectados por la invasión del mejillón cebra, dentro de la totalidad del territorio de la cuenca hidrográfica del Ebro. La representación de la muestra diferenciada por sectores presenta unos altos porcentajes específicos, todos ellos superiores al 80 %: potencia eléctrica instalada, empresas no energéticas, superficie de regadío, empresas de deporte fluvial, organismos estatales y autonómicos y recursos hídricos consumidos en abastecimientos.

En este trabajo se analizan también las distintas tipologías de daños que originan los costes. Hay que advertir que los costes de las administraciones son costes de control que han ido di-

rigidos fundamentalmente a estudios para el conocimiento de la biología del invasor y para el desarrollo de métodos de control, seminarios, labores de información y concienciación, campañas de muestreos larvarios y de adultos para una detección precoz de la plaga, etc. En los restantes sectores prácticamente los costes se podrían denominar "reactivos", al responder directamente al descubrimiento de daños en las instalaciones y servicios.

Los costes económicos han superado los 11.6 millones de euros en el periodo de estudio, 2005-2009. De los costes totales cuantificados, las administraciones públicas han aportado el 55.1 %. Al sector energético le corresponde un 26.4 % del coste total estimado. Los mayores costes se presentan en las centrales hidráulicas, seguidos por las nucleares y térmicas. Las comunidades de regantes y empresas agrícolas representan el 8.3 % del coste total y las empresas industriales no energéticas, el 5.7 %. Los costes en el sector de usos lúdicos deportivos del agua suponen el 2.3 % de los costes totales. Finalmente, los abastecimientos, pioneros junto a las centrales energéticas en la lucha contra la expansión del mejillón cebra en 2001, representan el 2.2 % de la inversión total.

Los diferentes sectores socioeconómicos han incrementado sus recursos para controlar el mejillón cebra y poder superar los problemas que ocasiona esta especie invasora en sus instalaciones o en las zonas afectadas donde desarrollan sus actividades económicas. Por otra parte, la cuantificación de los costes asociados al mejillón cebra es la variable más eficaz a la hora de poner en marcha acciones de control y prevención para las distintas administraciones.

Como ha puesto de manifiesto este estudio, el coste económico asociado al control y gestión de la invasión por mejillón cebra es ya muy elevado. Por ello, los futuros esfuerzos deberían ir dirigidos a impulsar medidas de prevención en las zonas todavía indemnes.

AGRADECIMIENTOS

Los autores agradecen la colaboración desinteresada de los encuestados, que han hecho posible la realización de este estudio y, especialmente, la de Yolanda Gimeno, de la Comunidad General de Riegos del Alto Aragón, por su disponibilidad y ayuda.

BIBLIOGRAFÍA

ALTABA, C. R., P. J. JIMÉNEZ & M. A. LÓPEZ. 2001. El temido mejillón cebra empieza a invadir los ríos españoles desde el curso bajo del río Ebro. *Quercus*, 188: 50–51.

ÁLVAREZ HALCÓN, R. M. 2001. El mejillón cebra: una amenaza para el Ebro. *Ibón, Revista de naturaleza y divulgación ambiental*, 15: 16–20.

ARAUJO, R., & R. M. ÁLVAREZ. 2001. El mejillón cebra en el Ebro: Un grave caso de riesgo ambiental en Aragón. *Naturaleza Aragonesa*, diciembre.

BINIMELIS, R., W. BORN, I. MONTERROSO & B. RODRÍGUEZ-LABAJOS. 2007. Socioeconomic impacts and assessment of biological invasions. In: *Biological Invasions. Ecological Studies.* N. Nentwig (ed.): 331–348. Springer-Verlag Berlin Heidelberg. Berlin.

BOBAT, A. 2004. Zebra Mussel and Fouling Problems in the Euphrates Basin. *Turkish Journal of Zoology*, 28: 161–177.

BORN, W., F. RAUSCHMAYER & I. BRAUER. 2005. Economic evaluation of biological invasions-a survey. *Ecological Economics*, 55: 321–336.

CANADIAN BIODIVERSITY INFORMATION NETWORK. 2004. An invasive alien species strategy for Canada. Disponible en: http://www.ec.gc.ca/eee-ias/default.asp? lang= En& x ml =733437C8-1B65-400F-9074-E1F3EA692114.

CHE & KEMA. 2011. Control y mitigación del mejillón cebra dentro del marco normativo de la Unión Europea. Documento interno. 124 pp. Disponible en: http://www.chebro.es/contenido.visualizar.do?idContenido=28341&idMenu=4080.

COLLAUTTI, R. I., S. A. BAILEY & C. D. A. VAN OVERDIJK. 2006. Characterised and projected costs of nonindigenous species in Canada. *Biological Invasions*, 8: 45–59.

CONNELLY, N. A., C. R. O'NEILL JR., B. A. KNUTH & T. L. BROWN. 2007. Economic Impacts of Zebra Mussels on Drinking Water Treatment and Electric Power Generation Facilities. *Environmental Management*, 40: 105–112.

DURÁN, C., A. VIAMONTE, Y. BERNAT, L. DÍEZ-ANTOÑANZAS, C. JIMÉNEZ & A. ANADÓN. 2007. Mejillón cebra en aguas de la cuenca del Ebro. *Ambienta*, diciembre: 44–50.

DURÁN, C., & A. ANADÓN. 2008. The zebra mussel invasion in Spain and navigation rules. *Aquatic Invasions*, 3: 315–324.

DURÁN, C., M. LANAO, A. ANADÓN & V. TOUYÁ. 2010. Management strategies for the zebra mussel invasion in the Ebro River basin. *Aquatic Invasions*, 5(3): 309–316.

GOZLAN, R. E. 2010. The cost of non-native aquatic species introductions in Spain: fact or fiction? *Aquatic Invasions*, 5(3): 231–238.

HIGGINS, T. M., J. M. GRENNAN & K. T. MCCARTHY. 2008. Effects of recent zebra mussel invasion on water chemistry and phytoplankton production in a small Irish lake. *Aquatic Invasions*, 3(1): 14–20.

HUNTER, R. D., & J. F. BAILEY. 1992. *Dreissena polymorpha* (Zebra Mussel): Colonization of Soft Substrata and Some Effects on Unionid Bivalves. *The Nautilus*, 106(2): 60–67.

KARATAYEV, A. Y., L. E. BURLAKOVA & D. K. PADILLA. 1997. The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic Communities in Eastern Europe. *Journal of Shellfish Research*, 16(1): 187–203.

LOVELL, S. J., S. F. STONE & L. FERNANDEZ. 2006. The economic impact of aquatic invasive species: a review of the literature. *Agricultural Economics Research Review*, 35: 195–208.

MCLEOD, R. 2004. *Counting the cost: impact of invasive animals in Australia.* Cooperation Research Centre for Pest Animal Control. Camberra. 82 pp.

NAVARRO, E., M. BACARDIT, L. CAPUTO, A. PALAU & J. ARMENGOL. 2006. Limnological characterization and flow patterns of a three-coupled reservoir system and their influence on *Dreissena polymorpha* populations and settlement during the stratification period. *Lake and Reservoir Management*, 22(4): 293–302.

OLSON, L. J. 2006. The economics of terrestrial invasive species: a review of the literature. *Agricultural Economics Research Review*, 35: 178–194.

O'NEILL, C. R. 1997. Economic impact of zebra mussels. Results of the 1995 national zebra mussel information clearinghouse study. *Great Lakes Research Review*, 3(1): 35–45.

PÉREZ y PÉREZ, L. & C. CHICA. 2006. Estimación de los costes económicos de la invasión del mejillón cebra (*Dreissena polymorpha*) en la Cuenca del Ebro. *Fundación Economía Aragonesa (Fundear)*. DT 35/2006. Zaragoza. 48 pp.

PERRINGS, C., M. WILLIANSON & S. DALMAZONE. 2000. *The economics of biological invasions*. Edward Elgar. Cheltenham. United Kingdom. 249 pp.

PIMENTEL, D., L. LACH, R. ZÚÑIGA & D. MORRISON. 2000. Environmental and economic cost of non-indigenous species in the United States. *BioScience*, 53, vol. 50(1).

PIMENTEL, D., R. ZÚÑIGA & D. MORRISON. 2005. Update on the environmental and economic cost associated with alien-invasive species in the United States. *Ecological Economics*, 52: 273–288.

RESOLUCIÓN de 24 de septiembre de 2002, de la Confederación Hidrográfica del Ebro, sobre normas para la navegación en los embalses de Mequinenza, Ribarroja y Flix, tramos inferior del río Ebro por la aparición del mejillón cebra. Disponible en: http://www.chebro.es/contenido.visualizar.do?idContenido=21675&idMenu=3897.

RESOLUCIÓN de 15 de mayo de 2007, de la Confederación Hidrográfica del Ebro, sobre modificación de las normas de navegación con motivo de la expansión del mejillón cebra y nueva clasificación de embalses de la cuenca del Ebro. Disponible en: http://www.chebro.es/contenido.visualizar.do?idContenido=21675&idMenu=3897.

SOUSA, R., F. PILOTTO, D. R. ALDRIDGE. 2011. Fouling of European freshwater bivalves (Unionidae) by the invasive zebra mussel (*Dreissena polymorpha*). *Freshwater Biology*, 56: 867–876.

STRAYER, D. L. 1999. Effects of alien species on freshwater mollusks in North America. *Journal of the North American Benthological Society*, 18(1): 74–98.

US-OTA, United States-Office of Technology Assessment. 1993. Harmful non-indigenous species in the United States, OTA-F-565, NTIS order #PB9-107679, September, 397 pp.

U.S. ARMY. 2002. Economic impact of zebra mussel infestation. Disponible en: http://el.erdc.usace.army.mil/zebra/zmis/zmishelp/economic_impacts_of_zebra_mussel_infestation.htm.

VILÀ, M., C. BASNOU, P. PYŠEK, M. JOSEFSSON, P. GENOVESI, S. GOLLASCH, W. NENTWIG, S. OLENIN, A. ROQUES, D. ROY, E. PHI-

LIP & P. E. HULME. 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment*, 8: 135–144.

ANEXO I

Cuestionario

Sobre la base de la encuesta energética, las primeras 18 preguntas son comunes a todos los sectores socioeconómicos (11-15 adaptadas a las características de cada sector). A continuación se añaden las preguntas específicas de cada uno de ellos.

1. A modo de introducción, le vamos a mencionar una serie de aspectos ambientales globales que usted puede considerar más o menos importantes. Le rogamos que valore su importancia en una escala de 1 a 5, siendo 1 nada importante y 5 muy importante:

Aspectos ambientales	**Valoración**				
	1	**2**	**3**	**4**	**5**
La extinción de especies y degradación del paisaje	□	□	□	□	□
La contaminación de los ríos	□	□	□	□	□
La invasión de especies foráneas acuáticas	□	□	□	□	□

2. ¿En qué tramo y margen de la cuenca del Ebro se ubica su actividad?

   * Hay tres tipos de **tramo**:

   - **Alto Ebro** (cabecera-desembocadura del río Aragón en Alfaro).
   - **Ebro Medio** (desembocadura del río Aragón-desembocadura del río Segre en Mequinenza).
   - **Bajo Ebro** (desembocadura del río Segre hasta el mar).

   * A su vez, dentro de cada tramo hay tres opciones en función del **eje del Ebro**:

   - **Eje Ebro**, en el propio cauce del río Ebro.
   - **Margen Derecha**: en dirección a su desembocadura (afluentes como el Najerilla, Alhama, Jalón, Huerva, Matarraña etc.).
   - **Margen Izquierda**, en dirección a su desembocadura (afluentes como el Zadorra, Aragón, Gállego, Cinca, Segre, etc.).

(Marque la opción elegida atendiendo a la zonificación efectuada):

ALTO EBRO		**EBRO MEDIO**		**BAJO EBRO**	
Eje Ebro	□	**Eje Ebro**	□	**Eje Ebro**	□
Margen Derecha	□	**Margen Derecha**	□	**Margen Derecha**	□
Margen Izquierda	□	**Margen Izquierda**	□	**Margen Izquierda**	□

3. ¿Sabe si se ha detectado la presencia del mejillón cebra en las proximidades de sus instalaciones (en instalaciones que no son las suyas)? *(Marque la opción elegida)*

No □
Si □ En caso afirmativo, ¿podría especificar dónde y quién/es son los afectados?

4. ¿Ha detectado la presencia del mejillón cebra en sus instalaciones? *(Marque la opción elegida)*

Si □
No □ (Vaya directamente a las preguntas 11 y siguientes)

5. ¿En qué año detectó por primera vez la presencia del mejillón cebra en sus instalaciones?

Año: 200_

6. ¿En qué año empezó por primera vez a tomar medidas para combatir las afecciones provocadas por el mejillón cebra?

Año: 200_

7. A partir de entonces, ¿qué otros años ha debido tomar medidas para luchar contra la invasión?

□ **2005**
□ **2006**
□ **2007**
□ **2008**
□ **2009**

8. ¿Qué parte/s de su instalación han sido afectadas por el mejillón cebra? *(Marque la opción/es elegida/s)*

□ Rejas de la toma
□ Compuertas
□ Conducciones circuito hidro
□ Tuberías, válvulas circuitos control
□ Bombas de presión y elevación
□ Filtros y membranas
□ Contraincendios
□ Otros (especificar)……

9. ¿Qué tipología de costes origina la lucha contra el mejillón cebra en sus instalaciones? *(Marque la opción/es elegida/s)*

□ Inversión en construcción de componentes del sistema: filtros, rejas…
□ Materiales, productos químicos de control o extracción
□ Incremento de mano de obra en mantenimiento y explotación
□ Pérdidas económicas por paradas originadas por efectos del mejillón cebra
□ Investigación y desarrollo
□ Otros (especificar):……

10. ¿Podría indicar los costes (aproximados) que le ha supuesto la invasión del mejillón cebra? (en euros)

2005:	**€**	**2006:**	**€**
2007:	**€**	**2008:**	**€**
Previsión 2009:	**€**		

11. ¿Dónde se localiza la toma de agua de la central hidroeléctrica o del circuito de refrigeración de la central? *(Marque la opción elegida)*

□ Directamente de un cauce fluvial
□ De un embalse, balsa de regulación o depósito de acumulación
□ De un canal de usos múltiples: riego, abastecimientos, industrias
□ De pozo mediante bombeo

12. Como casos singulares, si la toma se efectúa en un cauce fluvial importante o embalse en el propio río. ¿Podría especificar el nombre?

Río: Embalse:

13. ¿Cuál es el caudal máximo de la toma de agua? *(Marque la opción elegida)*

□ Menos de 1 m^3/seg
□ Entre 1 y 5 m^3/seg
□ Entre 5 y 10 m^3/seg
□ Entre 10 y 20 m^3/seg
□ Entre 20 y 40 m^3/seg
□ Entre 40 y 70 m^3/seg
□ Entre 70 y 120 m^3/seg
□ Más de 120 m^3/seg

14. ¿Cuál es el volumen de agua anual derivado por la industria/central/instalación? (en metros/hectómetros cúbicos)

15. ¿Cuántos km de tubería cerrada hay desde la captación hasta la industria/central/instalación?

16. Aclaraciones a alguna pregunta, observaciones…

17. Dirección postal, Municipio de la sede social:

18. Persona y teléfono de contacto.

SECTOR ENERGÉTICO:

19. Su central de producción eléctrica, ¿dentro de qué tipología puede encuadrarse?

□ Hidráulica, convencional o reversible
□ Térmica
□ Nuclear
□ Nuevas Tecnologías

SECTOR AGRÍCOLA:

19. ¿Cuántas balsas de almacenamiento de agua tiene?

20. ¿Cuál es el volumen total de ellas? **(en metros cúbicos)**

21. ¿Qué superficie se riega? *(Marque la opción elegida)*

- Menos de 10 ha. □
- Entre 10 y 100 ha. □
- Entre 100 y 1.000 ha. □
- Entre 1.000 y 5.000 ha. □
- Entre 5.000 y 15.000 ha. □
- Entre 15.000 y 30.000 ha. □
- Más de 30.000 ha. □

22. ¿En qué proporción se divide el regadío? (observe que la suma a)+ b) + c) ha de ser= 100).

a) **Inundación a manta** (en %):

b) **Aspersión** (en %):

c) **Goteo** (en %):

SECTOR ABASTECIMIENTOS:

19. ¿Cuál es la población abastecida por la planta? (en habitantes).

SECTOR DE LAS ADMINISTRACIONES PÚBLICAS:

1. Nivel de la administración con responsabilidades en materia de aguas, u organismo involucrado.

□ Ministerial (Dirección General, etc.)
□ Organismo Autónomo estatal (CHE. . .)
□ Gobiernos Autónomos (Consejerías, Organismos Autónomos Autonómicos, Servicios...)
□ Universidades, Centros de Investigación. . .

2. ¿En qué año empezó por primera vez a tomar medidas para combatir las afecciones provocadas por el mejillón cebra, o intervino en su caracterización y estudio?

Año: 200_

3. A partir de entonces, ¿qué otros años ha realizado estudios o intervenciones para luchar contra la invasión?

Años:

4. ¿Qué tipología de costes origina la lucha contra el mejillón cebra? (Marque la opción/es elegida/s)

□ Inversión en construcción de instalaciones y subvenciones
□ Estudios y proyectos
□ Seminarios, Jornadas y publicaciones
□ Asistencia técnica en prospecciones, muestreos, diseños. . .
□ Información, folletos
□ Otros (especificar)

SECTOR LÚDICO:

Preguntas 1, 2, 10, 16, 17 y 18 de la parte común.

— ¿Qué tipología de costes origina la lucha contra el mejillón cebra? (Marque la opción/es elegida/s)

□ Inversión en material de desinfección
□ Lucro cesante por disminución de actividad o cese de actividad
□ Otros (Especificar)

— Número de embarcaciones y tipología.

Limnetica, 31 (2): 231-250 (2012)

Nutrient and sediment dynamics in a Mediterranean shallow lake in southwest Spain

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Received: 7/4/11 Accepted: 6/2/12

ABSTRACT

Nutrient and sediment dynamics in a Mediterranean shallow lake in southwest Spain

Temporal and spatial variations in the nutrient concentrations of lake water and surface sediments and in settling and resuspension rates were assessed in a Mediterranean shallow lake (Medina Lake, southern Spain) using a combination of short-term and long-time monitoring. Our results confirmed the high temporal (inter- and intra-annual) variability characterising Mediterranean shallow lakes, which is also enhanced by water level fluctuations. The results also underlined the crucial role of phosphorus (P) exchange across the sediment-water interface in controlling P dynamics in lake water. This statement is supported by (i) the existence in the upper 1 cm of the sediment of 18 times the mass of TP of the whole water column and, hence, the high potential impact of P released from the sediment into the overlying column and by (ii) the strong P limitation of planktonic primary production, as reflected by a DIN:TP atomic ratio much higher than 16. Resuspension, co-precipitation with $CaCO_3$ and adsorption onto iron hydroxides (FeOOH) all had major effects on the P exchange across the sediment-water interface. Wind-induced resuspension (31 ± 13 % of the settled matter) explained the extremely high gross sedimentation rates (40 ± 11 g m^{-2} d^{-1}) recorded for a 24 h period. P adsorption onto FeOOH controlled internal P loading during the winter (FeOOH: P_{mobile} > 15). During the summer, the low availability of FeOOH (Fe:P_{mobile} < 15) reflected the inability of FeOOH to control P adsorption. The SRP concentrations in lake water were much higher than necessary for $CaCO_3$ and P co-precipitation, explaining the high contribution of P bound to $CaCO_3$ (P_{HCl}) to the total P in the sediment of the study site and demonstrating the importance of $CaCO_3$ precipitation for removing P from lake water.

Key words: Mediterranean shallow lakes, phosphorus, sediment, resuspension.

RESUMEN

Dinámica de los nutrientes y del sedimento en un lago somero Mediterráneo

En este trabajo se estudia la distribución temporal y espacial de los nutrientes en el agua y en el sedimento superficial así como las tasas de sedimentación y resuspensión en una laguna somera Mediterránea (laguna de Medina, Sur de España). Para ello se ha empleado una doble aproximación basada en un seguimiento a corto (muestreos intensivos) y a largo plazo (seguimiento estacional). Nuestros resultados han confirmado la elevada variabilidad temporal (inter e intra-anual) que caracteriza a los lagos someros mediterráneos, y que es favorecida por las fluctuaciones en el nivel de agua. Además, se ha observado el importante papel que juega el intercambio de fósforo (P) a través de la interfase agua-sedimento sobre la dinámica de este nutriente en la columna de agua. Esta afirmación se sustenta en: (i) la existencia en el sedimento superficial (1 cm) de 18 veces la masa de TP presente en toda la columna de agua; y en (ii) la fuerte limitación de la producción primaria planctónica por P, reflejada por una razón atómica DIN:TP muy superior a 16. La resuspensión, la precipitación con carbonato cálcico ($CaCO_3$) y la adsorción sobre hidróxidos de hierro (FeOOH) son los procesos físicos y químicos más relevantes que afectan al intercambio de P en la interfase agua-sedimento. La resuspensión (31 ± 13 % del material sestónico) inducida por el viento es el principal factor responsable de la extremadamente elevada tasa de sedimentación de partículas en la laguna de Medina (40 ± 11 g $m^{-2}d^{-1}$), registradas durante períodos de 24h. Por otro lado, la adsorción de P sobre FeOOH limita la carga interna de P durante el invierno (FeOOH: $P_{móvil}$ > 15); mientras que durante el verano, la escasa disponibilidad de FeOOH (Fe:$P_{móvil}$ < 15) indica un papel secundario de los FeOOH en el control de la carga interna de P. Finalmente, la existencia de concentraciones de fósforo reactivo soluble (SRP) en la columna de agua muy superiores a las estimadas como necesarias

para que tenga lugar la co-precipitación con $CaCO_3$, es la responsable de que la fracción más importante de P sedimentario sea la asociada al $CaCO_3$, confirmando la importancia de este proceso químico para la retención de P en el sedimento.

Palabras clave: *Lagos someros Mediterráneos, fósforo, sedimento, resuspensión.*

INTRODUCTION

Shallow lakes can be defined as more or less permanent standing water bodies that are shallow enough to potentially allow light penetration to the lake bottom and are frequently colonised by higher aquatic plants (Meerhoff & Jeppesen, 2009). Shallow lakes are also defined as polymictic, as they do not stratify for long periods in the summer and the entire water column is frequently mixed (Scheffer, 1998). The average depth of most of these aquatic ecosystems is less than 3 m. Since the 1990s, it has generally been accepted that, over a range of nutrient concentrations, shallow temperate lakes can have two alternative equilibrium states: a clear state dominated by aquatic vegetation and a turbid state characterised by high algal biomass (Scheffer *et al*., 1993). Aquatic vegetation can stabilise a clear-water state in shallow lakes up to relatively high nutrient loadings, but once the system has switched to a turbid state, a strong nutrient reduction is required to enable recolonisation by plants (Scheffer, 1998). The high surface area to maximum depth ratio and the typical polymixis that characterise shallow lakes are also responsible for an intense benthic-pelagic coupling. In fact, shallow lake functioning is subject to much temporal variability, and a major factor contributing to their marked instability is the close link between bottom sediments and overlying waters (de Vicente *et al*., 2006a). This sediment-water interaction is extremely important for understanding the nutrient dynamics of the water column (Ryding, 1985; Boström et al., 1988).

On a global scale, shallow lakes constitute a larger proportion of inland waters than hitherto believed (i.e., Downing, 2010). Their relevance is even greater in the Iberian Peninsula due to the scarcity of natural inland waters. Mediterranean shallow lakes are characterised by extreme natural fluctuations in water levels in response to irregular precipitation patterns (Álvarez-Cobelas *et al.*, 2005). The Mediterranean climate is characterised by dry, hot summers and mild winters with irregular precipitation, most of which occurs from October to February. As a consequence of the water level fluctuations, a portion of the lake sediment is exposed to air-drying in dry years when the water table becomes low, affecting those phosphate-binding properties of the lake sediment that are related to iron and aluminium oxides/hydroxides (de Vicente *et al.*, 2010a). Accordingly, water level fluctuations are likely to enhance the intense nutrient exchange across the sediment-water interface that characterises shallow lakes.

Sediments may affect water quality as a consequence of their dynamic and active character, resulting from a great variety of biogeochemical reactions and transformations. The resuspension of unconsolidated sediment usually plays a fundamental role in shallow lakes, where sediments are often subjected to continuous wave action (Kristensen *et al.*, 1992; Nõges *et al.*, 1999; Weyhenmeyer & Bloesch, 2001; de Vicente *et al.*, 2010b). Evidence for the importance of resuspension is plentiful (Kristensen *et al.*, 1992; Bloesch, 1995; Weyhenmeyer *et al.*, 1995). Resuspension rates can be estimated using different methodological approaches. Because sedimentation traps provide an estimation of the gross sedimentation flux rather than the net sedimentation flux (Bloesch, 1982), two different methods for estimating the contribution of resuspended matter to settled matter have been developed. First, and assuming that in relatively deep lakes resuspension only affects the bottom waters, the comparison between the settling rates measured at traps located close to the surface of the sediment with

those measured at traps farther above provides information about the resuspension rate (Bloesch, 1995; Kleeberg, 2002). However, the application of this method is limited in shallow lakes because the upper traps may also be affected by resuspended matter at certain times, which reveals the inherent difficulties in identifying an appropriate reference level (Bloesch, 1994). A second methodological approach for estimating resuspension rates is based on the use of Fe as a sediment tracer due to its generally low concentration in settled organic material (Jensen, pers. comm.). Hence, the contribution of resuspended matter to settling rates can be estimated by comparing the total iron (TFe) concentrations of both materials (surface sediments and settled matter) during periods without any inflow.

Apart from wind-induced resuspension, P cycling in shallow lakes strongly depends on biological processes, as most of the organic matter produced in the water column reaches the sediment without being mineralised, and also on chemical reactions (adsorption and precipitation) that are essentially mediated by iron oxides (FeOOH) and calcium carbonate ($CaCO_3$). The study of the chemical processes occurring at the sediment-water interface in deeper lakes has traditionally focused on the chemistry of Fe and P compounds, which ultimately depends on O_2 availability (Mortimer, 1941) and on the Fe:P ratio (i.e., Jensen *et al.*, 1992; Gächter & Wehrli, 1998; Gächter & Müller, 2003). However, $CaCO_3$ precipitation is a very common process in hard water lakes and ultimately affects P dynamics (Otzuki & Wetzel, 1972; Koschel *et al.*, 1983; Rodrigo *et al.*, 1993; Dittrich & Koschel, 2002). Therefore, the endorheic nature, and thus the highly mineralised waters, of most Iberian shallow lakes suggests that P removal from the water column mediated by $CaCO_3$ precipitation may be a crucial mechanism affecting P availability in these ecosystems.

The present study was carried out in a Mediterranean shallow lake (Medina Lake) located in a calcareous endorheic area (Jerez de la Frontera, south-western Spain). As a consequence of its morphometry and geographic location (a low-lying, windy area), this lake represents an ideal site for achieving a better understanding of the temporal variability in the interactions between meteorology, biogeochemistry and physics. In addition, the P limitation of primary production in the study site (see below) makes it vital to gain knowledge about P exchange across the sediment-water interface. In particular, the aims of this study are the following: i) to study the spatial and temporal (on a daily and on a two-year scale) variations in dissolved inorganic and total nutrients (N and P), total suspended matter and chlorophyll *a*; ii) to determine the gross and net settling flux by assessing the contribution of resuspended matter; and iii) to quantify the spatial and temporal distribution of sedimentary P fractions to estimate

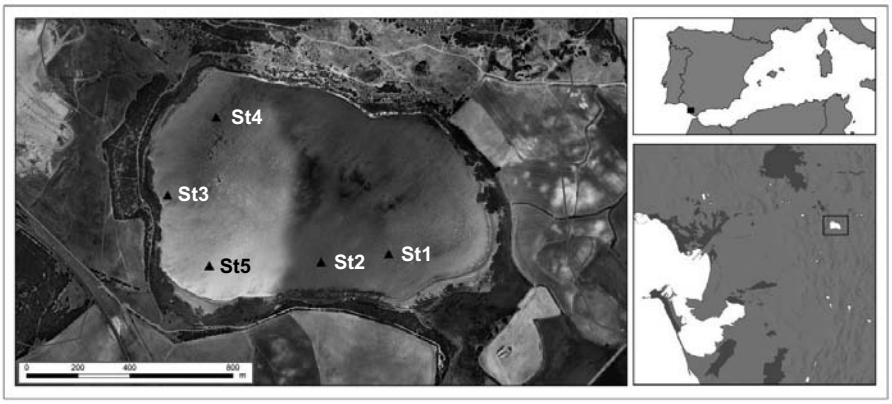

Figure 1. Geographic location of Medina Lake (Cádiz, Spain). Triangles indicate the 5 sampling stations. Localización geográfica de la laguna de Medina (Cádiz, España). *Los triángulos indican las 5 estaciones de muestreo.*

the potential contribution of sedimentary P to the availability of P in the water column.

MATERIAL AND METHODS

Study site

Medina Lake (c. 120 ha) is the second largest inland playa lake in Andalusia (Table 1, Fig. 1). Although there is no universal definition for playa lakes (Smith, 2003), Rodríguez-Rodríguez (2007) defined them as shallow water bodies without outlets and with a closed (endorheic) watershed made up of permeable or semi-permeable materials. More than 85 % of the Medina watershed is occupied by low-permeability marls and clays deposited during the Triassic period and then thrust upward, forming rocks known as olistolites (Benavente *et al.*, 2005). The substratum over which the playa lake formed inhibits downward percolation and groundwater recharge (Rodríguez-Rodríguez *et al.* 2011). Thus, Medina Lake can be considered a discharge playa lake (Yecchieli & Wood 2002), where the main form of water output is evapotranspiration. The hydroperiod is altered by an artificial overflow that is linked to a ditch and was constructed to prevent the flooding of adjacent fields (Rodríguez-Rodríguez *et al.*, 2011). Medina Lake has suffered marked fluctuations in depth and salinity over the last 9000 years (Reed *et al.*, 2001). The closed basin or watershed of 1748 ha is utilised primarily for wheat cultivation (Rodríguez-Rodríguez *et al.*, 2011). The great importance of Medina Lake for water birds (e.g., Amat, 1984; Martínez-Haro *et al.*, 2011) led to its protection as a nature reserve and its declaration as a Wetland of International Importance under the Ramsar Convention in 1989. Owing to formerly intense hunting activity, the lake sediments are highly contaminated with spent lead shot (Mateo *et al.*, 2007). Recent management activities include the removal in September 2007 with rotenone of invasive and allochthonous carp (*Cyprinus carpio*, Linnaeus, 1758), which became established in the study site in 2003. In addition, 20 ha of crops in the area adjacent to the eastern shoreline were expropriated, enabling the restoration of natural vegetation from November 2007 onwards. Despite marked inter-annual variations in its limnological characteristics, some general features emerge. It is a polymictic lake. Its shallowness and the intensity and frequency of prevailing winds lead to thermal homogeneity in the vertical profile and a corresponding low mechanical resistance of the water column to mixing for most of the annual cycle. Medina Lake has a basic pH and a high alkalinity (Table 1). The lake waters are highly mineralised, with an ionic composition dominated by SO_4^{-2}-Cl^--Na^+-Mg^{+2} (Ca^{+2}). Water transparency is particularly variable, with the highest values during the spring and summer, associated with the extensive development of macrophytes, especially *Potamogeton pectinatus* (Linnaeus, 1753) and *Zannichellia obtusifolia* (Talavera, García Murillo and Smit, 1986).

Table 1. Primary limnological features of Medina Lake. *Min-Max (Median) for the period 2002-2006 (n = 10). TA is total alkalinity. Morphometric features are those present when the lake is at full capacity. Data provided by Consejería de Medio Ambiente, Junta de Andalucía. **Características limnológicas principales de la Laguna Medina. Min-Max (Mediana) durante el periodo 2002-2006 (*n = 10). TA es la alcalinidad total. Las características morfométricas presentadas son aquellas cuando la laguna se encuentra al máximo de su capacidad. Datos proporcionados por la Consejería de Medio Ambiente, Junta de Andalucía.*

Lake area (ha)	120
Maximum length (m)	1500
Maximum width (m)	750
Watershed area (ha)	1800
Maximum depth (m)	3.5
Mean depth (m)	1.8
Volume (hm^3)	3.610
T (ºC)*	10.80-28.30 (20.65)
Cond (mS cm^{-1})*	4.65-12.88 (6.11)
pH*	7.60-8.90 (7.98)
O_2 (mg l^{-1})*	3.84-12.01 (10.22)
SD (m)*	0.08-2.62 (0.44)
TSS (mg l^{-1})*	3-510 (72)
Ca^{2+} (mg l^{-1})*	268.2-709.0 (407.5)
Mg^{2+} (mg l^{-1})*	206.8-720.0 (320.0)
K^+ (mg l^{-1})*	16.4-48.4 (22.3)
Na^+ (mg l^{-1})*	421.0-1735.0 (638.6)
Cl^- (mg l^{-1})*	820.5-2914.9 (1238.8)
SO_4^{2-} (mg l^{-1})*	1146.0-3994.0 (1887.7)
TA (meq l^{-1})*	0.80-2.60 (2.13)

Meteorological Data and Morphometry

Daily data on rainfall, evaporation, daily average wind speed and wind direction were provided by www.juntadeandalucia.es/agriculturaypesca/ifapa/ria for the period 01/01/2008-11/10/2009. In addition, during our intensive, short-term monitoring periods (31/01/2008-01/02/2008 and 30/03/2008-01/04/2008), a meteorological station (HOBO Micro Station Logger [H21-002]) was placed nearby to record wind speed and wind direction every 15 min. Data on morphometric variables were obtained from Consejería de Medio Ambiente (2007) (Table 1). Water level data were collected on a monthly basis by a limnimetric station.

Water Column Monitoring

From the winter of 2008 to the summer of 2009, eight surveys were conducted using a combination of short-term (daily) and long-term (two-years) monitoring to characterise the water column, settling/resuspension of particles and surface sediment. Two intensive samplings were carried out: 31/01/08-01/02/08 and 31/03/08-01/04/08. On 31/01/08, samples were collected at 17:00 and on 01/02/08 samples were collected at 10:00, 13:00 and 17:00, whereas from 31/03/08-01/04/08, samples were only collected once per day at 17:00. Because no significant changes occurred during the first intensive sampling period, only one result for each day (those measured at 17:00) is shown (see "Results" section). For the 2-year monitoring, seasonal samples (one per season) were collected.

Lake water samples were collected using a Van Dorn sampler at two different depths in the vertical profile (10 cm below the surface and 20 cm above sediments) and at five sampling stations (Fig. 1). Once at the laboratory, total phosphorus (TP) and total nitrogen (TN) were directly determined from non-filtered water. TP was analysed as molybdate reactive P (Murphy & Riley, 1972) after persulfate digestion (APHA, 1995), and TN was determined after alkaline digestion by using the UV spectrophotometric method (APHA, 1995). A subsample was filtered for the analysis of dissolved nutrients. Total dissolved phosphorus (TDP) and total dissolved nitrogen (TDN) were determined in filtered waters following the above methods for TP and TN, respectively. Soluble reactive phosphorus (SRP) was measured using the molybdenum blue method described by Murphy & Riley (1972). Nitrate (NO_3^-) and nitrite (NO_2^-) were analysed using UV spectrophotometry after acidification (1N HCl) and using the sulphanilamide and naphtil methods, respectively (Rodier, 1989). A phenol-hypochloride reaction was used for the determination of ammonium (NH_4^+) (Rodier, 1989). Total particulate P (TPP) was estimated as the difference between TP and TDP. In addition, alkalinity was measured using the titrimetric method of determination (METROHM 716 DMS) for the filtered subsample. Chl *a* concentration was measured using the trichromatic method of Jeffrey & Humphrey (1975). Finally, total suspended solids (TSS) were quantified using a gravimetric method. The organic matter concentration in the suspended solids (particulate organic matter = POM) was quantified using the ignition method (LOI) based on the difference in weight before and after the ignition of dried sediment (520°C, 3 h). Analytical error was 0.01 %. Particulate inorganic matter (PIM) was estimated by subtracting POM from TSS.

Resuspension and settling fluxes

Cylindrical sedimentation traps (height/ diameter = 6.2) were deployed in pairs 20 cm above the bottom at the five sampling stations (Fig. 1). The settled material was collected on two occasions (31/01/2008-01/02/2008 and 31/03/2008-01/04/2008). The short exposure time (24 h) of the sedimentation traps allowed us to assume that mineralisation losses were minor. In the laboratory, the suspension was filtered through Whatman GF/C glass fibre filters and dried (104 °C, 24 h). The sinking flux (S) of particulate material (g DW m^{-2} d^{-1}) was calculated as,

$$S = M \cdot V_T \cdot V_F^{-1} \cdot A^{-1} \cdot T^{-1} \qquad (1)$$

where M is the mass of particulate material quantified as the difference in the dry weight of the

filters before and after filtering a known volume (V_F) of the homogenised suspension sample; V_T is the trap volume, 0.45 l; A is the collection area, 15.2 cm^2 and T is the time of trap exposure.

In the spring of 2008 (31/03/2008-01/04/2008), resuspended matter was sampled using a horizontal Van Dorn sampler, which was used to strike the lake bottom a few times to resuspend the sediment (Doremus & Clesceri, 1982). Organic matter (OM) and TFe concentrations were determined in both the settling and resuspended matter. The concentration of OM (%) was quantified as LOI (520°C, 3 h). TFe was determined by igniting (520°C, 3 h) 0.1 g of dry material followed by hot 1 M HCl extraction (104°C, 1 h). Finally, TFe was measured spectrophotometrically using the ferrozine method (Gibbs, 1979). Considering Fe as a sediment tracer, the contribution of resuspended matter to settling rates was estimated by comparing the TFe concentrations in both materials during periods without any inflow.

Chemical characterisation of surface sediment

On two occasions (December 2008 and July 2009), three sediment cores were collected in acrylic tubes using a Kajak sampler at the five sampling stations. Once in the laboratory, sediment cores were sectioned and the upper sediment (0-0.5 cm) sections from the three cores corresponding to the same station were pooled before analysis. Fresh sediment was analysed for OM concentration, TFe and Fe (extracted in bicarbonate-dithionite (BD) solution) and the different sedimentary P fractions. All analyses were run in duplicate.

P speciation was determined using a slight modification of the sequential extraction method proposed by Paludan & Jensen (1995), where the use of 1 M $MgCl_2$ was replaced with distilled water for the extraction of weakly adsorbed P in the first step. In summary, this method is based on 5 sequential steps where 7 different forms of P may be discriminated: 1) water extractable P (P_{H_2O}), 2) reductant extractable P (P_{BD}), 3) NaOH soluble, molybdate-reactive P (iP_{NaOH}), 4) NaOH extractable non-reactive (organic) P (nrP_{NaOH}), 5) P recovered in humic precipitate (Humic-P), 6) HCl extractable P (P_{HCl}), and 7) residual P (Res-P_{HCl}) extracted from the sediment residue after ignition and boiling with 1 M HCl. For P fractionation, 1 g of wet sediment was shaken with 25 ml of each extractant solution. In the first three extractions (H_2O, BD and NaOH), inorganic and organic P (non-reactive) fractions were distinguished by digesting (organic and inorganic P) or not digesting (inorganic P) the supernatants before measuring P as molybdate-reactive P (Murphy & Riley, 1972). From the difference between TP and SRP in the P_{H_2O}, P_{BD}, and P_{NaOH} extracts, the nrP was calculated. The sum of nrP in the three extracts is believed to represent labile P compounds (Reitzel *et al*., 2005). As Golterman (2001) noted, the addition of NaOH may cause the formation of hydroxi-apatite and the hydrolysis of organic compounds when the extraction time for NaOH is too long. However, in this study, the short extraction time (1 h) may have reduced the hydrolysis of organic compounds. The total P in the sediment (TP_{sed}) was determined for parallel non-extracted sediment samples by igniting (520°C, 3 h) 0.1 g of dry sediment followed by a hot 1 M HCl extraction (104°C, 1 h). The sum of the seven P-pools never varied more than 10 % from the parallel measurement of TP_{sed}. As the latter measurement is considered more accurate, we normalised the sediment P-pools so that the sum of the pools equalled this value. Normalisation consisted of multiplying each sedimentary P fraction by the TP_{sed} and dividing by the sum of the P pools.

Potentially mobile phosphorus (P mobile) was defined as the sum of porewater P (P_{H_2O}), iron-bound P (P_{BD}), and non-reactive P extracted in H_2O (nrP_{H_2O}), in BD (nrP_{BD}) and in NaOH (nrP_{NaOH}) because these fractions constitute the P that can be released during anoxic periods and through the degradation of organic matter (Reitzel *et al*., 2005).

Fe oxides were obtained from the BD extracts (Fe_{BD}) used for P speciation (Jensen & Thamdrup, 1993). For the determination of TFe, the sediment was combusted following the same methodology described for TP_{sed}. TFe and Fe_{BD} were measured spectrophotometrically using the

ferrozine method (Gibbs, 1979). For calculating the Fe:P ratio, the Fe and P sedimentary forms must be specified. As FeOOH (Fe_{BD}) is the most important Fe sedimentary pool contributing to P adsorption capacity and mobile P represents sedimentary P fractions that are more easily subject to mobilisation, we have examined the FeOOH: P mobile ratio.

OM concentration was quantified as LOI (520 °C, 3 h). C and N concentrations were determined using a CNH Elemental Analyser.

Quantification of macrophyte cover

For the period from January 2008 to December 2009, we used 20 satellite images taken by the TM and ETM+ sensors on board the Landsat 5 and Landsat 7 satellites, obtained from the United States Geological Survey. We applied the Normalised Difference Vegetation Index (NDVI, Mather, 1987), which estimates the fraction of active photosynthetic radiation that is intercepted by vegetation (Alcaraz-Segura *et al.*, 2008) and is based on the reflectance in the red (R) and near infrared (NIR) bands (bands 3 and 4, respectively, for Landsat images). Using ENVI 4.4 software, one mask was constructed for the total lake surface and a second mask for the vegetation cover. These masks were combined to obtain one that contained only aquatic vegetation. The mask area was quantified by the number of pixels (30 m × 30 m each).

Statistical Analysis

Statistical analysis was performed using Statistica 6.0 Software (StatSoft Inc, 1997). Student t-tests were used to evaluate differences between paired or unpaired datasets. The significance level was established at $p < 0.05$ unless otherwise stated.

When necessary, data were log-transformed to comply with normality assumptions. All chemi-

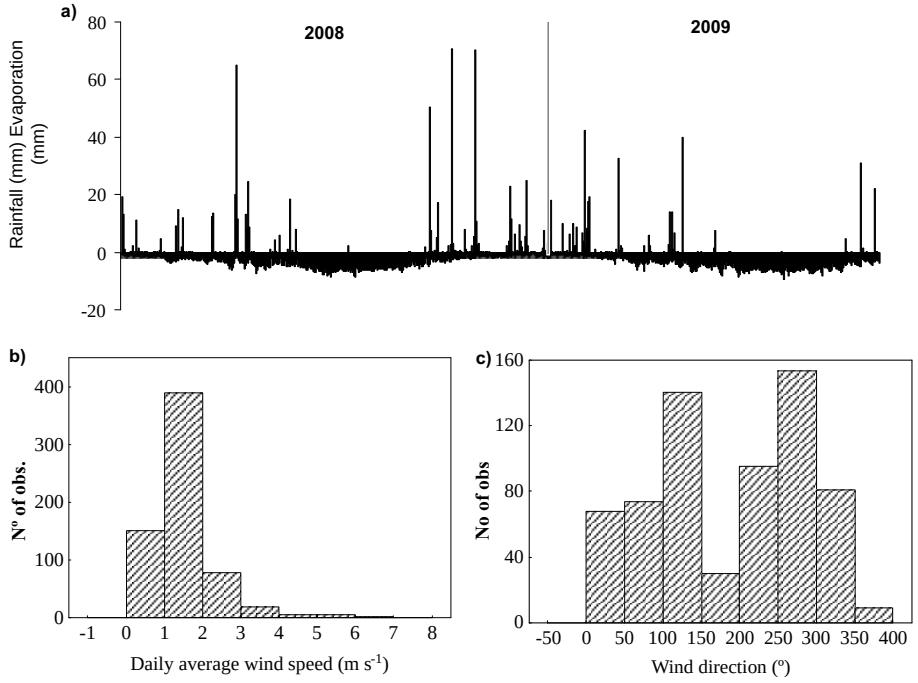

Figure 2. Temporal evolution of daily rainfall (positive) and daily evaporation (negative) (a) and histograms of daily average wind speed (b) and wind direction (c). All data are for the period 01/01/2008-11/10/2009. Data provided by www.juntadeandalucia.es/agriculturaypesca/ifapa/ria (Jerez de la Frontera, 36°38′38″ N, 06°00′44″ W). *Evolución temporal de la precipitación diaria (positiva) y de la evaporación diaria (negativa) (a) e histogramas del promedio diario de la velocidad del viento (b) y de la dirección del viento (c). Todos los datos corresponden al periodo 01/01/2008-11/10/2009. Datos proporcionados por www.juntadeandalucia.es/agriculturaypesca/ifapa/ria (Jerez de la Frontera, 36°38′38″ N, 06°00′44″ W).*

cal analyses were performed in duplicate (coefficient of variation, CV = 8 %).

RESULTS

Medina Lake is subject to the typical temporal fluctuations in weather forcings that characterise the Mediterranean climate (Fig. 2a). Sporadic and strong peaks in rainfall occur during the spring and autumn. In fact, during just one day (31/10/2008), up to 10 % of the year's accumulated rainfall was recorded. Evaporation rates were highest in the summer as a consequence of high air temperatures. The study site is relatively windy (Fig. 2b for daily average wind speed). Most of the observations correspond to values ranging from 1 to 2 m s^{-1}, although 3 % of the

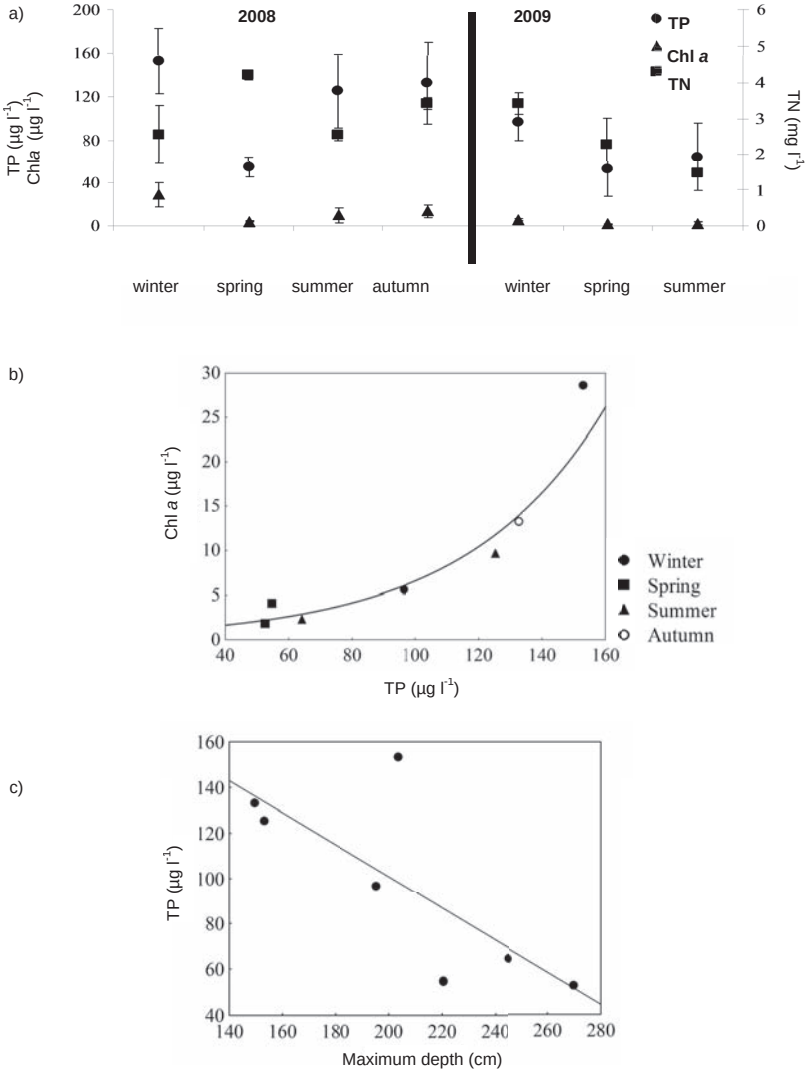

Figure 3. TP, TN and Chl *a* concentrations (a) and scatterplots of TP vs. Chl *a* (b) and maximum water depth vs. TP (c). The vertical bars in (a) represent the SD considering the surface and bottom waters at the 5 sampling stations. The data points in (b) refer to mean values from figure 3a ($r = 0.87$; $p < 0.05$). *Concentración de TP, TN y Chl* a *(a) y regresión entre TP y Chl* a *(b) y entre la profundidad máxima y la concentración de TP (c). Las barras verticales en (a) representan la desviación estándar (SD) considerando muestras de agua de superficie y de fondo en las 5 estaciones de muestreo. Los datos representados con puntos en (b) se refieren a los valores promedios de la figura 3a (*r = 0.87; p < 0.05*).*

observed values were greater than 4 m s^{-1}. Wind direction was primarily south-east (100-150°) and west (250-300°) (Fig. 2c). Thus, wind frequently blows along the line of maximum fetch (W-E) (Fig. 1).

Two-year and daily monitoring of the water column

Marked inter- and intra-annual fluctuations in TN, TP and Chl *a* concentration were observed (Fig. 3a). In general, TP and Chl *a* concentrations showed similar temporal patterns over the study period, with the highest values recorded during the winter of 2008 and the lowest during the spring of 2009. The two variables were positively correlated ($r = 0.87$; $p < 0.05$) (Fig. 3b). Although not shown in the figure, the spatial homogeneity was highest during the spring of 2008, reflected by the lowest value of the coefficient of variation (CV) for the TP and Chl *a* concentrations. In contrast, TN concentrations were highest during the spring of 2008 and lowest during the summer of 2009. TP concentrations in the water column were significantly and inversely related to maximum water depth ($r = -0.76$; $p < 0.05$; Fig. 3c).

Contrasting meteorological forcings occurred during both intensive samplings (winter and spring 2008). The maximum wind speed was significantly lower ($p < 0.001$) in the winter (3.5 m s^{-1}) than in the spring of 2008 (5.4 m s^{-1}) (Fig. 4). Similarly, significant differences in nutrient, Chl *a* and TSS concentrations were found (Figs. 5 and 6). TP and TDP were significantly higher ($p < 0.005$) in the winter of 2008, whereas an inverse tendency was observed for SRP, TN, TDN, NO_3^- and NH_4^+ concentrations. SRP comprised less than 1 % of the TDP in the winter of 2008, but this percentage increased to 22 % in the spring of 2008. A change in the dissolved inorganic nitrogen (DIN) fraction was also observed, with a predominance of NO_3^- in the winter of 2008 (27 % of the TDN) and of NH_4^+ in the spring of 2008 (62 % of the TDN). Despite these differences, the DIN:SRP atomic ratio was much greater than 16 during both intensive surveys, indicating strong P limitation of primary production. Chl *a* and POM concentrations were also significantly higher in the winter of 2008 than in the spring of 2008. In fact, the average Chl *a* concentration was 8 times higher in the winter of 2008. In contrast, no differences in PIM concentrations were observed. A

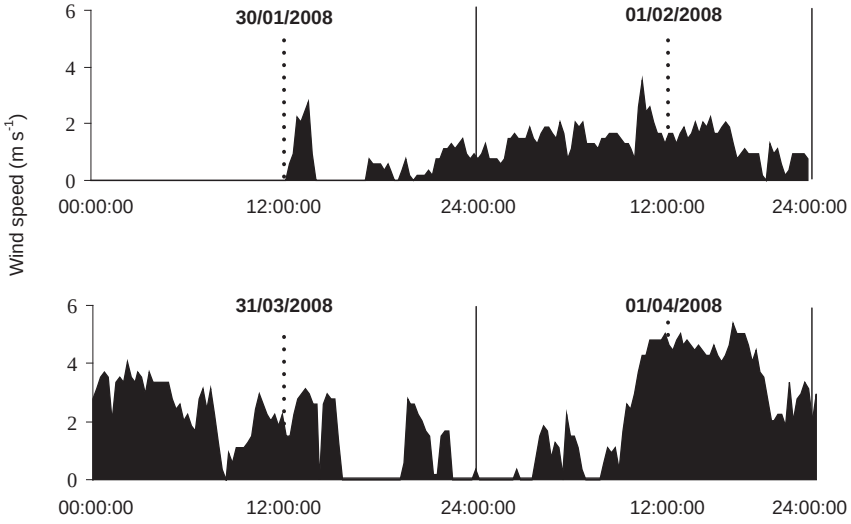

Figure 4. Temporal variation in wind speed during the intensive surveys. Data are shown for every 15 min. *Variación temporal de la velocidad del viento durante los muestreos intensivos. Datos mostrados cada 15 minutos.*

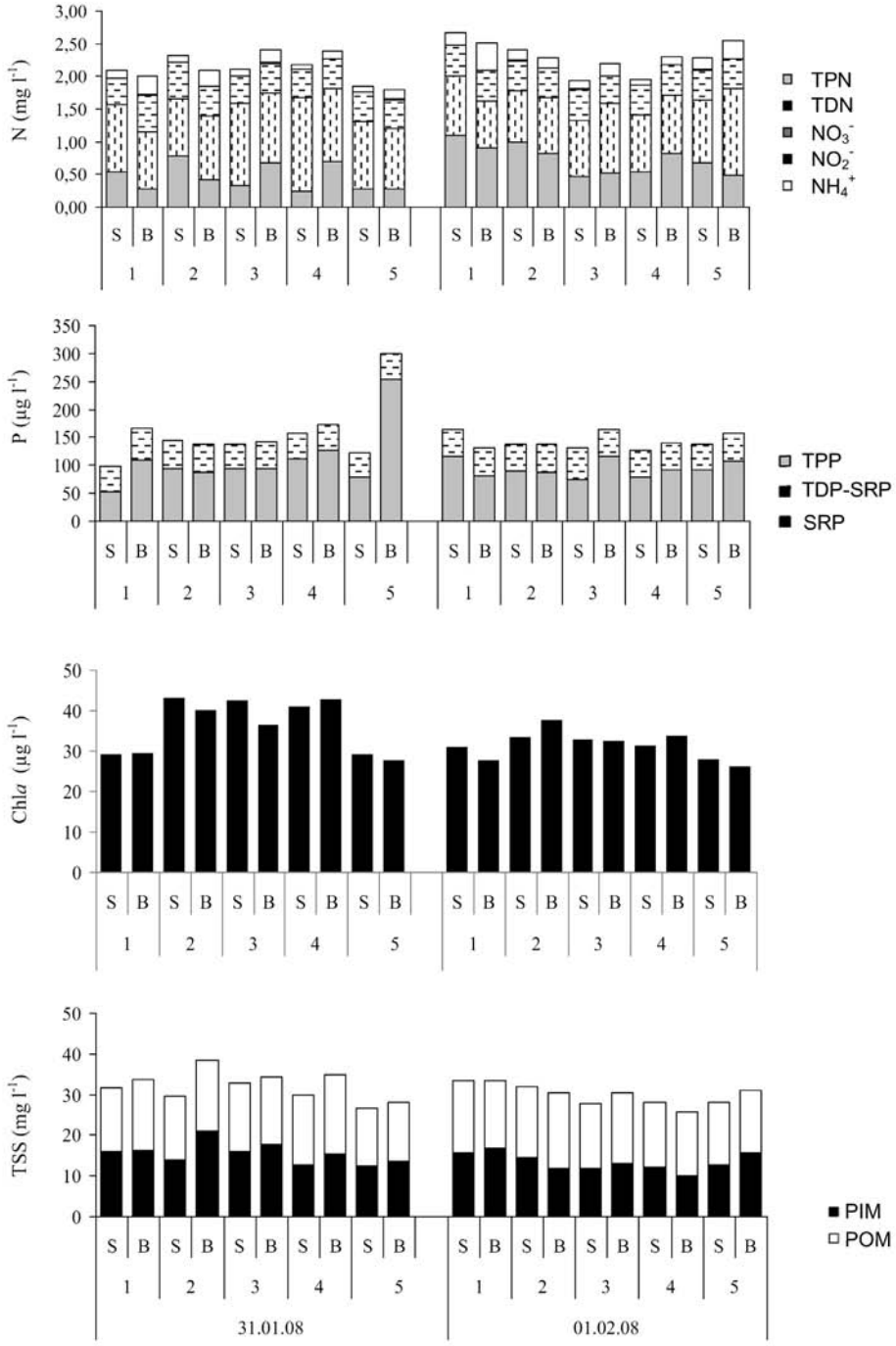

Figure 5. Results of the intensive survey carried out during 31/01/2008-01/02/2008. Only the results from samples collected at 17:00 h on each day are shown. S and B = surface (10 cm below surface) and bottom waters (20 cm above sediments), respectively; 1-5: sampling stations. TPN was estimated as the difference between TN and TDN. *Resultados de los muestreos intensivos realizados durante 31/01/2008-01/02/2008. Sólo se muestran los datos de las muestras tomadas, cada día, a las 17:00 h. S y B = agua superficial (10 cm desde la superficie) y agua de fondo (20 cm por encima del sedimento); 1-5: estaciones de muestreo. TPN fue estimado como la diferencia entre TN y TDN.*

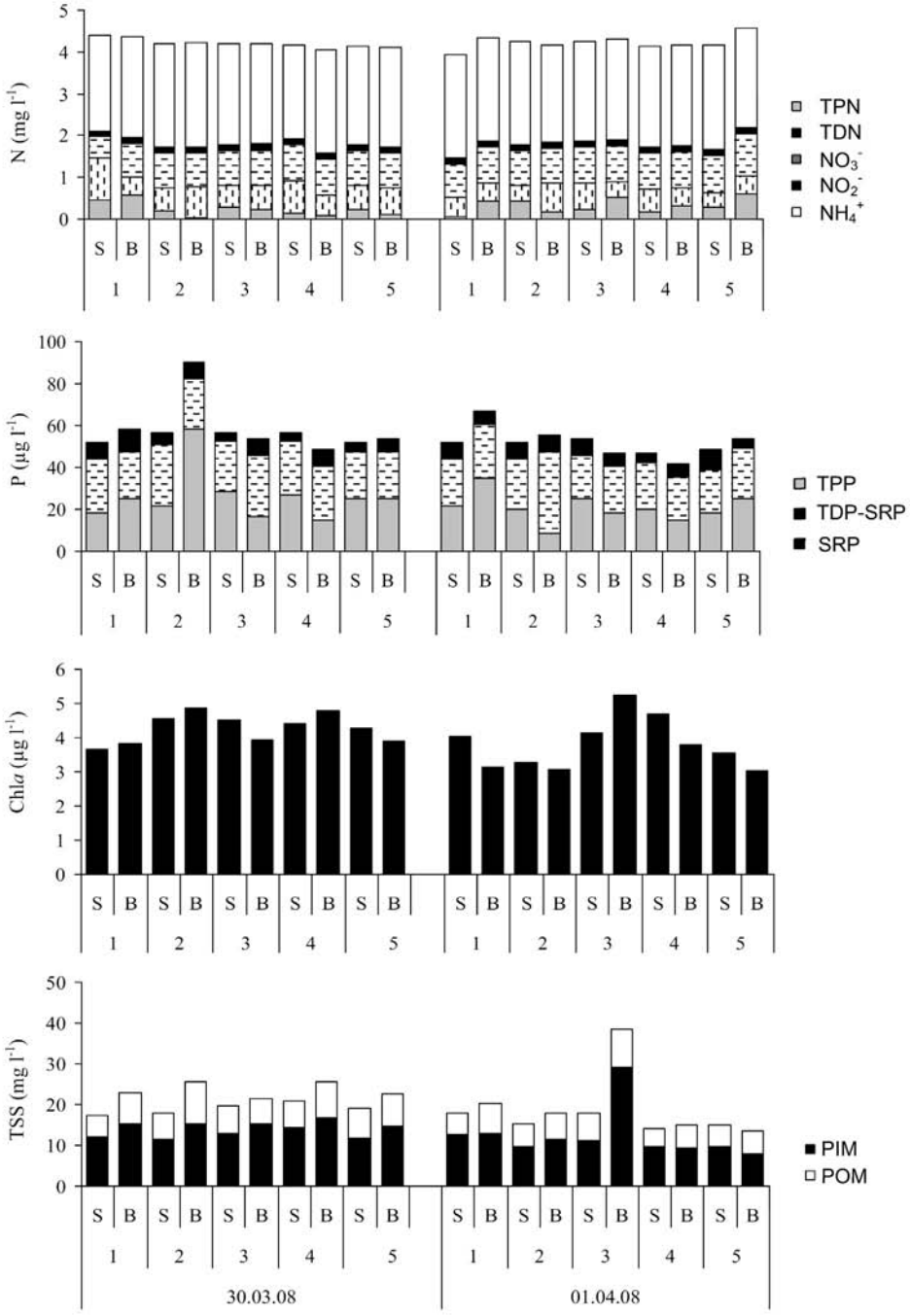

Figure 6. Results of the intensive survey carried out during 31/03/2008-01/04/2008. S and B = surface (10 cm below surface) and bottom waters (20 cm above sediments), respectively; 1-5: sampling stations. TPN was estimated as the difference between TN and TDN. *Resultados de los muestreos intensivos realizados durante 31/03/2008-01/04/2008. S y B = agua superficial (10 cm desde la superficie) y agua de fondo (20 cm por encima del sedimento); 1-5: estaciones de muestreo. TPN fue estimado como la diferencia entre TN y TDN.*

Table 2. Daily settling rates, percentage of resuspension (% Res) and chemical characterisation of both resuspended (RM) and settling matter (SM) during two intensive sampling periods (winter 2007-2008 and spring 2008). *Tasa diaria de sedimentación, porcentaje de resuspensión (% Res) y caracterización química del material resuspendido (RM) y de la materia sedimentada (SM) durante dos muestreos intensivos (invierno 2007-2008 y primavera 2008).*

	Station	Depth (m)	Sample	OM (%)	TFe (mg g^{-1} dw)	Sed. flux (g m^{-2} d^{-1})	Res (%)
31/01-01/02/2008	1	1.8	SM	28.5	—	31.0	—
	2	1.9	SM	35.0	-	26.5	—
	3	1.9	SM	33.8	—	30.6	—
	4	1.8	SM	36.8	—	31.3	—
	5	1.7	SM	32.7	—	40.0	—
31/03-01/04/2008	1	1.6	RM	7.9	15.64	47.9	36.6
			SM	23.3	5.73		
	2	1.6	RM	8.2	18.95	59.9	47.0
			SM	21.1	8.91		
	3	1.7	RM	15.8	20.51	51.1	35.5
			SM	21.6	7.29		
	4	1.6	RM	14.5	15.87	48.5	13.8
			SM	25.7	2.19		
	5	1.5	RM	18.3	18.19	38.7	23.2
			SM	23.4	4.23		

strong positive correlation ($r = 0.95$; $p < 0.001$) between POM and Chl *a* was found when merging all data from the two intensive samplings. Overall, no clear horizontal or vertical pattern in nutrient, Chl *a* and TSS concentrations emerged from the intensive surveys.

Resuspension and settling fluxes

Daily settling rates were significantly higher ($p < 0.005$) in the spring of 2008 (49.2 ± 7.6 g DW $m^{-2}d^{-1}$) than in the winter of 2008 (31.9 ± 4.9 g DW $m^{-2}d^{-1}$) (Table 2). Spatial variability in settling rates was similar during both intensive samplings, as reflected by a similar coefficient of variation (15 %). There was no clear spatial trend in sedimentation patterns in any of the surveys. The OM concentration in settling matter was significantly higher in winter (33.4 ± 3.1 %) than in the spring of 2008 (23.0 ± 1.8 %). Settling matter (23.0 ± 1.8 %) was significantly more enriched in OM than resuspended matter (13.0 ± 4.7 %), whereas the TFe concentration was significantly lower ($p < 0.001$) in settling matter (5.7 ± 2.6 mg Fe g^{-1} DW) than in resuspended matter (17.8 ± 2.0 mg Fe g^{-1} DW) (Table 2). Resuspension rates ranged from 13.8 % at Station 4 to 47.0 % at Station 2.

Surface sediment characterisation

The OM concentration was significantly higher ($p < 0.005$) in the winter (6.0±1.1 %) than the summer (3.1±1.0 %) (Fig. 7a). In fact, the OM concentration was more than twice as high in the winter at Stations 3, 4 and 5 than in the summer. Spatial heterogeneity was more pronounced in July (CV = 32 %), with higher OM concentrations in the eastern part of the lake (Station 1).

Fe_{BD} was also significantly higher ($p < 0.005$) in the winter (3.64±0.50 mg Fe g^{-1} DW) than the summer (1.25±0.72 mg Fe g^{-1} DW) (Fig. 7b). The Fe_{BD} concentration was extremely heterogeneously distributed in the summer (CV = 58 %), when peaks of Fe_{BD} were again found in the eastern site of the lake (Station 1). In contrast, no significant differences were observed in TFe concentration between the winter (30.40±7.01 mg Fe g^{-1} DW) and the summer (29.23±12.72 mg Fe g^{-1} DW). A more homogeneous spatial distribution was observed during winter sampling (CV = 23 %) than during the summer (CV = 43 %), when the highest concentration was measured at Station 3.

In general, Fe_{BD} represented a small fraction of TFe. However, remarkable differences between the two sampling periods emerged. A

significantly higher contribution of Fe_{BD} to the TFe pool was found in the winter (13±4 %) than in the summer (5±4 %). The Fe_{BD}: P_{BD} atomic ratio ranged from 11 to 19 in the winter and from 2 to 10 in the summer. Accordingly, significantly higher values were measured in the winter (14±3) than in the summer (4±3). Extreme spatial heterogeneity was observed in the summer (CV = 86 %), when the highest values were measured at Station 1.

No significant temporal differences were observed in TP concentration in any of the sedimentary P fractions (Fig. 7c). The P concentration in the sediment consisted primarily of P_{HCl}, which accounted, on average, for 48 % and 53 % of TP during the winter and summer, respectively. P mobile was significantly higher in the winter (394 ± 53 μg P g^{-1} DW) than in the summer (283 ± 84 μg P g^{-1} DW), comprising from 25 % (summer) to 37 % (winter) of the TP.

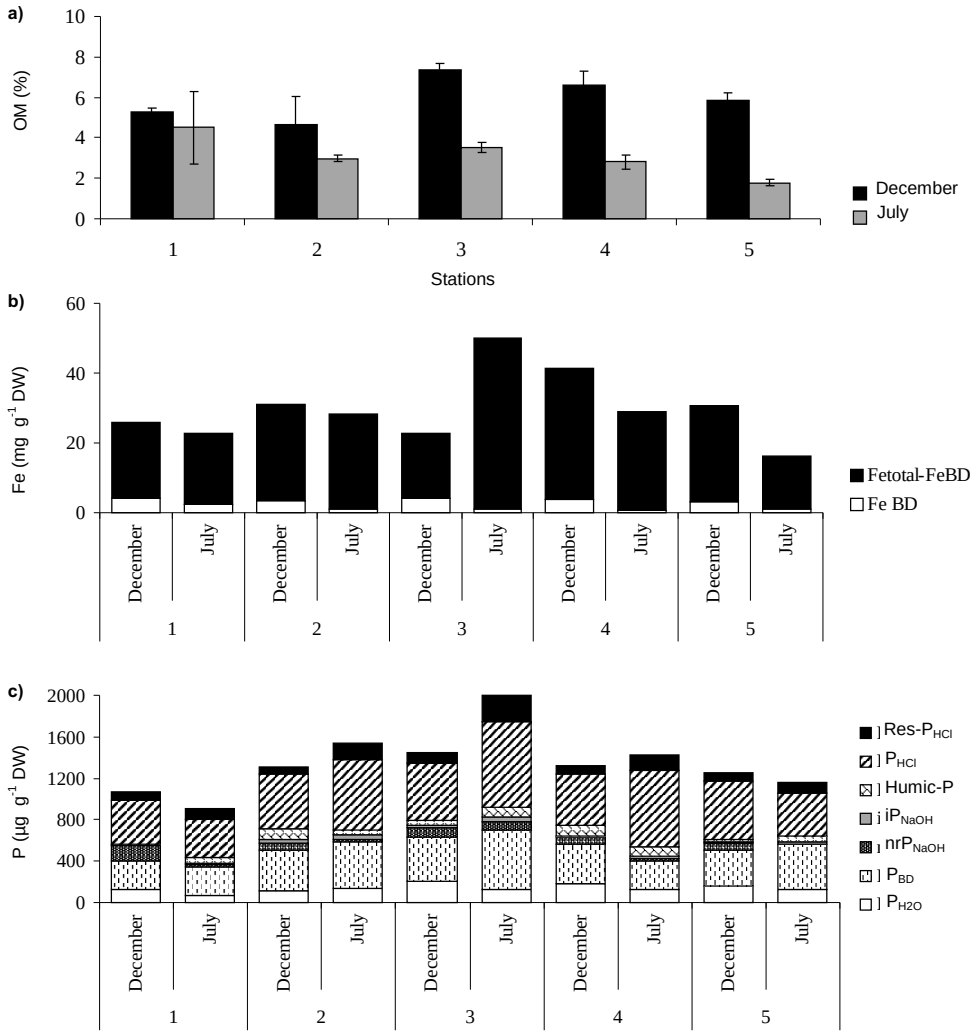

Figure 7. Variations in OM concentration (a) including vertical bars that represent the SD of duplicates, TFe and Fe oxides (Fe_{BD}) (b) and in sedimentary P fractions (c) of the surface sediment (0-0.5 cm). *n* = 3 per station. *Variaciones en el contenido de materia orgánica (a) incluyendo en barras verticales la SD de las réplicas, TFe y óxidos de Fe (Fe_{BD}) (b) y en fracciones de P sedimentario (c) en el sedimento superficial (0-0.5 cm).* n = *3 en cada estación.*

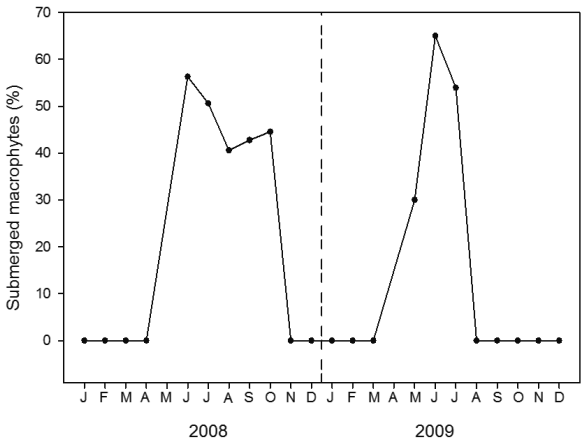

Figure 8. Development of macrophyte cover in Medina Lake according to an analysis of Landsat satellite images. No images were available for January or December 2008, but field visits showed that no macrophytes were present. *Variación temporal de la cobertura por macrófitos acuáticos en la laguna de Medina mediante el análisis de imágenes de satélite. A pesar de la ausencia de imágenes en Enero y Diciembre de 2008, los muestreos rutinarios nos permitieron reconocer la ausencia de macrófitos.*

Changes in macrophyte cover

The proportion of the lake surface covered with submerged macrophytes varied from zero in winter months to 30-65 % in summer months (Fig. 8).

DISCUSSION

This study confirmed the high temporal (inter and intra-annual) variability of the nutrient and sediment dynamics characterising Mediterranean shallow lakes (i.e., de Vicente *et al.*, 2006b). Due to this variability, the study of shallow lakes may require a greater reliance on lake-specific research results and less inter-lake generalisation than is possible for deeper systems. However, our knowledge of shallow lakes, especially Mediterranean shallow lakes, is still limited (Becares *et al*., 2004; Beklioglu *et al*., 2007). A major factor contributing to the marked temporal variability of these ecosystems is water level fluctuations. In fact, as recorded in other Mediterranean lakes (García-Jurado, 2012), in Medina Lake we found a significant and inverse relationship between TP concentrations in the water column and maximum water depth, reflecting the effects of both nutrient concentration and resuspension when the water level becomes low.

Short-term monitoring at the study site revealed that not only meteorological forcing but also biological structure are crucial for whole-lake functioning. Therefore, although maximum wind speed was much higher in the spring, the existence of dense macrophyte beds reduced the impact of wind-induced Resuspension, as reflected by the lower TSS concentrations. In addition to affecting sediment and water interactions by limiting wind-induced resuspension and taking up interstitial P through their root systems, macrophytes also critically affect plankton dynamics (Scheffer *et al.*, 1993). In plant-dominated shallow lakes, macrophytes can limit the growth of phytoplankton and periphyton by competing with algae for nutrients (Ozimek *et al*., 1993), shading their competitors (Kairesalo, 1984; Sand-Jensen & Borum, 1991; Cattaneo *et al*., 1998) and by harbouring grazers (Timms & Moss, 1984; Lauridsen *et al*., 1996). This explains why we found very low values of Chl *a* concentrations in Medina Lake, especially during the summer. The higher water temperatures, the reduction in water depth (up to 35 % and 22 % reductions during the summers of 2008 and 2009, respectively) and the higher light availability compared to the rest of the year enable the persistence of aquatic plants during the spring and summer periods (Green *et al*., 2009), promoting a clear-water phase. As a result, based on the annual average Chl *a* concentration and following the thresholds for shallow lakes proposed by Moss *et al.* (2003), we could classify Medina Lake as being of high water quality. In contrast, a strong discrepancy exists when evaluating trophic state considering annual average TP concentrations (from poor water quality during 2008 to moderate during 2009). These results highlight the need for further research for establishing more specific thresholds for Mediterranean shallow lakes, where the mild climate can allow macrophyte beds to persist for longer periods.

A major factor contributing to the marked instability characterising shallow lake functioning

is the close link between bottom sediments and overlying waters. The potential importance of sediment-water interactions in the P cycling of Medina Lake is illustrated by a simple comparison of available P forms in lake water and lake sediments. Considering the whole lake, the upper 1 cm sediment layer holds 6.53 Tm of mobile P, which is 18 times the mass of TP in the lake water. In fact, this calculation is an underestimate, as some authors consider that the mobile P contained in the upper 10 cm can potentially be released into lake water (Reitzel *et al*., 2005). The bioturbation of sediments by water birds in Medina Lake may promote such P release from deeper sediments (Rodríguez-Pérez & Green, 2006). Additionally, and although other specific approaches are recommended in the literature, there exists a strong P limitation of planktonic primary production in the study site, as reflected by a DIN:SRP atomic ratio well over 16 (Morris & Lewis, 1988). Based on these results, P exchange across the sediment-water interface represents a crucial process for explaining P availability in the water column.

Sediments can act either as a sink or as a source of P according to the net consequences of a complex set of processes. Resuspension, precipitation with $CaCO_3$ and adsorption onto FeOOH are among the most relevant physical and chemical processes affecting P exchange across the sediment-water interface. Sediment resuspension can significantly modify the biogeochemistry of shallow aquatic ecosystems (e.g., Kristensen *et al*., 1992; Evans, 1994; Bloesch, 1995; Weyhenmeyer *et al*., 1995; Scheffer, 1998; Golterman, 2004). As a consequence of resuspension, the concentration of particulate matter in the water column increases, leading to reduced light penetration. To clarify the role of wind-induced resuspension on the turbidity of Medina Lake, we correlated the maximum wind speed recorded during a 48 hour period before the sampling (ws_{48}) and TSS and total particulate phosphorus (TPP) concentrations. We found a positive and statistically significant relationship between ws_{48} and TSS ($r = 0.77$; $p < 0.05$; $n = 8$), showing the role of wind forcing on the light climate in the study site. However, the positive relationship observed between TSS and TPP was not statistically significant ($r = 0.66$; $p > 0.05$; $n = 6$), reflecting the variety of other processes involved in P cycling. The almost flat bottom of the study site is responsible for horizontal homogeneity in resuspension rates. However, the existence of prevailing winds blowing along the main axis (E-W) caused a slight increase in resuspension rates at stations located along this axis (1, 2 and 3), whereas lower values are exhibited at stations closer to the shoreline (4 and 5).

In addition, P adsorption by resuspended matter is a crucial process for retaining this nutrient in lake sediments. The effectiveness of P adsorption critically depends on several factors. Among them, the degree of saturation is particularly important, and this, in turn, can be related to the Fe:P ratio and reflects the number of free adsorption sites (Jensen & Andersen, 1992; Jensen *et al*., 1992). The 3.5-fold higher FeOOH: P mobile ratio (by weight) in the winter (25) compared to the summer (7) suggests a higher capacity of Medina sediments to adsorb P in winter when there are more free adsorption sites. Furthermore, our results show that, as according to Jensen *et al*. (1992), internal P-loading may be controlled by P adsorption onto oxidised surface sediments in the winter (Fe:P > 15), whereas in the summer, the low ratio (Fe:P < 15) reflects the lack of sufficient FeOOH to control P adsorption. The seasonal reduction in the FeOOH: P mobile ratio was a consequence of a notable reduction in FeOOH concentrations in the summer. This observation has frequently been made elsewhere during anoxic conditions in the summer months (Boström *et al*., 1982). As a result, P mobile that is partly bound to FeOOH was notably reduced (30 % reduction) during the summer. The close coupling between the sediment and water in Medina Lake is reflected by the 3-fold increase in SRP concentrations in the water column in the summer compared to the winter. It is also noteworthy that the most important organic P pool (nrP_{NaOH}) drastically decreased from winter to summer as a consequence of the intense OM mineralisation promoted by higher water temperatures.

Because the most important sedimentary inorganic P pool in Medina Lake is represented by P bound to Ca (P_{HCl}), it is important to study

the precipitation process in detail. As suggested by Golterman (2004), the "apatite" compound is most likely a mixture of $CaCO_3$ with apatite ($Ca_5(PO_4)_3 \cdot OH$). The small $Ca_5(PO_4)_3 \cdot OH$ crystals may be adsorbed onto the much larger $CaCO_3$ particles, both being traditionally abbreviated as $P \approx CaCO_3$. The maximum SRP concentration in the absence of $CaCO_3$ precipitation can be calculated as a function of Ca^{2+} concentration and pH (Golterman, 2004). In Medina Lake, based on the average lake water pH (7.98), temperature (21°C) and Ca^{2+} concentration (400 mg l^{-1}), the maximum SRP concentration would be lower than 5 μg l^{-1}, a value well below the average SRP concentration measured in the lake during the study period (11 μg l^{-1}), indicating the relevance of $CaCO_3$ precipitation for removing P from lake water. Thus, the existence of SRP concentrations in lake water that are much higher than the threshold for $CaCO_3$ and P co-precipitation is responsible for the high contribution of P bound to $CaCO_3$ (P_{HCl}) to the Tot-P in the study site.

Sedimentation is a fundamental process connecting plankton with benthic communities (Bloesch & Uehlinger, 1986). Although seasonal fluctuations and vertical variations in settling rate are recognised as important and have been widely studied (i.e., Hupfer *et al*., 1995; Penn & Auer, 1997; de Vicente *et al*., 2005), horizontal differences have rarely been taken into account (Bloesch, 1982; Weyhenmeyer *et al*., 1997). In addition, although the exposure time for collecting settled matter has been identified as a key issue, most of the existing studies consider exposure times longer than two weeks (Pejrup *et al*., 1996; Weyhenmeyer *et al*., 1997). Owing to these limitations in previous studies, in this paper, horizontal variability in sedimentation rates was estimated considering an exposure time of 24 hours, thus assuring low losses by OM mineralisation. The daily settling rates measured in this study are among the highest values reported in the literature for natural inland waters (Tartari & Biasci, 1997). Apart from confirming the positive relationship between trophic state and settling flux observed in natural water bodies (Tartari & Biasci, 1997; de Vicente *et al*., 2005), these high values for settling rates corroborate the contribution of resuspended matter to gross sedimentation fluxes.

Overall, the large proportion of P mobile to the overall sedimentary P pool and its strong seasonal variability (a reduction of 32 % from winter to summer) suggest that the P-limited Medina Lake is especially dependent on physical (wind-induced resuspension) and chemical ($CaCO_3$ precipitation and P adsorption on FeOOH) processes affecting P exchange across the sediment-water interface.

ACKNOWLEDGMENTS

This research was funded by the Spanish Ministry of Science and Technology (DISPAR, CGL2005-00076) and by a contract with Ingeniería de Protección Ambiental, S.L. to investigate the success of restoration work (to AJG).

REFERENCES

ALVAREZ-COBELAS, M., C. ROJO & D. G. ANGELER. 2005. Mediterranean limnology: current status, gaps and the future. *J. Limnol.*, 64: 13–29.

APHA. 1995. *Standard methods for examination of water and wastewater, nineteenth edition*. APHA-AWWA-WPCF, Washington D.C., USA.

AMAT, J. A. 1984. Las poblaciones de aves acuáticas en las lagunas andaluzas: composición y diversidad durante un ciclo anual. *Ardeola*, 31: 61–79.

BÉCARES, E., A. CONTY, C. RODRÍGUEZ-VILLAFAÑE & S. BLANCO. 2004. Funcionamiento de los lagos someros mediterráneos. *Ecosistemas*, 2: (URL: http://www.aeet.org/ecosistemas/042/revision3.htm).

BEKLIOGLU, M., S. ROMO, I. KAGALOU, X. QUINTANA & E. BÉCARES. 2007. State of the art in the functioning of shallow mediterranean lakes: workshop conclusions. *Hydrobiol.*, 584: 317–326.

BENAVENTE, J., F. MORAL & M. RODRÍGUEZ-RODRÍGUEZ. 2005. *Definition of the hydrogeological setting of Andalusian wetlands.* Playa-lakes of the province of Cadiz. Seville: Guadalquivir River Basin Authority. 182 pp.

BLOESCH, J. 1982. Inshore-offshore sedimentation differences resulting from resuspension in the

eastern basin of Lake Erie. *Can. J. Fish. Aquat. Sci.,* 39: 748–759.

BLOESCH, J. 1994. A review of methods used to measure sediment resuspension. *Hydrobiol.,* 284: 13–18.

BLOESCH, J. 1995. Mechanisms, measurement and importance of sediment resuspension in lakes. *Mar. Fresh. Res.,* 46: 295–304.

BLOESCH, J. & U. UEHLINGER. 1986. Horizontal sedimentation differences in a eutrophic Swiss lake. *Limnol. Oceanogr.,* 31: 1094–1109.

BOSTRÖM, B., M. JANSSON & C. FORSBERG. 1982. Phosphorus release from lake sediments. *Arch. Hydrobiol. Beih. Ergeb. Limnol.*, 18: 5–59.

BOSTRÖM, B., J. M. ANDERSEN, S. FLEISCHER & M. JANSSON. 1988. Exchange of phosphorus across the sediment-water interface. *Hydrobiol.*, 170: 229–244.

CATTANEO, A., G. GALANTI & S. ROMO. 1998. Epiphytic algae and macroinvertebrates on submerged and floating-leaved macrophytes in an Italian lake. *Freshwat. Biol.*, 39: 725–740.

DE VICENTE, I., V. AMORES, C. ESCOT, A. BASANTA & L. CRUZ-PIZARRO. 2005. Temporal and spatial trends in the sedimentation process in a canyon-type reservoir (El Gergal, Seville, Spain). *Arch. Hydrobiol.*, 163: 241–257.

DE VICENTE, I., V. AMORES & L. CRUZ-PIZARRO. 2006a. Instability of shallow lakes: a matter of the complexity of factors involved in sediment and water interactions? *Limnetica*, 25: 253–270.

DE VICENTE, I., E. MORENO-OSTOS, F. J. RUEDA, V. AMORES & L. CRUZ-PIZARRO. 2006b. Low predictability in the dynamics of shallow lakes: implications for their management and restoration. *Wetlands*, 26: 928–938.

DE VICENTE, I., F. Ø. ANDERSEN, H. C. B. HANSEN, L. CRUZ-PIZARRO & H. S. JENSEN. 2010a. Water level fluctuations may decrease phosphate adsorption capacity of the sediment in oligotrophic high mountain lakes. *Hydrobiol.*, 651: 253–264.

DE VICENTE, I., L. CRUZ-PIZARRO & F. J. RUEDA. 2010b. Sediment resuspension in two adjacent shallow coastal lakes: controlling factors and consequences on phosphate dynamics. *Aquat. Sci.,* 72: 21–31.

DITTRICH, M. & R. KOSCHEL. 2002. Interaction between calcite precipitation (natural and artificial) and phosphorus cycle in the hardwater lake. *Hydrobiol.,* 469: 49–57.

DOREMUS, C. & L. S. CLESCERI. 1982. Microbial metabolism in surface sediments and its role in the inmobilization of phosphorus in oligotrophic lake sediments. *Hydrobiol.*, 91: 261–268.

DOWNING, J. A. 2010. Emerging global role of small lakes and ponds: little things means a lot. *Limnetica*, 29: 9–24.

EVANS, R. D. 1994. Empirical evidence of the importance of sediment resuspension in lakes. *Hydrobiol.*, 284: 5–12.

GARCÍA-JURADO, F., I. DE VICENTE, A. GALOTTI, A. REUL, F. JIMÉNEZ-GÓMEZ & F. GUERRERO. 2012. Effect of drought conditions on plankton community and on nutrient availability in an oligotrophic high mountain lake. *Artic, Antartic and Alpine Res.* (in press).

GÄCHTER, R. & B. WEHRLI. 1998. Ten years of artificial mixing and oxygenation: no effect on the internal phosphorus loading of two eutrophic lakes. *Environ. Sci. Technol.,* 32: 3659–3665.

GÄCHTER, R. & B. MÜLLER. 2003. Why the phosphorus retention of lakes does not necessarily depend on the oxygen supply to their sediment surface. *Limnol. Oceanogr*., 48: 929–933.

GIBBS, M. M. 1979. A simple method for the rapid determination of iron in natural waters. *Wat. Res.*, 13: 295–297.

GOLTERMAN, H. L. 2001. Fractionation and bioavailability of phosphates in lacustrine sediments: a review. *Limnetica*, 20: 15–29.

GOLTERMAN, H. L. 2004. *The chemistry of phosphate and nitrogen compounds in sediments*. Kluwer Academic Publishers, Dordrecht/ Boston/ London. 246 pp.

HUPFER, M., R. GÄCHTER & R. GIOVANOLI. 1995. Transformation of phosphorus species in settling seston and during early sediment diagenesis. *Aquat. Sci.,* 57: 305–324.

JENSEN, H. S. & F. Ø. ANDERSEN. 1992. Importance of temperature, nitrate and pH for phosphorus release from aerobic sediments of four shallow eutrophic lakes. *Limnol. Oceanogr.,* 37: 577–589.

JENSEN, H. S., P. KRISTENSEN, E. JEPPENSEN & A. SKYTTHE. 1992. Iron:phosphorus ratio in surface sediment as an indicator of phosphate release from aerobic sediments in shallow lakes. *Hydrobiol.,* 235/236: 731–743.

JENSEN, H. S. & B. THAMDRUP. 1993. Iron-bound phosphorus in marine sediments as measured by

bicarbonate-dithionite extraction. *Hydrobiol.*, 253: 47–59.

JEFFREY, S. W. & G. F. HUMPHREY. 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochem. Physiol.*, 167: 191–194.

KAIRESALO, T. 1984. The seasonal succession of epiphytic communities within an *Equisetum fluviatile* stand in lake Pääjarvi, Southern Finland. *Int. Rev. Gesam Hydrobiol.*, 69: 475–505.

KLEEBERG, A. 2002. Phosphorus sedimentation in seasonal anoxic Lake Scharmützel, NE Germany. *Hydrobiol.*, 472: 53–65.

KOSCHEL, R., B. JURGEN, G. PROFT & F. RECKNAGEL. 1983. Calcite precipitation as a natural control mechanism of eutrophication. *Arch. Hydrobiol*., 98: 380–408.

KRISTENSEN, P., M. SØNDERGAARD & E. JEPPESEN. 1992. Resuspension in a shallow eutrophic lake. *Hydrobiol.*, 228, 101–109.

LAURIDSEN, T. L., L. J. PEDERSEN, E. JEPPESEN & M. SONDERGAARD. 1996. The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake. *J. Plank. Res*., 18: 2293–2294.

MARTÍNEZ-HARO, M., A. J. GREEN, P. ACEVEDO & R. MATEO. 2011. Use of grit supplements by waterbirds: an experimental assessment of strategies to reduce lead poisoning. *Eur. J. Wildl. Res.*, 57: 475–484.

MATEO, R., A. J. GREEN, L. LEFRANC, R. BAOS & J. FIGUEROLA. 2007. Lead poisoning in wild birds from southern Spain: a comparative study of wetland areas and species affected, and trends over time. *Ecotoxicol. Environ. Saf.*, 66: 119–126.

MEERHOFF, M. & E. JEPPESEN. 2009. *Shallow lakes and ponds*. Encyclopedia of Inland Waters, Vol. 2: 645–655.

MORRIS, D. P. & M. W. LEWIS. 1988. Phytoplankton nutrient limitation in Colorado mountain lakes. *Freshwat. Biol*., 20: 315–327.

MORTIMER, C. H. 1941. The exchange of dissolved substances between mud and water in lakes. *J. Ecol*., 30: 280–329.

MOSS, B., D. STEPHEN, C. ÁLVAREZ, E. BÉCARES, W. VAN DE BUND, S. E. COLLINGS, E. VAN DONK, E. DE EYTO, T. FELDMANN, C. FERNÁNDEZ-ALÁEZ, M. FERNÁNDEZ-ALÁEZ, R. J. M. FRANKEN, F. GARCÍA-CRIADO, E. M. GROSS, M. GYLLSTRÖM, L. A. HANSSON, K. IRVINE, A. JÄRVALT, J. P. JENSEN, E. JEPPESEN, T. KAIRESALO, R. KORNIJÓW, T. KRAUSE, H. KÜNNAP, A. LAAS, E. LILL, B. LORENS, H. LUUP, M. R. MIRACLE, P. NÕGES, T. NÕGES, M. NYKÄNEN, I. OTT, W. PECZULA, E. T. H. M. PEETERS, G. PHILLIPS, S. ROMO, V. RUSSELL, J. SALUJÕE, M. SCHEFFER, K. SIEWERTSEN, H. SMAL, C. TESCH, H. TIMM, L. TUVIKENE, I. TONNO, T. VIRRO, E. VICENTE & D. WILSON. 2003. The determination of ecological status in shallow lakes-a tested system (ECOFRAME) for implementation of the European Water Framework Directive. *Aquatic Conserv. Mar. Freshw. Ecosyst*., 13: 507–549.

MURPHY, J. & J. P. RILEY. 1962. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim . Acta*, 27: 31–36.

NÕGES, P., L. TUVIKENE, T. NÕGES & A. KISAND. 1999. Primary production, sedimentation and resuspension in large shallow Lake Võrtsjärv. *Aquat. Sci*., 61: 168–182.

OTZUKI, A. & R. G. WETZEL. 1972. Coprecipitation of phosphate with carbonates in a marl lake. *Limnol. Oceanogr.*, 17: 763–767.

OZIMEK, T., E. VAN DONK & R. D. GULATI. 1993. Growth and nutrient uptake by two species of *Elodea* in experimental conditions and their role in nutrient accumulation. *Hydrobiol.,* 251: 13–18.

PALUDAN, C. & H. S. JENSEN. 1995. Sequential extraction of phosphorus in freshwater wetlands and lake sediment: significance of humic acids. *Wetlands*, 15: 365–373.

PENN, M. R. & M. T. AUER. 1997. Seasonal variability in phosphorus speciation and deposition in a calcareous, eutrophic lake. *Mar. Geol*., 139: 47–59.

PEJRUP, M., J. VALEUR & A. JENSEN. 1996. Vertical fluxes of particulate matter in Aarhus Bight, Denmark. *Cont. Shelf Res*., 16: 1047–1064.

REED, J. M., A. C. STEVENSON & S. JUGGINS. 2001. A multi-proxy record of Holocene climatic change in southwestern Spain: the Laguna de Medina, Cadiz. *Holocene*, 11: 707–719.

REITZEL, K., J. HANSEN, F. Ø. ANDERSEN & H. S JENSEN. 2005. Lake restoration by dosing aluminum relative to mobile phosphorus in the sediment. *Environ. Sci. Technol*., 39: 4134–4140.

RODIER, J. 1989. *Análisis de las aguas*. Ed. Omega, Barcelona, Spain. 1059 pp.

RODRIGO, M. A., E. VICENTE & M. R. MIRACLE. 1993. Short-term calcite precipitation in the karstic meromictic lake La Cruz (Cuenca, Spain). *Verh. Int. Verein. Limnol.*, 25: 711–719.

RODRÍGUEZ-PÉREZ, H. & A. J. GREEN, A. J. 2006. Waterbird impacts on widgeongrass *Ruppia maritima* in a Mediterranean wetland: comparing bird groups and seasonal effects. *Oikos*, 112: 525–534.

RODRÍGUEZ-RODRÍGUEZ, M. 2007. Hydrogeology of ponds, pools and playa-lakes of Southern Spain. *Wetlands*, 27: 819–830.

RODRÍGUEZ-RODRÍGUEZ, M., A. J. GREEN, R. LÓPEZ & S. MARTOS-ROSILLO. 2011. Changes in water level, land use, and hydrological budget in a semi-permanent playa lake, southwest Spain. *Environmental Monitoring and Assessment*, DOI 10.1007/s10661-011-2002-1.

RYDING, S. O. 1985. Chemical and microbiological processes as regulators of the exchange of substances between sediments and water in shallow eutrophic lakes. *Int. Rev. Ges. Hydrobiol.*, 70: 657–702.

SAND-JENSEN, K. & J. BORUM. 1991. Interactions among phytoplankton, periphyton and macrophytes in temperate freshwaters and estuaries. *Aquat. Bot.*, 41: 137–175.

SCHEFFER, M. 1998. *Ecology of shallow lakes*. Chapman and Hall, London. 345 pp.

SCHEFFER, M., S. H. HOSPER, M. L. MEIJER, B. MOSS & E. JEPPESEN. 1993. Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution*, 8: 275–279.

STATSOFT Inc. 1997. *Statistica for Windows* (computer program manual). Tulsa, Oklahoma, USA.

SMITH, L. M. 2003. *Playas of the Great Plains*. University of Texas Press, Texas, TX, USA.

TARTARI, G. & G. BIASCI. 1997. Trophic status and lake sedimentation fluxes. *Wat. Air Soil Pollut.*, 99: 523–531.

TIMMS, R. M. & B. MOSS. 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. *Limnol. Oceanogr.*, 29: 472–486.

WEYHENMEYER, G. A., M. MEILI & D. C. PIERSON. 1995. A simple method to quantify sources of settling particles in lakes: Resuspension versus new sedimentation of material from planktonic production. *Mar. Fresh. Res.*, 46: 223–231.

WEYHENMEYER, G. A., L. HAKÅNSON & M. MEILI. 1997. A validated model for daily variations in the flux, origin and distribution of settling particles within lakes. *Limnol. Oceanogr.*, 42: 1517–1529.

WEYHENMEYER, G. A. & J. BLOESCH. 2001. The pattern of particle flux variability in Swedish and Swiss lakes. *Sci. Tot. Environ.*, 266: 69–78.

YECHIELI, Y. & W. W. WOOD. 2002. Hydrogeologic processes in saline systems: playas, sabkhas, and saline lakes. *Earth-Science Reviews*, 58: 343–65.

Limnetica, 31 (2): 251-260 (2012)
 ISSN: 0213-8409

The Gulf Stream position influences the functional composition of phytoplankton in El Gergal reservoir (Spain)

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Received: 25/2/12 Accepted: 18/6/12

ABSTRACT

The Gulf Stream position influences the functional composition of phytoplankton in El Gergal reservoir (Spain)

The latitudinal position of the north-wall of the Gulf Stream influences the climatic conditions in the Atlantic North and Western Europe. Southerly movements of the Gulf Stream (low Gulf Stream Index values, GSI) typically induce unstable meteorological conditions in this region, while north displacements of the oceanic current (high GSI values) are associated with stable weather. In the present article we explore a seven years data set including annual GSI, meteorological records and phytoplankton community composition and abundance to demonstrate that the year-to-year changes in the position of the Gulf Stream and its influence on the prevailing weather conditions have an effect on the long-term variability of phytoplankton community in El Gergal reservoir, an ecosystem located in the Atlantic coast of Andalusia (SW Spain). Furthermore, we describe the response of each considered phytoplankton functional groups to changes in the Gulf Stream position. Thus, northerly displacements of the north-wall increased the abundance of $H + S_1$ cyanobacteria through a non-linear function with two marked GSI thresholds. GSI and L_m dinoflagellates abundance depicted a significant positive linear correlation, while groups B + P diatoms abundance was negatively linear correlated with GSI. Groups Y cryptophytes and X_1 + J chlorophytes abundance remained nearly constant for most of the studied years but developed an exponential increase at high GSI years. Implications for water quality management are pointed out.

Key words: Gulf Stream Index (GSI), Teleconnection, Climate, Long-term study, Phytoplankton functional groups, El Gergal reservoir.

RESUMEN

La posición de la Corriente del Golfo influye en la composición funcional del fitoplancton en el embalse de El Gergal (España)

Las condiciones climáticas en la fachada Atlántica europea están influidas por las variaciones temporales en la posición latitudinal de la Corriente del Golfo en el océano Atlántico. Así, el desplazamiento hacia el Sur de la Corriente del Golfo (valores bajos del Índice de la Corriente del Golfo, GSI) induce condiciones de inestabilidad meteorológica en la Europa occidental, mientras que los desplazamientos septentrionales de la corriente oceánica (elevados valores del GSI) están asociados con mayor estabilidad meteorológica en esta región. Este artículo estudia la influencia de los cambios interanuales en la posición de la Corriente del Golfo sobre la comunidad fitoplanctónica del embalse de El Gergal, un ecosistema localizado en la costa atlántica andaluza (SW España). Para ello, a lo largo de siete años se han registrado valores anuales de GSI, información meteorológica y datos sobre la composición y biovolumen del fitoplancton. El análisis de esta información permite describir cómo las variaciones anuales en la posición de la Corriente del Golfo afectan a las condiciones meteorológicas en el área de estudio, influyendo de esta manera sobre el biovolumen de cada uno de los grupos funcionales de fitoplancton considerados. Los desplazamientos hacia el Norte de la Corriente del Golfo favorecieron el incremento del biovolumen de cianobacterias de los grupos $H + S_1$ a través de una función no lineal con dos valores críticos de GSI bien

definidos. Por su parte, se encontró una relación lineal positiva entre el GSI y el biovolumen de dinoflagelados del grupo L_m, mientras que las diatomeas de los grupos B + P se relacionaron de forma inversa con el GSI. Aunque el biovolumen de clorofitas de los grupos X_1 + J y de criptofitas del grupo Y permaneció estable durante la mayor parte de los años estudiados, se registró un notable incremento del mismo en aquellos años en los que el GSI mostró sus valores más elevados. Finalmente se apuntan algunas consideraciones sobre posibles implicaciones en la gestión de la calidad del agua embalsada.

Palabras clave: *Índice de la Corriente del Golfo (GSI), Teleconexión, Clima, Estudio a largo plazo, Grupos funcionales de fitoplancton, Embalse de El Gergal.*

INTRODUCTION

It is well known that climatic conditions in the maritime Northern and Western Europe are strongly determined by the latitudinal position of the Gulf Stream (Taylor, 1996; Taylor, 2011; Taylor *et al.*, 1992; Taylor & Stephens, 1998; Taylor *et al.*, 2002), which depicts a marked annual variability (Taylor, 2011; Willis *et al.*, 1995). The Gulf Stream Position Index (GSI) characterizes the position of the north-wall of the Gulf Stream (Taylor & Stephens, 1980; Taylor, 1996) and is commonly related to regional-scale variations in weather conditions. Southward displacements of the Gulf Stream (low GSI values) are typically associated to unstable weather conditions, whilst northerly movements (high GSI values) induce a more stable weather pattern (George, 2000). In this context, Taylor (1996, 2002) reported that the sea level pressure and the distribution of storm tracks over the NE Atlantic in spring differed in extreme positive and negative GSI years. Thus, northwards displacements of the north wall are typically accompanied by high spring sea level pressure in the NE Atlantic region and the opposite occurs during low GSI years. Taylor (1996) also found that the number of storms in the North Atlantic were significantly lower when the Gulf Stream was located north.

Ecosystems act as integrators of subtle climatic signals and could be sensitive sensors of climatic processes (Taylor, 2011; Taylor *et al.*, 2002). Thus, this quasi-cyclical regional scale process influencing year-to-year weather variations have profound effects on the dynamics of diverse biological communities such as terrestrial vegetation (Willis *et al.*, 1995), marine plankton (Taylor & Stephens, 1980; Taylor *et al.*, 1992; Taylor, 1995; Planque & Taylor, 1998; Borkman & Smayda, 2009) and fish (Lavín *et al.*, 2007). It has also been demonstrated that annual variability in the Gulf Stream position influences the hydrological (Noges, 2004), physical (George & Taylor, 1995; George, 2000), biogeochemical (George, 2002; Jennings & Allott, 2006) and plankton dynamics of Northern Europe lakes (George & Taylor, 1995; Planque & Taylor, 1998; George & Hewitt, 1998; George, 2000; George *et al.*, 2010). Nevertheless, there is a lack of research on the effect of GSI variations on freshwater ecosystems in the Atlantic Southern Europe. Taking our wide knowledge on the factors influencing the phytoplankton dynamics in El Gergal reservoir (Atlantic coast of Andalucía, Southern Spain) as a starting point (Vidal *et al.* 2010, Moreno-Ostos *et al.* 2009a, Moreno-Ostos *et al.* 2009b, Hoyer *et al.* 2009, Moreno-Ostos *et al.* 2008, Moreno-Ostos *et al.* 2007, Moreno-Ostos *et al.* 2006, Cruz-Pizarro *et al.* 2005), in this paper we suggest that the year-to-year changes in this community could be significantly influenced by the Gulf Stream position. To achieve this objective, we have explored the long-term relationship between GSI, meteorological conditions and phytoplankton functional composition in El Gergal during a seven years period (2000-2006).

MATERIAL AND METHODS

Study site

El Gergal (37°34′13″ N; 6°02′57″) is a medium size (surface area: 250 ha; volume: 35 hm^3; maximum depth: 37 m; mean depth: 15.7 m)

water supply reservoir located in the Rivera de Huelva basin, a tributary of the Guadalquivir River in the Atlantic coast of Andalucía (Southern Spain) (Fig. 1). The thermal regime of the reservoir has previously been described as warm monomictic (Moreno-Ostos *et al.*, 2009a; 2009b) and the functional composition and seasonal succession of phytoplankton is strongly associated to the development of the water column thermal structure and variations in the turbulent mixing dynamics (Hoyer *et al.*, 2009). Further information on the physical, chemical and biological features of El Gergal reservoir can be found elsewhere (Cruz-Pizarro *et al.*, 2005; Moreno-Ostos *et al*. 2006; Moreno-Ostos *et al.*, 2007; Moreno-Ostos *et al.*, 2008; Moreno-Ostos *et al.*, 2009a; Moreno-Ostos *et al.*, 2009b).

Environmental conditions

Hourly variations in surface water temperature, air temperature, wind speed and atmospheric pressure were recorded by a meteorological station mounted on a buoy as part of an automatic water-quality monitoring station (AWQMS) and deployed near the deepest point of the reservoir (see Moreno-Ostos *et al.*, 2009b). To record surface water temperature (among other water quality variables) the AWQMS was fitted with an YSI 6920 multiple-parameter sonde (Yellow Springs Instruments). Wind speed was measured with a Vector Instruments A100L2-WR cup anemometer. A Vector Instruments T302 aspirated platinum resistance sensor was used to measure air temperature. Barometric pressure was measured using a Druck PDCR 1830 semiconductor strain gauge. All the acquired meteorological data were stored in a Campbell Scientific data logger CR23X.

Estimates of the characteristic vertical turbulent velocity within the upper layers of the water column were derived using the familiar shear velocity (u^*) approximation (Denman & Gargett, 1983; Reynolds, 1997):

$$u* = (\rho_a \, c_1 \, u_{10}^2 / \rho_w)^{-0.5} \qquad (1)$$

where ρ_a is the density of air, c_1 is the dimensionless coefficient for frictional drag upon water ($1.3 \cdot 10^{-3}$), u_{10} is the wind speed at 10 meters above the water surface and ρ_w is the density of water at the surface. The wind speed at 10 meters

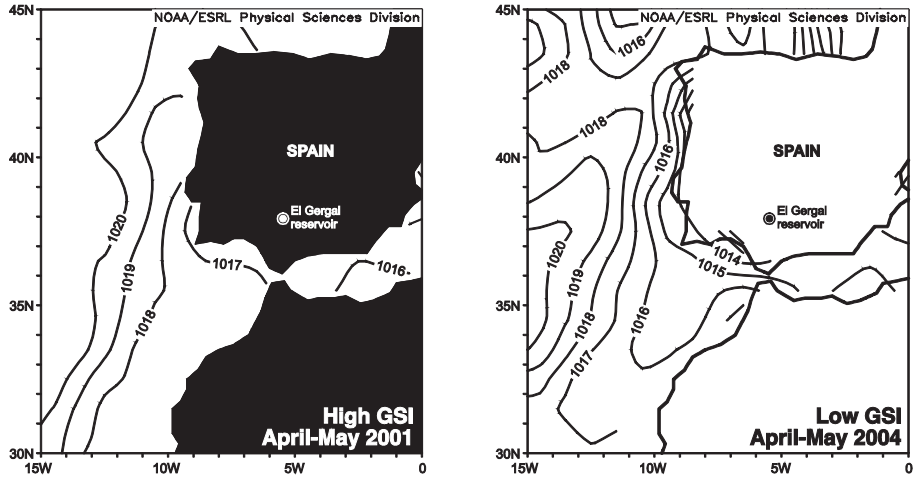

Figure 1. Geographical location of El Gergal reservoir and April-May averaged Sea Level Pressure (mbar) obtained from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) available at the Earth System Research Laboratory of NOAA (http://www.esrl.noaa.gov). Left panel correponds with the high GSI year 2001. Right panel corresponds with the low GSI year 2004. *Localización geográfica del embalse de El Gergal y valores medios de presión atmosférica a nivel del mar (mbar) en Abril-Mayo obtenidos del International Comprehensive Ocean-Atmosphere Data Set (ICOADS), disponible en el Earth System Research Laboratory de NOAA (http://www.esrl.noaa.gov). El panel izquierdo corresponde al año 2001 (alto valor de GSI). El panel derecho corresponde al año 2004 (bajo valor de GSI).*

above the water surface (u_{10}) was calculated from the wind speed at 2 m (u_2) using equation 2,

$$u_{10} = u_2 \ln(10/Z_0)/\ln(2/Z_0) \quad (2)$$

where Z_0 is a dimensionless constant equal to 0.000115 (Brookes *et al.*, 2003)

Phytoplankton community composition and biovolume

During the studied period (2000-2006) water samples for phytoplankton analysis were collected every two weeks from the same sampling station. On each occasion, water samples were collected from discrete depths of 0, 2, 5, 10, 15, 20, 25 and 30 m using a 5 L Van-Dorn water sampler. The samples were preserved in lugol's iodine solution and the cells indentified and counted under inverted microscope following Utermöhl's method (1958).

Morphological measurements were carried out using an inverted Leica DMIL microscope attached to an Allied Pike F145C-IRF16 digital camera and a Sanyo B/W CCD VC-2512 video camera. Images were processed using the Fotomaton II software (University of Málaga). At least 100 microscope measurements of cells/colonies length and width were made for each phytoplankton species at every sample. Cell volumes were calculated from the obtained morphological data following Hillebrant *et al.* (1999).

The species encountered in the samples were classified into functional groups following Reynolds(1997; 2002), a well-known and widely-recognised methodology previously applied to El Gergal phytoplankton (Moreno-Ostos *et al.* 2009b, Hoyer *et al.* 2009). Group biovolume were estimated by adding the biovolume corresponding to the member species at each depth and then averaging the biovolume encountered at all depths. Finally, year-to-year variations in mean annual group biovolume were calculated.

Gulf Stream Position

The annual mean latitude of the north wall of the Gulf Stream was studied using the Gulf Stream Index (GSI) described by Taylor & Stephens (1980). In this procedure, the latitude of the north wall is read from each chart at six longitudes (79° W, 75° W, 72° W, 70° W, 67° W and 65° W) and an index of position constructed using principal component analysis. The first principal component typically accounts for a high proportion of the variance and constitutes the best estimate of the latitudinal displacement of the Gulf Stream (George, 2000). Annual GSI data were obtained from the Plymouth Marine Laboratory (PML) at http://www.pml.ac.uk/gulfstream.

RESULTS

The Gulf Stream position influences the long-term local weather conditions

During the studied period mean annual GSI ranged between 1.467 in 2001 (north mode of the Gulf Stream) and –0.847 in 2004 (south mode of the Gulf Stream) (Fig. 2a), a range of

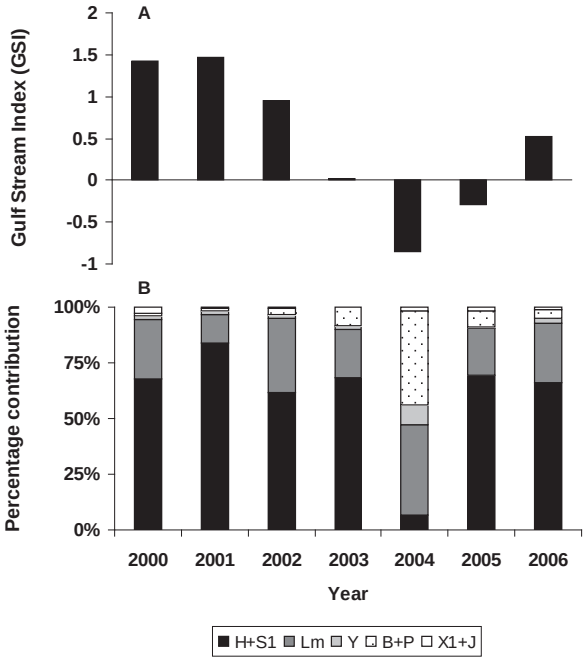

Figure 2. A) Annual average GSI values. B) The relative contribution of each considered phytoplankton functional group to total phytoplankton biovolume. *A) Valores medios anuales de GSI. B) Contribución relativa de cada grupo funcional considerado al biovolumen fitoplanctónico total.*

GSI values consistent with those previously considered in the literature (i.e. George 1995, 2000; Taylor & Stephens, 1998; Taylor, 2011). A large-scale picture of April-May averaged Sea Level Pressure (mbar) obtained from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) available at the Earth System Research Laboratory of NOAA revealed that north mode of the Gulf Stream was related to high pressure conditions in the Atlantic coast of the Iberian Peninsula, whilst south displacements of the oceanic current coincided with lower pressure and higher pressure gradient in this area (Fig. 1). Accordingly, meteorological and physical records in El Gergal suggest that the Gulf Stream position significantly influenced the local weather and mixing conditions. Again, north mode of the Gulf Stream was related with stable conditions in El Gergal, while south displacements of the Gulf Stream induced a more unstable environment. Thus, GSI was positively correlated with mean annual atmospheric pressure ($r = 0.91$; $p < 0.005$) and mean annual air temperature ($r = 0.93$; $p < 0.001$), and negatively correlated with mean annual shear velocity ($r = -0.90$; $p < 0.001$) and with the number of wind events (wind speed >4 ms^{-1}) per year ($r = -0.89$; $p < 0.05$).

The influence of the Gulf Stream position on the functional composition of phytoplankton

Long-term changes in meteorological forcing initiated by the Gulf Stream latitude influenced the relative biovolume of components of the phytoplankton community in El Gergal reservoir (Fig. 2b). Thus, during high GSI years the warm and calm conditions favoured the development of a phytoplankton community governed by functional groups H + S_1 (positively buoyant filamentous cyanobacteria) and L_m (swimming dinoflagellates). However, during

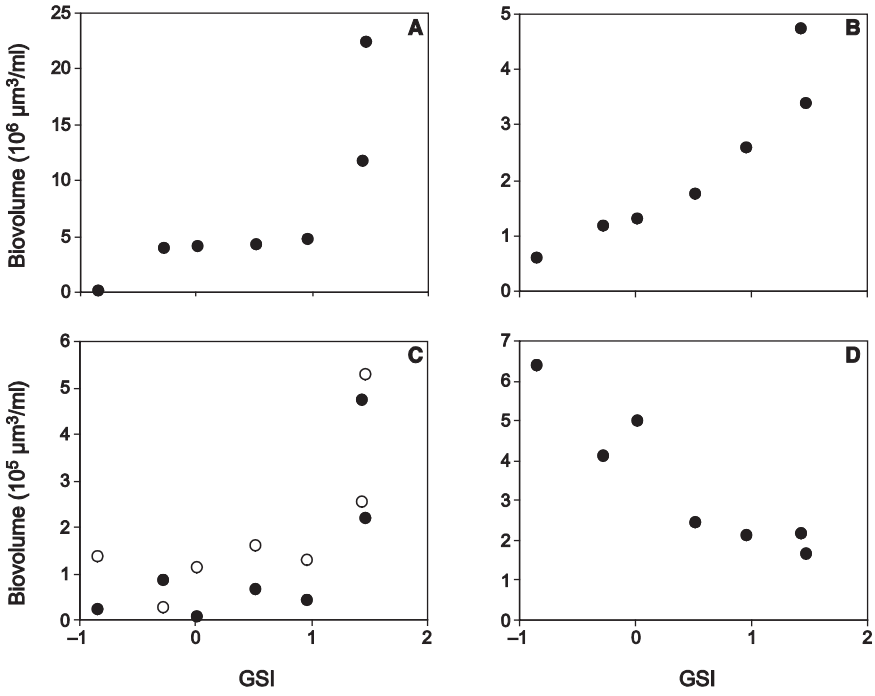

Figure 3. The influence of GSI on different phytoplankton functional groups (Reynolds 2002) biovolume in El Gergal reservoir. A) groups H + S_1 cyanobacteria; B) group L_m dinoflagellates ; C) groups X_1 + J chlorophytes (black circles) and Y cryptophytes (white circles); D) groups B + P diatoms. *Influencia del valor del GSI en el biovolumen diferentes grupos funcionales de fitoplancton en el embalse de El Gergal. A) Cianobacterias de los grupos H + S_1; B) dinoflagelados del grupo L_m; C) clorofilas de los grupos X_1 + J (círculos negros) y criptofitas del grupo Y (círculos blancos); D) diatomeas de los grupos B + P.*

the unstable low GSI years these functional groups were less abundant and functional groups B+P (negatively buoyant diatoms) increased their percentage contribution to total biovolume. The percentage contribution of groups X_1+J (neutrally buoyant chlorophytes) and Y (cryptophytes) remained always low although it slightly increased during high GSI years.

The response of different phytoplankton functional groups to variations in the Gulf Stream position

Each different phytoplankton functional group considered in this study developed a particular response in terms of biovolume to the long-term changes in the weather conditions induced by annual variations in GSI (Fig. 3). In this sense, the response of functional groups $H+S_1$ to changes in GSI was characterized by a typical catastrophic (*sensu* Scheffer *et al.* 2001) non-linear function with rapid state transitions through two marked GSI thresholds (Fig. 3a). When the Gulf Stream moves to the south (GSI < −0.3) the enhanced wind-induced turbulent mixing prevents the development of filamentous cyanobacteria, while their abundance dramatically increased when the oceanic current is located well to the north (GSI > 1) and shear stress decreases. During years when GSI was within these two thresholds values the cyanobacteria biovolume remained nearly constant around $4.3 \cdot 10^6$ μm^3/ml and coexistence with other phytoplankton groups occurred.

Dinoflagellates abundance depicted a similar response to long-term changes in GSI, with the highest abundances recorded during the low turbulent mixing and stable weather conditions prevailing in the reservoir during high GSI years and the lowest during the unstable low GSI years. Interestingly, GSI threshold levels were in agreement with those described for cyanobacteria, although the character of the dinoflagellates response was smoother and the critical GSI levels for transitions between states were fuzzier (Fig. 3b).

The response of groups Y and X_1+J abundance to changes in GSI was also catastrophic, although just one GSI "breakpoint" around GSI 1.4 was identified. Thus, cryptophytes and chlorophytes abundance remained low and roughly constant in those years when GSI < 1.4, while it sharply increased above this threshold value (Fig. 3c).

By contrast, a significant continuous (rather than catastrophic) negative linear correlation was found between GSI and functional groups B+P biovolume ($r = 0.93$; $p < 0.0001$; $n = 7$) (Fig. 3d) thus revealing that the turbulent conditions prevailing during low GSI years enhanced the development of negatively-buoyant diatoms.

DISCUSSION

Long-term changes in the existing meteorological conditions (i.e. temperature, wind speed, turbulent mixing) have a profound effect on the freshwater plankton communities development (Margalef, 1980; Catalan & Fee, 1994; George *et al.*, 1998, George, 2000). In this context, it has been suggested that the position of the Gulf Stream should be considered as a relevant factor influencing phytoplankton dynamics in the lakes located in the Atlantic coast of Western Europe (Taylor *et al.*, 1992; Taylor, 2002; Taylor *et al.*, 2002; Taylor, 2011; Jennings & Allott, 2006; George *et al.*, 2010). Previous studies (George & Taylor, 1995; Taylor, 2002) have reported that the mediating factor seems to be the subtle changes in the spring and early summer weather induced by the Gulf Stream position, especially in the wind speed dynamics (Noges, 2004, see also George & Hewitt, 1998).

Our results suggest that the phytoplankton community composition and the success of certain functional groups are indirectly linked to the Gulf Stream position, which significantly influences the local meteorological forcing over the reservoir. As far as we know from the literature, this is the first study revealing the interaction between the Gulf Stream position and the phytoplankton community dynamic in a freshwater ecosystem in SW Europe. Previous results reported by Moreno-Ostos *et al.* (2009b) using a high-resolution autonomous monitoring device highlighted the influence of wind mixing on the cyanobacteria and diatoms dynamics

in El Gergal reservoir. Now we show that the South displacements of the Gulf Stream were associated with stronger turbulent mixing in El Gergal and favoured the development of negatively buoyant diatoms, while a North position of the Gulf Stream influenced a less intense wind-induced mixing and, consequently, the growth of positively buoyant cyanobacteria and swimming dinoflagellates populations in the reservoir. In this context, George (2000) reported the occurrence of intense *Aphanizomenon* sp. blooms during high GSI years in Esthwaite Water (England, UK), while during low GSI years the phytoplankton community was mainly governed by microalgae. These climate-induced changes in phytoplankton community could also propagate through the trophic web influencing zooplankton composition. Thus, George (2000) demonstrated that during low GSI years the enhanced small edible algae populations sustained higher abundances of *Daphnia* during the early summer in Esthwaite Water, while the increased cyanobacteria populations during high GSI years avoided the large-sized cladocera growth. A comparable effect was reported in the North Basin of Windermere Lake by George & Taylor (1995).

Our study reveals that the abundance of many phytoplankton functional groups in El Gergal reservoir (i.e. cyanobacteria, dinoflagellates, cryptophytes and chlorophytes) responds catastrophically to gradual changes in GSI. From a reservoir management scope this is especially relevant in the case of cyanobacteria, a harmful phytoplankton group which develops sudden and persistent surface blooms with deleterious effects on the stored water quality. Although more research is needed, in this study we have delimited the GSI threshold value for the occurrence of dense cyanobacteria blooms. On the basis of this knowledge, reservoir managers should forecast GSI as an early-warning signal of approaching catastrophic shift to cyanobacteria dominance and implement water management strategies to avoid the development of surface blooms during high GSI years. In this context, Taylor & Stephens (1998) obtained a multiple regression empirical model to predict GSI from the NAO index recorded two years previously and the previous year's Gulf Stream position.

Ecosystem state shifts can cause large losses of ecological and economical resources, and restoring a desired state may require drastic and expensive intervention (Scheffer *et al.*, 2001; Scheffer & Carpenter, 2003). As perturbations are difficult to control, the most pragmatic and effective way to manage ecosystems is to build and maintain resilience of desired ecosystem state (Scheffer *et al.*, 2001). In El Gergal reservoir case, while meteorological forcing (i.e. wind mixing) is naturally imposed, not manageable and strongly linked to annual changes in the Gulf Stream position, selective water withdrawal constitutes a valuable tool for reservoir managers to influence the phytoplankton community composition in the reservoir (Hoyer *et al.*, 2009) and sustain a low cyanobacteria abundance stability domain. As the mixed layer depth of reservoirs submitted to selective withdrawal operations is strongly influenced by the water withdrawal depth (Moreno-Ostos *et al.*, 2008), during the thermally-stratified period of high GSI years hypolimnetic withdrawal could disband the positive-buoyant cyanobacteria patches throughout the enlarged mixed layer, promoting the shift to a phytoplankton community governed by innocuous chlorophytes and diatoms.

ACKNOWLEDGMENTS

This study has been funded by the project CGL2005-04070 (Ministerio de Ciencia e Innovación, Gobierno de España). We acknowledge the Plymouth Marine Laboratory (UK) for providing annual mean GSI data, and the Earth System Research Laboratory of NOAA (USA) for averaged Sea Level Pressure charts. The weekly data and part of the continuous monitoring records used in this work belongs to EMASESA, and were collected as part of their reservoir water quality monitoring program. Logistical support was provided by the Seville water supply company (EMASESA).

REFERENCES

BORKMAN, D. G. & T. J. SMAYDA. 2009. Multidecadal (1959–1997) changes in *Skeletonema* abundance and seasonal bloom patterns in Narragansett Bay, Rhode Island, USA. *Journal of Sea Research*, 61: 84–94.

BROOKES, J. D., R. H. REGEL & G. G. GANF. 2003. Changes in the photochemistry of Microcystis aeruginosa in response to light and mixing. *New Phytologist*, 158: 151–164

CATALAN, J. & E. J. FEE. 1994. Interannual variability in limnetic ecosystems: origin, patterns and predictability. In: *Limnology Now: A paradigm of planetary problems*. R. Margalef (ed.): 81–97. Elsevier. Amsterdam.

CRUZ-PIZARRO, L., A. BASANTA, C. ESCOT, E. MORENO-OSTOS & D. G. GEORGE. 2005. Temporal and spatial variations in the quality of water in El Gergal reservoir, Seville, Spain. *Freshwater Forum*, 23: 62–77.

DENMAN, K. L. & A. E. GARGETT. 1983. Time and space scales of vertical mixing and advection of phytoplankton in the upper ocean. *Limnology and Oceanography*, 28: 801–815.

GEORGE, D. G. 2000. The impact of regional-scale changes in the weather on the long-term dynamics of *Eudiaptomus* and *Daphnia* in Esthwaite Water, Cumbria. *Freshwater Biology*, 45: 111–121.

GEORGE, D. G. 2002. Regional-scale influences on the long-term dynamics of lake plankton. In: *Phytoplankton productivity: carbon assimilation in marine and freshwater ecosystems*. P. J. le B. Williams, D. N. Thomas & C. S, Reynolds (eds): 265–290. Blackwell Science Ltd. Oxford (UK).

GEORGE, D. G. & A. H. TAYLOR. 1995. UK lake plankton and the Gulf Stream. *Nature*, 378: 139.

GEORGE, D. G. & D. P. HEWITT. 1998. The influence of year-to-year changes in position of the Atlantic Gulf Stream on the biomass of zooplankton in Windermere North Basin, UK. Management of lakes and reservoirs during global climate change. Proceedings of the NATO Advanced Research Workshop. November 11–15, 1995. Prague, Czech Republic: 223–244.

GEORGE, D. G., T. L. CONSTANTINESCU, J. DURAS, D. GERDEAUX, S. HORICKA & T. OZIMEK. 1998. Managing water quality in a changing world. In: *Managing lakes under conditions of global change*. D. G. George, D. W. Sutcliffe, C. S. Reynolds, J. W. G. Jones & P. Puncochar (eds.): 301–306. NATO ASI Series. Kluwer, Dordrecht (The Nethertlands).

GEORGE, D. G. & D. P HEWITT. 1999. The influence of the year-to-year variations in the winter weather on the dynamics of *Daphnia* and *Eudiaptomus* in Esthwaite Water, Cumbria. *Functional Ecology*, 13: 45–54.

GEORGE, D. G, E. JENNINGS & N. ALLOTT. 2010. The impact of climate change on lakes in Britain and Ireland. In: *The impact of climate change on European lakes.* D. G. George (ed.): 359–386. Aquatic Ecology Series, 4. Springer-Verlag. The Netherlands.

HILLEBRANT, H., C. D. DÜRSELEN, D. KIRSCHTEL, U. POLLINGHER & T. ZOHARY. 1999. Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology*, 35: 403–424.

HOYER, A. B. E. MORENO-OSTOS, J. VIDAL, J. M. BLANCO, R. L. PALOMINO-TORRES, A. BASANTA, C. ESCOT & F. J. RUEDA. 2009. The influence of external perturbations on the fucntional composition of phytoplankton in a Mediterranean reservoir. *Hydrobiologia*, 627:1–17.

JENNINGS, E. & N. ALLOTT. 2006. Position of the Gulf Stream influences lake nitrate concentrations in SW Ireland. *Aquatic Science*, 68: 482–489.

LAVÍN, A., X. MORENO-VENTAS, V. ORTIZ DE ZÁRATE, P. ABAUNZA & J. M. CABANAS. 2007. Environmental variability in the North Atlantic and Iberian Waters and its influence on horse mackerel (*Trachurus trachurus*) and albacore (*Thunnus alalunga*) dynamics. *ICES Journal of Marine Science*, 64: 425–438.

MARGALEF, R. 1980. *La biosfera: entre la termodinámica y el juego*. Omega. Barcelona. 236 pp.

MORENO-OSTOS, E., L. CRUZ-PIZARRO, A. BASANTA, C. ESCOT, D. G. GEORGE. 2006. Algae in the motion: spatial distribution of phytoplankton in thermally stratified reservoirs. *Limnetica*, 25(1-2): 205–217.

MORENO-OSTOS, E., J. A. ELLIOTT, L. CRUZ-PIZARRO, C. ESCOT, A. BASANTA & D. G. GEORGE. 2007. Using a numerical model (PROTECH) to examine the impact of water transfers on phytoplankton dynamics in a Mediterranean reservoir. *Limnetica*, 26: 1–11.

MORENO-OSTOS, E., L. CRUZ-PIZARRO, A. BASANTA & D. G. GEORGE. 2008. The spatial distribution of different phytoplankton functional groups in a Mediterranean reservoir. *Aquatic Ecology*, 42: 115–128.

MORENO-OSTOS, E., L. CRUZ-PIZARRO, A. BASANTA & D. G. GEORGE. 2009a. Spatial heterogeneity of cyanobacteria and diatoms in a thermally stratified canyon-shaped reservoir. *International Review of Hydrobiology*, 94(3): 245–257.

MORENO-OSTOS, E., L. CRUZ-PIZARRO, A. BASANTA & D. G. GEORGE. 2009b. The influence of wind-induced mixing on the vertical distribution of buoyant and sinking phytoplankton species. *Aquatic Ecology*, 43: 271–284.

NOGES, T. 2004. Reflection of the changes of the North Atlantic Oscillation Index and the Gulf Stream Position Index in the hydrology and phytoplankton of Vortsjärv, a large, shallow lake in Estonia. *Boreal Environment Research*, 9: 401–407.

PLANQUE, B. & A. H. TAYLOR. 1998. Long-term changes in zooplankton and the climate of the North Atlantic. *ICES Journal of Marine Science*, 55: 644–654.

REYNOLDS, C. S. 1997. *Vegetation processes in the pelagic: a model for ecosystem theory*. Excellence in Ecology, 9. Ecology Institute, Oldendorf/luhe, Germany. 371 pp.

REYNOLDS, C. S. 2002. Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research*, 24(5): 417–428.

SCHEFFER, M., S. CARPENTER, J. A. FOLEY, C. FOLKE & B. WALKER. 2001. Catastrophic shifts in ecosystems. *Nature*, 413: 591–596.

SCHEFFER, M. & S. R. CARPENTER. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution*, 18 (12): 648–656.

TAYLOR, A. H. 1995. North-soth shifts of the Gulf Stream and climatic connection with the abundance of zooplankton in the UK and its surroundings seas. *ICES Journal of Marine Science*, 52: 711–721.

TAYLOR, A. H. 1996. North-South shifts of the Gulf Stream: Ocean-Atmosphere interactions in the North Atlantic. *International Journal of Climatology*, 16: 559–583.

TAYLOR, A. H. 2002. North-tlantic climatic signals and the plankton of the European continental shelf. In: *Large marine ecosystems of the North Atlantic: Changing states and sustainability*. K. Sherman & H. R. Skjoldal (eds.): 3–26. Elsevier Science. London. UK.

TAYLOR, A. H. 2011. *The dance of air and sea. How oceans, weather and life link together*. Oxford University Press Inc. New York. USA. 288 pp.

TAYLOR, A. H. & J. A. STEPHENS. 1980. Latitudinal displacements of the Gulf Stream (1966 to 1977) and their relation to changes in temperature and zooplankton in the NE Atlantic. *Oceanologica Acta*, 3: 145–149.

TAYLOR, A. H. & J. A. STEPHENS. 1998. The North Atlantic Oscillation and the latitude of the Gulf Stream. *Tellus*, 50A: 134–142

TAYLOR, A. H., J. M. COLEBROK, J. A. STEPHENS & N. G. BAKER. 1992. Latitudinal displacements of the Gulf Stream and the abundance of plankton in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 72: 919–921.

TAYLOR, A. H., J. I. ALLEN & P. A. CLARK. 2002. Extraction of weak climatic signal by an ecosystem. *Nature*, 416: 629–632.

UTERMÖHL, H. 1958. Zur Vervollkommung der Quantitativen Phytoplankton-Methodik. *Mitteilungen Internationale Vereinigung für Theoretische und Angewandte Limnologie*, 9:1–39.

VIDAL, J., E. MORENO-OSTOS, C. ESCOT, R. QUESADA & F. RUEDA. 2010. The effects of diel changes in circulation and mixing on the longitudinal distribution of phytoplankton in a canyon-shaped Mediterranean reservoir. *Freshwater Biology*, 55 (9): 1945–1957.

WILLIS, A. J., N. P. DUNNETT, R. HUNT & J. P. GRIME. 1995. Does Gulf Stream position affect vegetation dynamics in Western Europe? *Oikos*, 73: 3.

Limnetica, 31 (2): 261-272 (2012)
 ISSN: 0213-8409

An assessment of the changes in water chemistry and in the macroinvertebrate community produced during the creation of the new Llobregat river mouth (Barcelona, NE Spain)

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Received: 6/3/12 Accepted: 29/6/12

ABSTRACT

An assessment of the changes in water chemistry and in the macroinvertebrate community produced during the creation of the new Llobregat river mouth (Barcelona, NE Spain)

In 1999, a set of coordinated projects and investments whose principal objective was to transform Barcelona into one of the main distribution points of southern Europe resulted in the relocation of the Llobregat River mouth. The mouth was relocated by draining the old river mouth and constructing a new one. The aim of this study was to characterise the physico-chemical properties and the aquatic macroinvertebrate communities of the new river mouth and to monitor the changes experienced by the estuarine environment during its creation. A sampling point was established in the river 1.8 km upstream from its connection with the new mouth, and two sampling points were established in the new mouth. Samples of water and macroinvertebrates were collected every two months from May 2004 to June 2005, covering the periods before (from May to September 2004) and after (from September 2004 to June 2005) the new mouth was connected to the river and the sea. During the period before its connection to the river and the sea, the new mouth was functionally similar to a lagoon, with clear waters, presence of *Chara* and a rich invertebrate community. After the connection was completed, seawater penetrated the river mouth and extended to the connection point with the river (approximately 3.9 km upstream). An increase in conductivity from 4-6 mS cm^{-1} to 24-30 mS cm^{-1} caused important changes in the macroinvertebrate community of the new mouth. An initial defaunation was followed by a colonisation of the new mouth by brackish-water and marine invertebrate species. Due to its design (which allows the penetration of the sea) and the decreased discharge from the lower part of the Llobregat River, the new mouth has become an arm of the sea.

Key words: River diversion, river mouth, human impact, aquatic macroinvertebrates, chironomids.

RESUMEN

Caracterización de las propiedades físico-químicas y la comunidad de macroinvertebrados acuáticos de la nueva desembocadura del Río Llobregat (Barcelona, NE España)

En 1999 la desembocadura del Río Llobregat fue desviada como consecuencia de una acción coordinada de proyectos cuyo principal objetivo era el de transformar Barcelona en uno de los principales puntos de distribución de mercancías del sur de Europa. En el presente estudio se caracterizan las propiedades físico-químicas y la comunidad de macroinvertebrados acuáticos de la nueva desembocadura, y se monitorizan los cambios experimentados por el ecosistema durante su creación. Un punto de muestreo se situó en el Río Llobregat, 1.8 km aguas arriba de su conexión con la nueva desembocadura, y dos puntos de muestreo se situaron en la nueva desembocadura. Se recogieron muestras de agua y de macroinvertebrados cada dos meses desde Mayo de 2004 hasta Junio de 2005, período que incluyó el antes (desde Mayo hasta Septiembre de 2004) y el después (desde Septiembre de 2004 hasta Junio de 2005) de que la nueva desembocadura fuera conectada al río y al mar. Durante el período anterior a su conexión con el río y el mar la nueva desembocadura funcionaba como una laguna, presentando aguas claras, presencia de Chara *y una comunidad de macroinvertebrados rica en especies. Después de ser conectada al río y el mar, el agua de mar penetró en la desembocadura hasta el punto de conexión con el río*

(aproximadamente unos 3.9 km aguas arriba). La conductividad de la desembocadura aumentó de 4-6 mS cm^{-1} a 24-30 mS cm^{-1}, causando importantes cambios en la comunidad de macroinvertebrados acuáticos. Se registró una pérdida de fauna inicial seguida de una colonización de fauna marina y de aguas salobres. Debido a su diseño (que permite la entrada de grandes cantidades de agua de mar) y al escaso caudal del tramo bajo del Llobregat, la nueva desembocadura se ha convertido en un brazo de mar.

Palabras clave: *Desvío del río, desembocadura, impacto humano, macroinvertebrados acuáticos, quironómidos.*

INTRODUCTION

Urban development is concentrated in the coastal zones of the world, and these coastal populations are growing more rapidly than the global average. Recent calculations showed that $2.69 \cdot 10^9$ people (44 percent of the world's population) live within the coastal zone (Crossland *et al*., 2005). The average human population density in coastal areas is approximately 80 persons per square kilometre, twice the global average (http://earthwatch.unep.ch/oceans/coastalthreats.php). This massive human presence along the coastline is translated into a wide variety of pressures (e.g., wastewater discharges, landscape fragmentation and habitat destruction) on coastal ecosystems. In certain areas, the growth of the population and the infrastructures is reaching a point at which there is no more available space and a reconfiguration of the natural landscape is required. The city of Barcelona and its metropolitan area (Spain) represent a clear example of this situation.

Barcelona is the second largest city in Spain (5 507 813 inhabitants in 2009 in the metropolitan area, according to the Spanish Institute of Statistics: http://www.ine.es), and it is a hotspot for the trade in goods and services within Europe. The growth of the population and the development of the economy have forced the city to expand. However, the expanding city faces four physical barriers: the Collserola Mountains in the West, the Mediterranean Sea in the East, the Besòs River in the North and the Llobregat River in the South. In 1999, the Delta Plan, a large-scale project costing 6750 million euros, was launched. The Delta Plan consisted of a set of coordinated projects and investments whose main objective was to transform Barcelona into "the main distribution point of southern Europe" (Catalonian Government, available at: http://www.gencat.net). The Delta Plan involved the expansion of Barcelona's port. The planned expansion would double the rate of the trade in goods by doubling the surface area of the port. This space requirement resulted in the relocation of the Llobregat River's estuary by draining the old river mouth and constructing a new one.

Aquatic macroinvertebrates were chosen as the focus of the study because this group of organisms is very rich in species (Barnes, 1995; Tachet *et al*., 2000) that can occur over a wide range of environmental conditions and can show rapid responses to any change in the environment (e.g., Merritt & Cummins, 1996; Batzer *et al*., 1999; Bilton *et al*., 2001; Basset *et al*., 2006; Jackson & Füreder, 2006). Aquatic macroinvertebrates have been widely used as indicators of water quality and ecosystem health status (Bonada *et al*., 2006), and they are one of the key elements of the European Water Framework Directive .(European Commission, 2000), intended to achieve a good water quality in all European water bodies. The objective of this study was to characterise the physico-chemical properties and the aquatic macroinvertebrate communities of the new river mouth and to monitor the changes experienced during its creation. The study sought to report the environmental effects of a group of large engineering projects. Such effects are rarely assessed, and they remain unpublished in most cases.

METHODS

Study site

The Llobregat River is the principal river in Barcelona (NE Spain). It forms a delta of 97 km^2 upon reaching the Mediterranean Sea. The excavation of a new river mouth began in 2001 and was completed in May 2004. The river mouth remained closed (to the river in its upper part and to the sea at its outlet) for several months. During this period, it was fed exclusively by groundwater. The inlet and outlet of the river mouth were opened in September 2004. The new river mouth is 3.9 km long and 250 m wide, with a mean depth of 2 m. Because the depth of the river was approximately 0.4 m, an extensive slope was formed at the junction of the river and the new mouth. The banks of the new mouth were constructed of granite blocks. Aquatic and terrestrial vegetation were completely absent. The right levee was designed to allow overflow by the river during flood episodes, based on a return period of 25 years (Sánchez-Juny & Dolz, 2004). The flood waters would inundate a wetland area that includes Special Protection Zones for Birds (Community Directive 79/409/EEC) and areas protected by the Catalonian Government.

Sampling design

A sampling point (station 3) was established in the river, 1.8 km upstream from its connection with the new mouth. Two additional sampling points were located in the new mouth, one near the sea (station 1) and the other (station 2) 3 km landwards from the coastline (Fig. 1). Initially, a sampling point was established a few hundred metres above the connection, but constant and unpredictable disturbances linked to the engineering projects invalidated the preliminary results obtained from this site and later made access to the site impossible. Previous surveys from the 80s (Prat *et al*., 1983) and from 2001 (Alonso *et al*., 2001) reported that invertebrates were absent from the old river mouth. The lower part of the Llobregat River was severely polluted by urban and industrial wastes coming from the catchment (Millet & Prat, 1984; Prat & Rieradevall, 2006) and registered anoxic conditions that prevented the establishment of invertebrate communities. These previous conditions cannot

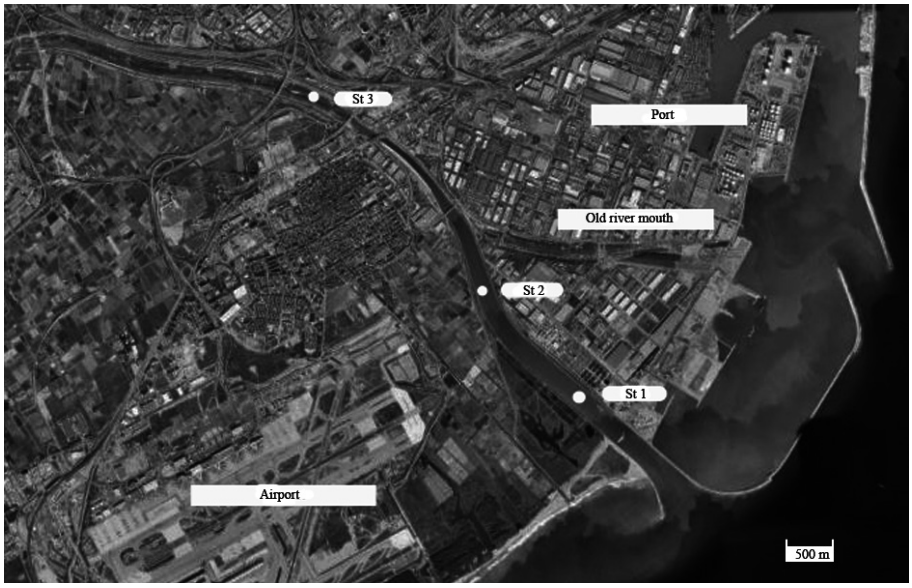

Figure 1. Study site. White dots mark the sampling stations in the new mouth (stations 1 and 2) and the river (station 3). Satellite image source: Institut Cartogràfic de Catalunya. *Zona de estudio. Los puntos blancos marcan las localidades de muestreo en la nueva desembocadura (localidades 1 y 2) y en el río (localidad 3). Fuente de la imagen de satélite: Institut Cartogràfic de Catalunya.*

be considered to represent a suitable goal in terms of environmental planning. After the recent initiation of wastewater control and the construction of a new large wastewater treatment plant (WTP) in the area, we expect an improvement in the water quality in the lower Llobregat River (similar to the current ecological status of nearby upstream stretches). Therefore, the upstream sampling site served to exemplify a relevant set of potential ecological conditions because of its communities of pollution- and salinity-tolerant invertebrate species (e.g., *Chironomus riparius*, *Cricotopus sylvestris*; see Cañedo-Argüelles & Rieradevall 2009 for pollution and salinity tolerances) that could colonise the new mouth. Water and macroinvertebrate samples were collected every two months from May 2004 to June 2005, covering the periods before (from May to September 2004) and after (from September 2004 to June 2005) the new mouth was connected to the river and the sea.

Physico-chemical characterisation

Water conductivity, pH, temperature and dissolved oxygen were measured *in situ* using a multi-parametric sensor (WTW, multiparameter model 197i). Transparency (Secchi disk) was also recorded in the field. One litre of surface water was collected and kept at a cold temperature for laboratory analyses of dissolved inorganic nutrients (NH_4^+, NO_3^-, NO_2^-, PO_4^{3-}, TP and Si^{2+}), total organic carbon (TOC), suspended solids (SSP) and major ions (SO_4^{2-}, Cl^-, Ca^{2+}, Mg^{2+}, Na^+, and K^+), following standard methods (Greenberg *et al*., 1999).

Collection and identification of aquatic macroinvertebrates

Multihabitat samples were collected by kicking at the substrate in all the available habitats for one minute and collecting the suspended material with a 250 μm mesh size dip net. To complement these samples, sediment was collected at the deepest points of stations 1 and 2 (maximum depth 2 meters) with a Van Veen grab sampler (area = 298.8 cm^{-2}). Three replicates of each sample type were collected at each sampling station. The samples were fixed in 4 % formaldehyde. In the laboratory, the samples were rinsed through a 250 μm mesh size net. The macroinvertebrates were removed and preserved in 90 % ethanol for identification. Most taxa were identified to species level. Oligochaetes and certain Diptera were identified to family level, and certain chironomids were identified to genus level.

Data analysis

Conductivity and oxygen profiles were constructed with SURFER 8.0 software (Golden Software). The macroinvertebrate community data were analysed using the Principal Response Curve (PRC) method (van den Brink & Ter Braak, 1999), which is designed to evaluate the temporal responses of communities to disturbance. The PRC method is a form of redundancy analysis and generates series of curves that represent the extent and direction of differences between the impacted communities and the controls. It is a useful method for visualising the trajectories of community responses to disturbance along time. The PRC analysis was performed in CANOCO version 4.5 (ter Braak & Šmilauer, 2002) with the average relative abundances of macroinvertebrates in the multihabitat samples from the three stations on each sampling date. The resulting PRC diagram displays the first principal component of the redundancy analysis over time and can be interpreted as the deviation of the impacted community (the new mouth) from the control (the upstream section of the Llobregat River). Two different groups of samples were then defined for the impacted communities: before (from May to September 2004) and after (from September 2004 to June 2005) the new mouth was connected to the river and the sea. After the groups were defined, an IndVal analysis was performed with PCORD 4.20 (McCune & Mefford, 1999) to identify the taxa significantly associated with each group. Indicator values analysis (IndVal) is based on the comparison of relative abundances and relative frequencies of taxa in the *a priori* defined site groups (Dufrêne & Legendre, 1997). Each taxon

is associated with an indicator value (IV value) that varies between 0 and 100 and a ρ-value obtained by Monte Carlo permutations (9999 runs). The ρ-value specifies the taxon's probability of assignment at random to the most probable of the defined site groups. Only taxa with a ρ-value of 0.05 were considered key taxa.

RESULTS

Physico-chemical characterisation

A smooth physico-chemical gradient could be observed in the new mouth throughout the study period. Upstream, conductivity decreased, whereas total phosphorus and suspended solids increased. The oxidized forms of nitrogen were dominant downstream, whereas the reduced forms were dominant upstream (Table 1). Before the connection of the new mouth to the river and to the sea, the physico-chemical characteristics of the new mouth resembled those of the river (Table 1); although conductivity was higher than at station 3, and nutrient concentrations were lower. After the connection was made, the new mouth showed a significant increase in water conductivity and in the concentrations of nutrients, suspended solids and major ions (Table 1). The increase in water conductivity was slightly higher at station 1 (closer to the sea) than at station 2, and no vertical stratification of salinity was recorded during the study period (Fig. 2). The connection of the mouth to the river and the sea also affected the dissolved oxygen concentrations, which decreased from saturation (100 %) to 40-60 % at stations 1 and 2, increasing again at the end of the study at station 1, where values greater than 300 % were recorded in June 2005 (Fig. 3).

Table 1. Physico-chemical characterization of the river (station 3) and the new mouth (stations 1 and 2) before and after its opening to the river and the sea. Only those variables which experienced a significant change (tested by ANOVA) after the connection are shown. In order to avoid redundant information soluble reactive phosphorous is not shown as being significantly correlated with total phosphorous (TP), and Ca^{2+}, Mg^{2+} and Na^{+} are not shown as being significantly correlated to K^{+} and Cl^{-}. *Características físico-químicas del río (localidad 3) y de la nueva desembocadura (localidades 1 y 2) antes y después de la conexión de esta última con el río y con el mar. Solo se muestran aquellas variables que registraron cambios significativos (analizados mediante ANOVA) después de la conexión. Para evitar redundancias el fósforo reactivo soluble (significativamente correlacionado con el fósforo total) y el Ca^{2+}, Mg^{2+} y Na^{+} (significativamente correlacionados con el K^{+} y el Cl^{-}) no se muestran en la tabla.*

	Conductivity mS cm^{-1}	NO_2^- mg l^{-1}	NO_3^- mg l^{-1}	NH_4^+ mg l^{-1}	TP mg l^{-1}
St 1					
Before connection	6.2 (± 0.6)	0.02 (± 0)	0.60 (± 0.14)	0.12 (± 0.03)	0.04 (± 0)
After connection	30.2 (± 4.9)	0.53 (± 0.12)	6.03 (± 2.24)	7.19 (± 1.95)	0.37 (± 0.10)
St 2					
Before connection	4.7 (± 0.2)	0.02 (± 0)	0.60 (± 0.14)	0.11 (± 0.03)	0.04 (± 0)
After connection	24.4 (± 5.1)	0.56 (± 0.11)	5.50 (± 2.33)	9.58 (± 2.31)	0.52 (± 0.10)
St 3					
Annual mean	1.7 (± 0.2)	0.87 (± 0.17)	7.58 (± 1.19)	12.14 (± 6.43)	0.78 (± 0.30)
	SSP mg l^{-1}	Cl^- g l^{-1}	SO_4^{2-} g l^{-1}	K^+ mg l^{-1}	Si^{2+} mg l^{-1}
St 1					
Before connection	0.03 (± 0)	0.73 (± 0.53)	0.40 (± 0.50)	24.5 (± 2.2)	0.41 (± 0.15)
After connection	0.20 (± 0.03)	8.33 (± 2.47)	2.22 (± 0.67)	145.3 (± 19.1)	0.73 (± 0.11)
St 2					
Before connection	0.06 (± 0)	1.30 (± 0.38)	0.53 (± 0.07)	32.7 (± 5.5)	0.44 (± 0.19)
After connection	0.34 (± 0.09)	6.44 (± 1.49)	1.90 (± 0.54)	165.9 (± 31.8)	0.86 (± 0.05)
St 3					
Annual mean	0.11 (± 0.02)	0.40 (± 0.99)	0.23 (± 0.03)	32.4 (± 3.4)	1.36 (± 0.25)

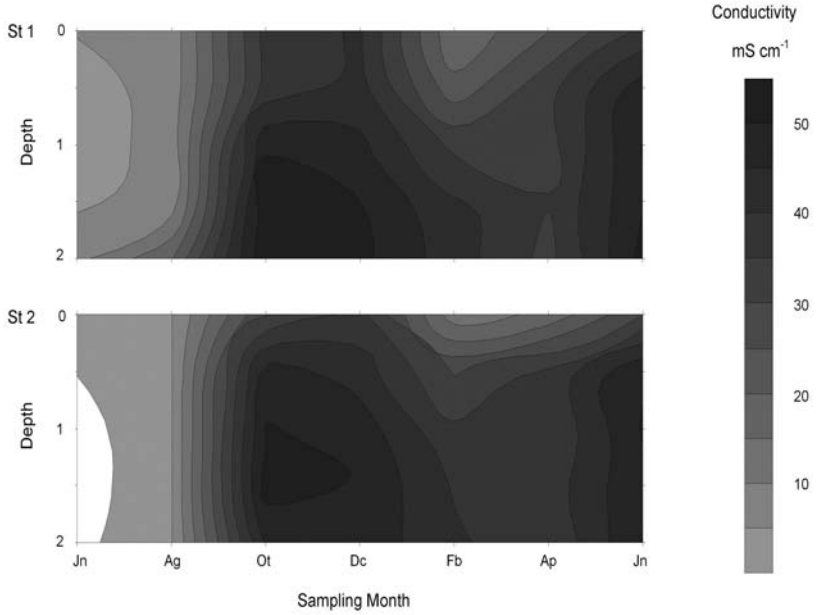

Figure 2. Depth conductivity profile (measured in mS cm^{-1}) for the new river mouth (stations 1 and 2) along the study period (June 2004-June 2005). *Perfil vertical de conductividad (medida en mS cm^{-1}) de la nueva desembocadura localidades 1 y 2) durante el período de estudio (Junio 2004-Junio 2005).*

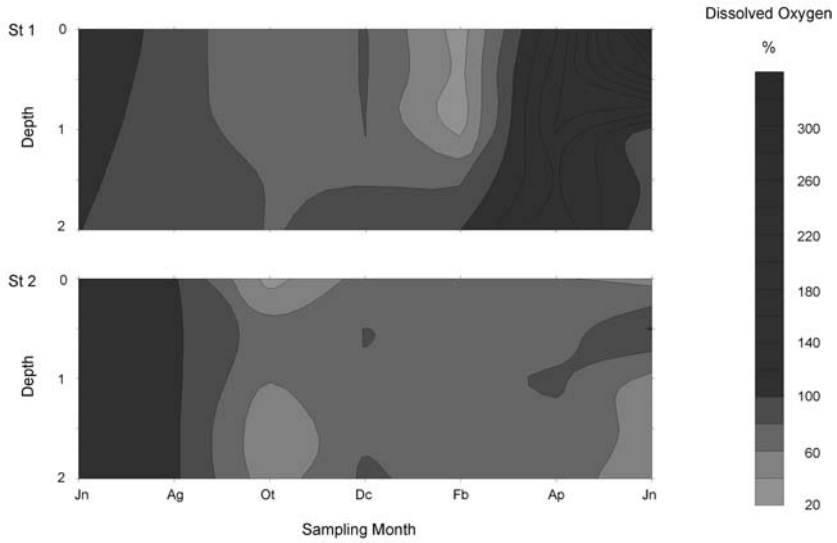

Figure 3. Depth oxygen profile (measured in %) for the new river mouth (stations 1 and 2) along the study period (June 2004-June 2005). *Perfil vertical de oxígeno (medido en %) de la nueva desembocadura (localidades 1 y 2) durante el período de estudio (Junio 2004-Junio 2005).*

Aquatic macroinvertebrates

A total of 39 macroinvertebrate taxa were recorded, of which 11 (28 %) were shared between the new mouth (stations 1 and 2) and the upstream river channel (station 3) before their connection, whereas only 2 (5 %) were shared after the connection. The connection of the new mouth with the river and the sea produced a drastic decrease in the densities of aquatic macroinvertebrates (from 1005 ± 393 to 101 ± 39 individuals per square metre in the sediment samples). According to the PRC analysis, the commun-

ities of the mouth resembled those of the river before the connection, whereas they became increasingly different afterwards (Fig. 4). The difference between the mouth and the riverine communities was highest at station 1, which was closest to the sea. Before the connection, both the littoral and the sediment communities of the new mouth were characterised by a dominance of chironomids (84 % and 73 % of total abundance, respectively) and other insects (9 and 21 % of total abundance, respectively) (Fig. 5). After the connection, oligochaetes (primarily Enchytraeidae) dominated the sediment (89 % of total abundance) and the littoral (97 % of total abundance), and no insects were recorded in the new mouth other than Ceratopogonidae (1 % of total abundance) and *Chironomus salinarius* (1 % of total abundance) in the multihabitat samples (Fig. 5). Although their abundances were low, certain brackish-water species (e.g., *Nereis diversicolor* and *Orchestia gammarellus*) and certain marine bivalve species (e.g., *Acanthocardia tuberculata* and *Mytilus galloprovincialis*) colonised and were recorded in the new mouth (Fig. 5).

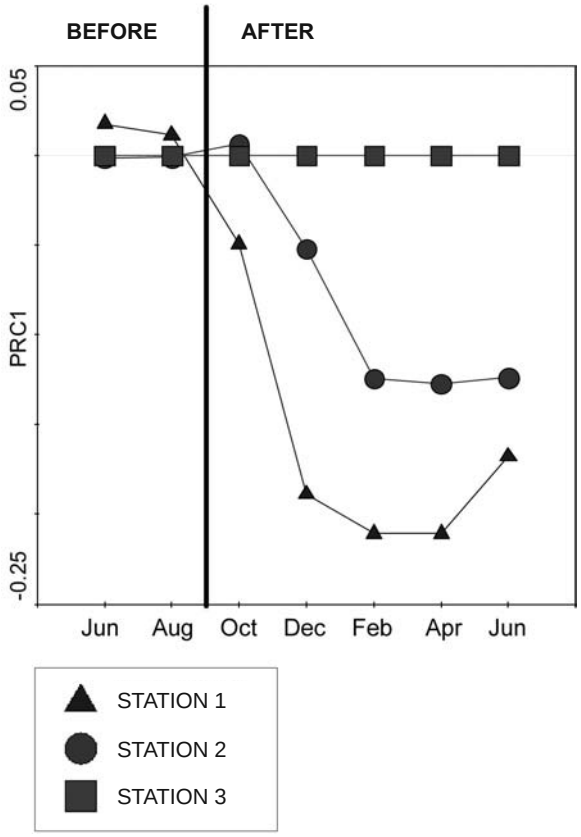

Figure 4. Principal response curve (PRC) showing the trajectories of the invertebrate community along time, which can be interpreted as the deviation in the new mouth community (stations 1 and 2) from the upstream (station 3). *Curvas de respuesta principales (PRC) mostrando las trayectorias de las comunidades de invertebrados a lo largo del tiempo. Las trayectorias pueden interpretarse como la desviación de las comunidades de invertebrados de la nueva desembocadura (localidades 1 y 2) respecto de la del río (localidad 3).*

DISCUSSION

Based on the physico-chemical data and the aquatic macroinvertebrate communities, two different periods could be distinguished in the present study: before and after the new river mouth was connected to the river and the sea.

Before connection

During this period, the function of the new river mouth was similar to that of a lagoon. The new mouth was disconnected from the river and the sea and exclusively fed by the superficial aquifer. Because the percentage of species shared with station 3, located approximately 1.8 km upstream from station 2, was very low, it is possible that the primary route of colonisation by aquatic macroinvertebrates during this period was the surrounding lagoons. The chironomids *Ablabesmyia monilis*, *Polypedilum nubifer* and *Tanypus punctipennis*, the dominant species in the sediment of the new mouth (stations 1 and 2), were not recorded at station 3, whereas they have been recorded at high densities in the adjacent lagoon of Cal Tet (Cañedo-Argüelles & Rieradevall, 2011) and in several water bodies within the deltaic plain (Cañedo-Argüelles & Rieradevall, 2009; Sànchez-Millaruelo *et al*., 2009). The dominance of these species at stations 1 and 2 during this period and their absence from station 3 could have been related to the presence of charophytes in the new river mouth (personal observation) because they have been reported

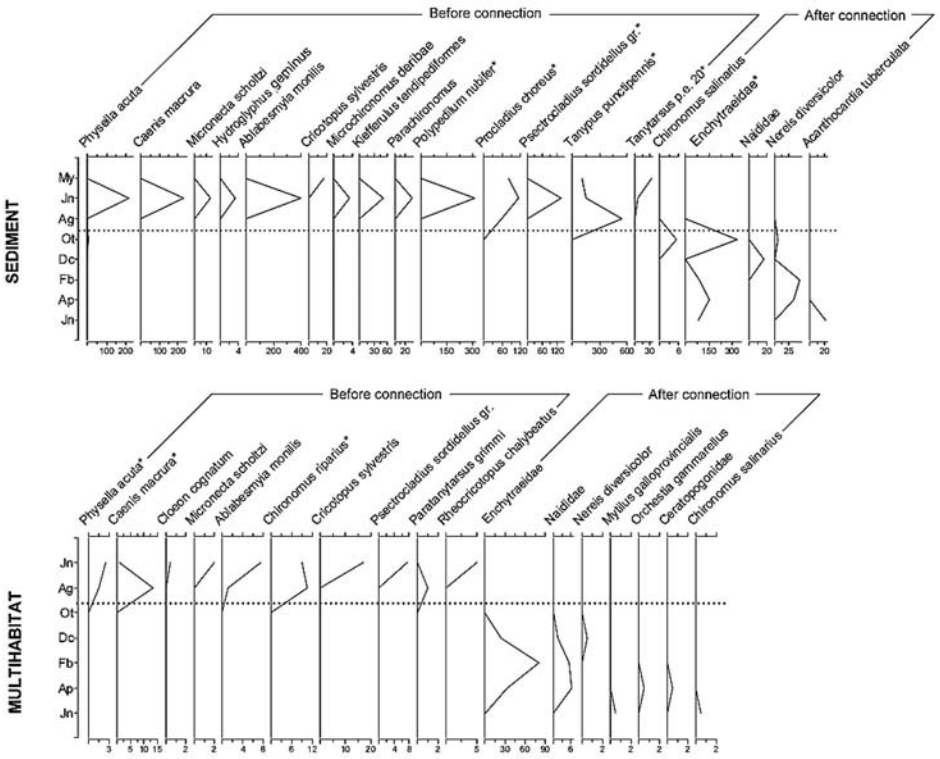

Figure 5. Macroinvertebrate abundances (individuals sample^{-1}) and densities (individuals m^{-2}), registered in the multihabitat and sediment samples respectively, collected in the new mouth (mean values of stations 1 and 2) along the study period (y axis). Taxa are grouped according to the most probable group (and after the connection of the new mouth to the river and to the sea) resulting from the IndVal analysis. The dashed line marks the moment of the opening (September 2004). * = taxa significantly associated to the group according to the IndVal analysis. *Abundancias (individuos muestra^{-1}) y densidades (individuos m^{-2}) de macroinvertebrados registradas en las muestras multi-hábitat y de sedimento, respectivamente, recolectadas en la nueva desembocadura (valores promedio para las localidades 1 y 2) durante el período de estudio (eje de las Y). Los taxones están agrupados según su grupo de pertenencia más probable (antes o después de la conexión de la desembocadura con el río y el mar) según los resultados del análisis IndVal. Las líneas discontinuas marcan el momento en el que se produjo la conexión de la nueva desembocadura (Septiembre del 2004). * = taxones asociados de manera significativa al grupo de acuerdo con el análisis IndVal.*

to be positively correlated with the presence of *Chara* (Armitage *et al*., 1995; Jeppesen *et al*., 1998; Brodersen *et al*., 2001; Cañedo-Argüelles & Rieradevall, 2011). Chironomidae represented most of the macroinvertebrate relative abundance in the new mouth during this period. This dominance was most likely related to the high dispersal abilities of this group (Bilton *et al*., 2001) and their high growth and reproduction rates (Armitage *et al*., 1995), which allow them to rapidly colonise new habitats (Barnes, 1983; Christman & Voshell, 1993; Velasco *et al*., 1993; Koskenniemi, 1994; Solimini *et al*., 2003; Cañedo-Argüelles & Rieradevall, 2011).

After connection

The sudden increase in conductivity from 4-6 mS cm^{-1} to 24-30 mS cm^{-1} caused substantial changes in the macroinvertebrate community of the new mouth after its connection to the river and the sea. A replacement of freshwater taxa by brackish-water and marine taxa is known to occur beyond 5 ‰ salinities (≈ 6.58 mS cm^{-1}) in coastal environments (Remane & Schlieper, 1971; Barnes, 1989; Jeppesen *et al*., 2007). The change from one community to the other was not instantaneous. Defaunation occurred after the connection. Three months later, oligochaetes

of the family Enchytraeidae had completely colonised the new mouth at high levels of abundance. The rapid colonisation by oligochaetes was most likely related to their high growth rates and their asexual reproduction, which allow their populations to increase rapidly *(Tachet et al*., 2000; Verdonschot, 2006). Oligochaetes and polychaetes (which colonised the new mouth at the same time) are known to be opportunistic taxa and have been shown to colonise new habitats rapidly in defaunation experiments (Zajac & Whitlatch, 1982; Lu & Wu, 2000) and after massive macroinvertebrate mortalities during organic enrichment episodes or dystrophic crises (Pearson & Rosenberg, 1978; Santos & Simon, 1980; Warwick & Clarke, 1994; Reizopoulou *et al*., 1996; Lardicci *et al*., 1997). The dominance of these opportunistic taxa and the low richness and diversity of taxa recorded might have been linked to the inability of riverine macroinvertebrates to colonise the new mouth due to the restrictions imposed by high conductivities (Williams & Hamm, 2002; Kefford *et al*., 2007).

Deltas are riverine-dominated ecosystems (Day *et al*., 1997) in which sediment and water outflow occur in the river mouth area (Zaldívar *et al*., 2008). These areas show a longitudinal conductivity and productivity gradient regulated by the mixing of river and seawaters *(Levin et al*., 2001; Boyes & Elliott, 2006), which create a transition zone where estuarine (≈ brackish-water) fauna become established (Ysebaert *et al*., 1993; Rundle *et al*., 1998; Cognetti & Maltagliati, 2000; Williams & Hamm, 2002; Teske & Wooldridge, 2003). In the case of the Llobregat Delta estuary, previous studies from 1982 (Prat *et al*., 1983) reported conductivities ranging from 2 to 5 mS cm^{-1} and eutrophic waters a few hundred metres landwards. This information suggests a strong riverine influence along the estuary, as could be expected in a Mediterranean estuary with low tidal influence. According to the present study, the new mouth showed very different conditions. Estuarine conditions are created by the balanced mixture of freshwater coming from the river and seawater penetrating from the coast. The water fluxes in the new mouth were unbalanced due to the human intervention. The river flow has been substantially reduced by numerous dams and water diversions along the river catchment (Lloret, 2004). As a result, very low freshwater discharges enter the new river mouth. At the same time, seawater penetrated the mouth up to the connection point with the river (approximately 3.9 km upstream). This outcome was a result of the design of the new mouth. As previously mentioned, the new mouth is 250 m wide and has a mean depth of 2 m (contrasting with the 0.4 m of depth in the upper river section). This geometry produced an extensive slope at the connection point between the river and the new mouth and allowed a large-scale penetration of seawater and an accompanying salinisation of the new mouth. Consequently, a drastic change occurred from a diverse freshwater macroinvertebrate community to an impoverished community that included marine species such as *Acanthocardia tuberculata* and *Mytilus galloprovincialis*. It can be stated that after its connection with the river and the sea, the new mouth became an arm of the sea. The lower oxygen concentration recorded at station 1 relative to station 2 and the shift from the dominance of the oxidized to the reduced forms of nitrogen represented the development of a confinement gradient, typical of coastal waters with low water renewal (Guelorget & Perthuisot, 1992). The areas with lower water renewal have a higher oxygen demand due to the accumulation of organic material that must be degraded, and hypoxia is a frequent phenomenon (Tett *et al*., 2003; Newton & Mudge, 2005; Mudge *et al*., 2007; Cañedo-Argüelles *et al*., in press). Therefore, several management actions need to be considered if an estuarine ecosystem is to be established rather than a marine ecosystem. It is probable that the most desirable option would be to re-establish river flow. This option would mean that more freshwater entered the system, but sediments would also be transported to fill up the new mouth and reduce the penetration of seawater. The management goal should be to use the energy of natural pulses to guarantee the sustainability of the estuarine and the deltaic ecosystem (Day *et al*., 1997). However, given the location of crucial infrastructure near the margins

of the river mouth (i.e., the airport and the port), the design and management objectives have been chosen to avoid flooding episodes. To assess how far the Llobregat mouth is from natural conditions, further research during wet years and/or flooding episodes is necessary to understand the dynamics of the new mouth and to analyse the river's ability to break the resistance of the sea and create a strong salinity gradient. It is probable that such a gradient would produce major changes in the macroinvertebrate communities.

ACKNOWLEDGEMENTS

This project was financed by the Generalitat de Catalunya. We thank the Consorci del Delta del Llobregat and Taller d'Enginyeria Ambiental for providing logistical support. In addition, we thank Roser Farrés for her assistance with field work. Taxonomic advice was provided by Dr. J. Alba-Tercedor for Ephemeroptera and Dr. D. Martín for Polychaeta. Several UB undergraduate biology students also helped in the laboratory.

REFERENCES

ALONSO, M., CAMBRA, J., GIL, M., GONZÁLEZ, G., JUAME, D., PINO, J., REAL, M., RICO, E., SALÓ, E., VILASECA & J. 2001. *Estudio del impacto sobre los organismos aquáticos de las obras de ampliación del aeropuerto de Barcelona*. AENA, Barcelona. 194 pp.

ARMITAGE, P. D., CRANSTON, P. S. & L. C. V. PINDER. 1995. *The Chironomidae: Biology and Ecology of Non-biting Midges*. Chapman & Hall: London. 572 pp.

BARNES, L. E. 1983. The colonization of ball-clay ponds by macroinvertebrates and macrophytes. *Freshwater Biology,* 13: 561–578.

BARNES, R. 1995. *Brackish-Water Fauna of Northwestern Europe*. Cambridge University Press: Cambridge. 287 pp.

BARNES, R. S. K. 1989. What, if anything, is a brackish-water fauna? *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 80: 235–240.

BASSET, A., N. GALUPPO & L. SABETTA. 2006. Environmental heterogeneity and benthic macroinvertebrate guilds in italian lagoons. *Transitional Waters Bulletin,* 1: 48–63.

BATZER, D., R. RADER & S. WISSINGER. 1999. *Invertebrates in Freshwater Wetlands of North America: Ecology and Management*. John Wiley and Sons. 1100 pp.

BILTON, D. T., J. R. FREELAND & B. OKAMURA. 2001. Dispersal in Freshwater Invertebrates. *Annual Review of Ecology and Systematics,* 32: 159–181.

BONADA, N., N. PRAT, V. H. RESH & B. STATZNER. 2006. Developments in aquatic insect biomonitoring: a comparative analysis of recent approaches. *Annual Review of Entomology*, 51: 495–523.

BOYES, S. & M. ELLIOTT. 2006. Organic matter and nutrient inputs in the Humber Estuary, England. *Marine Pollution Bulletin*, 53: 136–143.

BRODERSEN, K. P., B. V. ODGAARD, O. VESTERGAARD & J. ANDERSON. 2001. Chironomid stratigraphy in the shallow and eutrophic lake Søbygaard, Denmark: chironomid-macrophyte cooccurrence. *Freshwater Biology*, 46: 253–267.

CAÑEDO-ARGÜELLES, M. & M. RIERADEVALL. 2009. Quantification of environment-driven changes in epiphytic macroinvertebrate communities associated to *Phragmites australis*. *Journal of Limnology,* 68: 229–241.

CAÑEDO-ARGÜELLES, M. & M. RIERADEVALL. 2011. Initial succession of the macroinvertebrate community in a shallow lake: response to changes in the habitat condition. *Limnologica,* 41: 363–370.

CAÑEDO-ARGÜELLES, M., M. RIERADEVALL, R. FARRÉS-CORELL & A. NEWTON. (In press). Annual characterisation of four Mediterranean coastal lagoons subjected to intense human activity. *Estuarine, Coastal and Shelf Science*.

COGNETTI, G. & F. MALTAGLIATI. 2000. Biodiversity and adaptive mechanisms in brackish water fauna. *Marine Pollution Bulletin,* 40: 7–14.

CROSSLAND, C., H. KREMER, H. LINDEBOOM, J. CROSSLAND & M. LE TISSIER. 2005. *Coastal Fluxes in the Anthropocene*. Springer-Verlag: New York. 232 pp.

CHRISTMAN, V. D. & J. R. VOSHELL. 1993. Changes in the benthic macroinvertebrate community in two years of colonization of new experimental ponds. *Internationale Revue der Gesamtem Hydrobiologie,* 78: 481–491.

DAY, J. W., J. F. MARTIN, L. CARDOCH & P. H. TEMPLET. 1997. System functioning as a basis for sustainable management of deltaic ecosystems. *Coastal Management,* 25: 115–153.

DUFRÊNE, M. & P. LEGENDRE. 1997. Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach. *Ecological Monographs,* 67: 345–366.

EUROPEAN COMMISSION. 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. *Official Journal of the European Communities,* 43: 1–72.

GOLDEN SOFTWARE, I.t.S., Golden, Colorado 80401-1866, U.S.A., *SURFER 8.0*.

GREENBERG, A. E., L. S. CLESCERI & A. D. EATON. 1999. *Standard methods for the examination of water and wastewater,* 20 ed. American Public Health Association. 1325 pp.

GUELORGET, O. & J. P. PERTHUISOT. 1992. Paralic ecosystems. Biological organization and functioning. *Vie et Milieu,* 42: 215–251.

JACKSON, J. K. & L. FÜREDER. 2006. Long-term studies of freshwater macroinvertebrates: a review of the frequency, duration and ecological significance. *Freshwater Biology,* 51: 591–603.

JEPPESEN, E., M. SØNDERGAARD, M. SØNDERGAARD & K. CHRISTOFFERSEN. 1998. *The structuring role of submerged macrophytes in lakes*. Springer: New York. 471 pp.

JEPPESEN, E., M. SØNDERGARD, A. R. PEDERSEN, K. JÜRGENS, A. STRZELCZAK, T. L. LAURIDSEN & L. S. JOHANSSON. 2007. Salinity induced regime shift in shallow brackish lagoons. *Ecosystems,* 10: 47–57.

KEFFORD, B., D. NUGEGODA, L. ZALIZNIAK, E. FIELDS & K. HASSELL. 2007. The salinity tolerance of freshwater macroinvertebrate eggs and hatchlings in comparison to their older life-stages: a diversity of responses. *Aquatic Ecology,* 41: 335–348.

KOSKENNIEMI, E. 1994. Colonization, succession and environmental conditions of the macrozoobenthos in a regulated, polyhumic reservoir, western Finland. *Internationale Revue der Gesamtem Hydrobiologie,* 79: 521–555.

LARDICCI, C., F. ROSSI & A. CASTELLI. 1997. Analysis of macrozoobenthic community structure after severe dystrophic crises in a Mediterranean coastal lagoon. *Marine Pollution Bulletin,* 34: 536–547.

LEVIN, L. A., D. F. BOESCH, A. COVICH, C. DAHM, C. ERSÉUS, K. C. EWEL, R. T. KNEIB, A. MOLDENKE, M. A. PALMER, P. SNELGROVE, D. STRAYER & J. M. WESLAWSKI. 2001. The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems,* 4: 430–451.

LU, L., & R. S. S. WU. 2000. An experimental study on recolonization and succession of marine macrobenthos in defaunated sediment. *Marine Biology,* 136: 291–302.

LLORET, R. 2004. La qualitat de l'aigua del riu Llobregat. Un factor limitant del passat, un element clau per al futur. In: *El Baix Llobregat: història i actualitat ambiental d'un riu*. N. Prat Fornells, E. Tello Aragay (Eds.): 94–141. Centre d'Estudis Comarcals del Baix Llobregat.

MCCUNE, B. & J. MEFFORD. 1999. *PCORD: Multivariate Analysis of Ecological Data,* 4.20 ed. MjM software, Oregon.

MERRITT, R. W. & K. W. CUMMINS. 1996. *An introduction to the aquatic insects of North America*. Kendall/Hunt Publishing: Iowa. 862 pp.

MILLET, X. & N. PRAT. 1984. Las comunidades de macroinvertebrados a lo largo del rio Llobregat. *Limnetica,* 1: 222–223.

MUDGE, S. M., J. D. ICELY & A. NEWTON. 2007. Oxygen depletion in relation to water residence times. *Journal of Environmental Monitoring,* 9: 1194–1198.

NEWTON, A. & S. M. MUDGE. 2005. Lagoon-sea exchanges, nutrient dynamics and water quality management of the Ria Formosa (Portugal). *Estuarine, Coastal and Shelf Science,* 62: 405–414.

PEARSON, T. H. & R. ROSENBERG. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology Annual Review,* 16: 229–311.

PRAT, N., M. A. PUIG & G. GONZÁLEZ. 1983. *Predicció i control de la qualitat de les aigües dels rius Besós i Lobregat. II. El poblament faunístic i la seva relació qualitat-aigües*. Diputació de Barcelona. Col. Monografies, Barcelona. 164 pp.

PRAT, N. & M. RIERADEVALL. 2006. 25-years of biomonitoring in two mediterranean streams (Llobregat and Besòs basins, NE Spain). *Limnetica,* 25: 541–550.

REIZOPOULOU, S., M. THESSALOU-LEGAKI & A. NICOLAIDOU. 1996. Assessment of disturbance in Mediterranean lagoons: an evaluation of methods. *Marine Biology,* 125: 189–197.

REMANE, A. & C. SCHLIEPER. 1971. *Biology of brackish water*. Wiley Interscience: New York. 372 pp.

RUNDLE, S. D., M. J. ATTRILL & A. ARSHAD. 1998. Seasonality in macroinvertebrate community composition across a neglected ecological boundary, the freshwater-estuarine transition zone. *Aquatic Ecology,* 32: 211–216.

SÁNCHEZ-JUNY, M. & J. DOLZ RIPOLLÉS. 2004. El riu, un camí dáigua. In: *El Baix Llobregat: història i actualitat ambiental d'un riu.* N. Prat Fornells, E. Tello Aragay (Eds.): 32–47. Centre d'Estudis Comarcals del Baix Llobregat.

SÀNCHEZ-MILLARUELO, N., M. CAÑEDO-ARGÜELLES & M. RIERADEVALL. 2009. *Avaluació de la biodiversitat i l'estat ecològic de les llacunes i canals del Delta del Llobregat mitjançant l'ús de les exúvies de quironòmids com a bioindicadors*, 5enes Jornades d'Estudi del Patrimoni del Baix Llobregat: Patrimoni en un entorn metropolità. Consorci del Prat, El Prat, Barcelona: 83–88.

SANTOS, S. L. & J. L. SIMON. 1980. Response of soft-bottom benthos to annual catastrophic disturbance in a South Florida Estuary. *Marine Ecology Progress Series,* 3: 347–355.

SOLIMINI, A. G., A. RUGGIERO, V. BERNARDINI & G. CARCHINI. 2003. Temporal pattern of macroinvertebrate diversity and production in a new man made shallow lake. *Hydrobiologia,* 506–509: 373–379.

TACHET, H., P. RICHOUX, M. OURNAUD & P. USSEGLIO-POLATERA. 2000. *Invertébrés d'eau douce: Systématique, biologie, écologie*. CNRS Editions: Paris. 587 pp.

TER BRAAK, C. & P. ŠMILAUER. 2002. *Canoco for Windows, version 4.5.,* 4.5. ed, Wageningen, The Netherlands.

TESKE, P. R. & T. H. WOOLDRIDGE. 2003. What limits the distribution of subtidal macrobenthos in permanently open and temporarily open/closed South African estuaries? Salinity vs. sediment particle size. *Estuarine, Coastal and Shelf Science,* 57: 225–238.

TETT, P., L. GILPIN, H. SVENDSEN, C. P. ERLANDSSON, U. LARSSON, S. KRATZER, E. FOUILLAND, C. JANZEN, J. Y. LEE, C. GRENZ, A. NEWTON, J. G. FERREIRA, T. FERNANDES & S. SCORY. 2003. Eutrophication and some European waters of restricted exchange. *Continental Shelf Research,* 23: 1635–1671.

VAN DEN BRINK, P. & C. TER BRAAK. 1999. Principal response curves: analysis of timedependent multivariate responses of a biological community to stress. *Environmental Toxicology and Chemistry,* 18: 138–148.

VELASCO, J., A. MILLÁN, & L. RAMÍREZ-DÍAZ. 1993. Colonización y sucesión de nuevos medios acuáticos II. Variación temporal de la composición y estructura de las comunidades de insectos. *Limnetica,* 9: 87–98.

VERDONSCHOT, P. F. M. 2006. Beyond masses and blooms: the indicative value of oligochaetes. *Hydrobiologia,* 564: 127–142.

WARWICK, R. M. & K. R. CLARKE. 1994. Relearning the ABC: taxonomic changes and abundance/biomass relationships in disturbed benthic communities. *Marine Biology,* 118: 739–744.

WILLIAMS, D. D. & T. HAMM. 2002. Insect community organisation in estuaries: the role of the physical environment. *Ecography,* 25: 372–384.

YSEBAERT, T., P. MEIRE, D. MAES & J. BUIJS. 1993. The benthic macrofauna along the estuarine gradient of the Schelde Estuary. *Netherlands Journal of Aquatic Ecology,* 27: 327–341.

ZAJAC, R. N. & R. B. WHITLATCH. 1982. Responses of estuarine fauna to disturbance. I. Spatial and temporal variation of initial recolonization. *Marine Ecology Progress Series,* 10: 1–14.

ZALDÍVAR, J. M., A. C. CARDOSO, P. VIAROLI, A. NEWTON, R. DE WIT, C. IBAÑEZ, S. REIZOPOULOU, F. SOMMA, A. RAZINKOVAS, A. BASSET, M. HOLMER & N. MURRAY. 2008. Eutrophication in transitional waters: an overview. *Transitional Waters Monographs,* 1: 11–78.

Limnetica, 31 (2): 273-288 (2012)
 ISSN: 0213-8409

References data on the growth and population parameters of brown trout in siliceous rivers of Galicia (NW Spain)

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Received: 15/3/12 Accepted: 22/6/12

ABSTRACT

References data on the growth and population parameters of brown trout in siliceous rivers of Galicia (NW Spain)

Brown trout is an important angling species worldwide, and its morphology, population structure and genetics can be highly variable from one location to another. In this study, we provide data for the establishment of reference range values for several population and growth parameters of brown trout in the Cantabrian-Atlantic siliceous rivers of Galicia (NW Spain). Additionally, this study tests the hypothesis that the population and growth parameters differ among sections of rivers with different exploitation statuses (unexploited, exploited-regulated and exploited-open sections). Our study revealed that such population parameters as biomass and production were higher in unexploited sections, but the differences in growth among the sections with different angling regulations were not consistent. The findings of this study are discussed in light of the present knowledge on the status of trout fisheries, as it is essential for the development of management plans. Additional studies are needed to clarify whether the differences in growth can be correlated to the angling regulations.

Key words: Population parameters, growth, reference categories, angling regulations, Iberian Peninsula, Water Framework Directive.

RESUMEN

Datos de referencia de crecimiento y parámetros poblacionales de trucha común en ríos silíceos de Galicia (NO España)

La trucha común es una especie muy apreciada por los pescadores deportivos en todo el mundo, y su morfología, estructura poblacional y características genéticas pueden variar considerablemente entre áreas geográficas próximas. En este estudio proporcionamos datos para el establecimiento de categorías de referencia de varios parámetros poblacionales y de crecimiento de la trucha común en ríos silíceos Cantábrico-Atlánticos de Galicia (NO España). Además, con la realización de este estudio se pretende verificar la hipótesis de que los parámetros poblacionales y el crecimiento pueden variar entre tramos de ríos con diferente tipo de regulación de pesca deportiva (tramos vedados o inexplotados, tramos de pesca acotados y tramos de pesca libre). Así, nuestro estudio reveló que algunos parámetros poblacionales como la biomasa y la producción fueron más elevados en los tramos vedados, pero las diferencias en el crecimiento entre tramos con diferente regulación de pesca deportiva no fueron consistentes. Los resultados de este trabajo se discuten teniendo en cuenta el conocimiento actual sobre el estado de las poblaciones de trucha común, pues son esenciales para el desarrollo de planes de gestión. No obstante, se requieren de más estudios para aclarar si las diferencias en crecimiento se pueden relacionar con el tipo de regulación de pesca deportiva.

Palabras clave: *Parámetros poblacionales, crecimiento, categorías de referencia, regulación de pesca deportiva, Península Ibérica, Directiva Marco del Agua.*

INTRODUCTION

Limnological studies of the Galician freshwater basins (NW Spain) have shown the homogeneity of the physicochemical characteristics of its watercourses (Membiela *et al*., 1991): the freshwaters in Galicia are generally acid and very soft (Martínez-Ansemil & Membiela, 1992) watersheds draining granite and schist (Membiela *et al*., 1991; Martínez-Ansemil & Membiela, 1992). Moreover, in terms of its freshwater fish biogeography, Galicia has been considered a region that is independent from the rest of the Iberian Peninsula (e.g., Hernando & Soriguer, 1992; Filipe *et al*., 2009). Indeed, as a consequence of the hierarchical characterisation of Spanish rivers for their classification in accordance with the Water Framework Directive of the European Union by González del Tánago & García de Jalón (2006), most of the Galician watercourses have been recently included in a category called "Cantabrian-Atlantic siliceous rivers" by the Spanish Hydrological Plan.

Brown trout (*Salmo trutta* Linnaeus, 1758) is an important angling species worldwide. The fish has an outstanding socio-economic importance, both in commercial and sport fisheries, and brown trout is frequently used as a tourist attraction (Aas *et al*., 2000; Butler *et al*., 2009). Although the management of the wild stocks is the responsibility of the regional governments in Spain, different researchers have proposed some management guidelines to improve the conservation status of the brown trout populations (e.g., Braña *et al*., 1992, 2004; Almodóvar & Nicola, 1998; Alonso-González & García de Jalón, 2001), with the growth and population parameters being the variables usually employed in fishery assessments (e.g., Almodóvar & Nicola, 2004; Oscoz *et al*., 2005). These parameters are well known for the brown trout populations in different regions of Spain and can be highly variable (e.g., García de Jalón *et al*., 1986; Lobón-Cerviá *et al*., 1986; Nicola & Almodóvar, 2004; Parra *et al*., 2009; Lobón-Cerviá, 2010; Alonso *et al*., 2011). Contrastingly, the growth and population parameters of the brown trout populations in the Cantabrian-Atlantic siliceous rivers of Galicia remain poorly investigated, and the limited information available comes mainly from Garcia de Jalón *et al*. (1990) and Hervella & Caballero (1999), thus impeding the comparison of parameters between similar populations or river types.

Density categories have been established for salmonid populations in North America (Joyce *et al*., 1990; Stanfield *et al*., 2006) and Europe (Niemelä, 2004), whereas several authors have standardised the growth parameters of the brown trout populations in some regions of Europe (Kennedy & Fitzmaurice, 1971; Pedicillo *et al*., 2010). Thus, a wider knowledge on the reference categories for the growth and population parameters would improve management plans, as the establishment of these categories for fish populations is essential before meaningful comparisons can be made among rivers (Klemetsen *et al*., 2003). Hence, the aim of this work is the establishment of reference categories for the growth and population parameters of brown trout in the Cantabrian-Atlantic siliceous rivers of Galicia (NW Spain). Additionally, we discuss the effects of angling exploitation on these parameters.

MATERIAL AND METHODS

Study area

For the purpose of this study five annual survey campaigns were conducted in the summer season (from June to September) between 2007 and 2011. A total of 32 siliceous rivers of Galicia (NW Spain) were studied. As shown in Appendix 1 and figure 1, the majority of the rivers were sampled once, but four of the sampling stations for three rivers were sampled twice (Rivers Tamuxe, Hospital and Deva). Thus, the selection of the sampling stations was with the intention of providing an ample spectrum of the temporal and spatial variations in the environmental conditions.

The sampling sites included exploited and unexploited reaches, with three different angling regulations: unexploited sections (fishing activities are forbidden); exploited-regulated sections (sections with a limited in the number of anglers

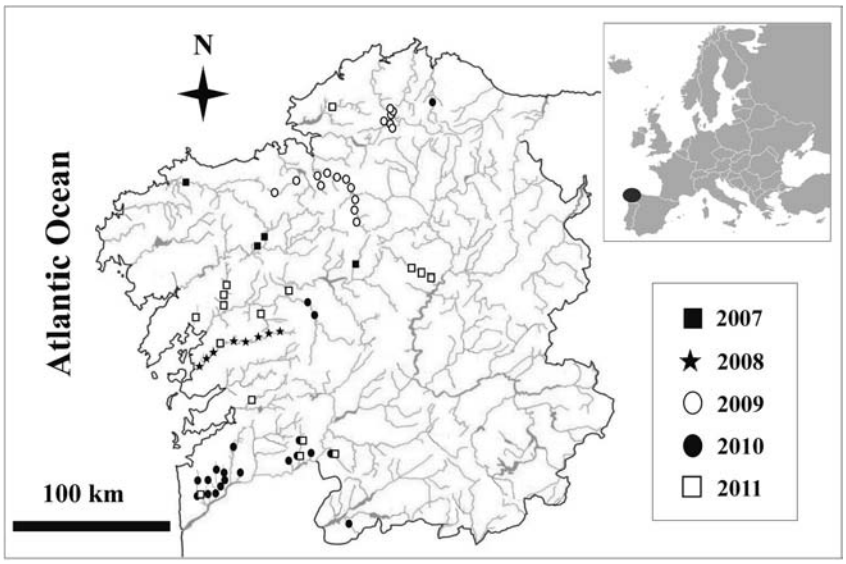

Figure 1. Location of the sampling sites. *Localización de las estaciones de muestreo.*

per day; anglers pay for a special permit for fishing) and exploited-open sections (free sections with no limitation in the number of anglers per day). Detailed information on the sampling sites is provided in Appendix 1 and figure 1.

Fish collection

The protocols used in this study conform to the ethical laws of the country and have been reviewed by the ethics committee of the University of Santiago de Compostela and the regional government (Xunta de Galicia). Fishes were collected using pulsed D.C. backpack electrofishing equipment (Hans Grassl GmbH, ELT60II) and anaesthetised with benzocaine (0.3 ml l^{-1}). The fishes were measured to the nearest 1 mm and weighed to the nearest 0.01 g. Scales were collected only from individuals > 10 cm. The ages of the fish were estimated by scale examination and using the Petersen's length-frequency method (Bagenal & Tesch, 1978). After manipulation, all of the fishes were returned to the river.

Growth and population parameters

Individuals of age-0+ and age-1+ were found in all of the sampling sites, with the exception of four rivers in 2010: River Tripes (only 0+ individuals) and Rivers Deva, Hospital and Tamuxe (only 1+ individuals). Consequently, only the density and biomass were estimated in these rivers. Age-2+ and age-3+ individuals were also present in a high number of populations (in 62 and 34 populations, respectively), but age-4+ individuals were only found in 12 populations. Older specimens were found (one 5+ trout in the River Barcés, one 6+ trout in the River Mandeo and one 7+ trout in the River Barcés), but it was impossible to calculate the specific growth rate (G) between these age classes. The condition factor (CF) for each fish was calculated according to Granado-Lorencio (1996) using the formula $CF = 100W/L^3$, where W is the wet weight (g) and L is the fork length (cm).

Growth was estimated using several methods. First, the Von Bertalanffy equation (Von Bertalanffy, 1938) assumes that a fish grows toward a theoretical maximum length or weight and that the closer the length is to the maximum, the slower is the rate of the change in size. Thus, the growth parameters L_∞ and k were calculated using the FISAT II (version 1.2.1) software package (Gayanilo *et al.*, 2005). Second, growth was measured as the specific growth rate (G) in body weight per year, as follows:

($G = (\ln W_2 - \ln W_1)/(t_2 - t_1)$), where W_1 and W_2 are the mean body weight at times t_1 and t_2 (Jensen *et al*., 1997). Third, because the comparison of growth among different organisms is often complex, we used the growth performance phi-prime index (Moura *et al*., 2009). Thus, according to Pedicillo *et al*. (2010), the index of the growth performance phi-prime Φ' was calculated by means of the following equation of Pauly & Munro (1984): $\Phi' = \log 10(k) + 2 \log 10(L_\infty)$, where k and L_∞ are the Von Bertalanffy growth parameters. Fourth, the weight-length relationship was calculated using the equation $W = aL^b$, where W is the total weight in g and L the total length in cm, with a being a coefficient related to the body form and b an exponent indicating isometric growth when equal to 3. The parameters a and b were estimated by the linear regression of the transformed equation: $\log W = \log a + b \log L$. The statistical significance level of r^2 was estimated, and the b-value for *S. trutta* was determined to verify whether the growth was different from the isometric ($b = 3$). When the value of b is other than 3, the weight increase is allometric (positive allometry if $b > 3$, negative allometry if $b < 3$) (Ricker, 1975).

The estimated density of each age class was calculated using the Zippin multiple-pass depletion method (Zippin, 1958; Zamora *et al*., 2009). The biomass was calculated using the mean weight per age class and the density of each age class. The total density and biomass were calculated as the sum of each age class density and biomass, respectively. According to García de Jalón *et al*. (1993), brown trout juveniles include 0+ and 1+ cohorts, and adults include individuals ≥ 2+. Hence, in this work, the density and biomass are reported for each age class, juveniles, adults and for the total of all of the individuals.

The annual production was estimated as the product of the specific growth rate (G) and biomass (B) using algebraic or graphic techniques, as outlined by Allen (1971). From the calculated estimates of total biomass and annual production, we calculated the turnover ratio (P/B) as the ratio between the production and biomass for the entire fish community.

The specific survival rate (S) for each age class was calculated using the formula $S = N_{t+1}/N_t$, where N_{t+1} and N_t are the number of individuals between consecutive age classes (t). In this work, S was calculated with the values of each age class and was presented as the mean value by sampling site. A graphical representation was used to determine the instantaneous mortality rate (Z). Thus, following Cowx & Frear (2004), we used the linear relationship between the natural logarithm of the number of fishes in each age class ($\ln N_t$) and age (t) to determine Z according to $\ln N_t = \ln N_0 - Z_t$.

Establishment of reference categories

To establish the reference categories for the growth and population parameters in the brown trout populations of the Galician siliceous rivers, all of the variables studied in this work (e.g., density, biomass) were collated and separated by percentiles following Pedicillo *et al*. (2010). Thus, five categories were established: 1) Very poor – when the value of the variable is below the 10th percentile; 2) Poor – when the value of the variable is between the 10th and the 30th percentile; 3) Normal – when the value of the variable is between the 30th and the 70th percentile; 4) High – when the value of the variable is between the 70th and the 90th percentile and 5) Very high – when the value of the variable exceeds the 90th percentile. References categories for the density and biomass of ages 5+, 6+ and 7+ were not calculated because only one individual was obtained for each age class (see above).

Statistical analysis

The statistical analyses were conducted using the programme PASW Statistics 18. The normality of the distribution and homogeneity of the variances were tested using Shapiro-Wilk and Levene's tests, respectively. Kruskal-Wallis tests for non-normal data were used to detect differences among the angling-regulation sections, and the Mann–Whitney U test was used for comparisons *a posteriori*. Additionally, the b-value of the weight–length relationship for each angling-

Table 1. Statistics and reference categories of growth parameters. The *CF* (condition factor), L_∞ and *k* (growth parameters calculated using FISAT II software package), specific growth rate (*G*), index of growth performance phi-prime (Φ′) and *b*-values of the weight-length relationship. *Calculated for one sampling site. Standard error (SE), minimum (Min) and maximum (Max). *Estadísticos y categorías de referencia de los parámetros de crecimiento.* CF *(factor de condición),* L_∞ *y* k *(parámetros de crecimiento calculados usando el software FISAT II), tasa de crecimiento específica (*G*), índice de crecimiento estándar phi prima (Φ′) y* b*-valores de la relación peso-longitud. *Calculados para una estación de muestreo. Error estándar (SE), mínimo (Min) y máximo (Max).*

	Statistics				Reference categories				
	Mean	SE	Min	Max	Very poor	Poor	Normal	High	Very high
CF	1.19	0.007	1.06	1.32	<1.11	1.11–1.16	1.16–1.23	1.23–1.27	> 1.27
k (g year^{-1})	0.21	0.011	0.05	0.41	<0.1	0.1–0.14	0.14–0.27	0.27–0.32	> 0.32
L∞ (cm)	48.15	1.73	29.15	116	<34.42	34.42–41.19	41.19–50.86	50.86–63.38	> 63.38
G_{0+-1+} (g year^{-1})	2.17	0.053	0.97	3.32	<1.73	1.73–1.94	1.94–2.30	2.30–2.83	> 2.83
G_{1+-2+} (g year^{-1})	1.06	0.037	0.64	1.82	<0.72	0.72–0.88	0.88–1.15	1.15–1.49	> 1.49
G_{2+-3+} (g year^{-1})	0.77	0.043	0.36	1.53	<0.48	0.48–0.63	0.63–0.84	0.84–1.09	> 1.09
G_{3+-4+} (g year^{-1})	0.69	0.085	0.36	1.16	<0.36	0.36–0.46	0.46–0.86	0.86–1.14	> 1.14
G_{4+-5+} (g year^{-1})*	0.74	—	—	—	—	—	—	—	—
Mean *G*(g year^{-1})	1.49	0.048	0.95	2.46	<1.10	1.10–1.23	1.23–1.58	1.58–2.12	> 2.12
Φ′	2.61	0.193	2.27	2.94	<2.41	2.41–2.49	2.49–2.72	2.72–2.81	> 2.81
b-values	3.02	0.01	2.83	3.21	<2.90	2.90–2.98	2.98–3.07	3.07–3.12	> 3.12

regulation section was tested using the t-test to verify whether it was significantly different from the isometric ($b = 3$). All of these tests were considered statistically significant at a p level < 0.05.

RESULTS

Growth and population parameters

In the present study, the range of condition factors was 1.06-1.32. We propose a normal category for the Galician populations, with values between 1.16 and 1.23 (Table 1). Differences among the angling regulation types were not significant (Table 2). The mean fork length of each age class varied: 0+ years, 2.3-11 cm; 1+ years, 8.2-21.6 cm; 2+ years, 14.1-26.5 cm; 3+ years 19-40.5 cm and 4+ years, 27-49 cm. Table 3 shows the descriptive statistics of the biometric measurements (size and weight) of all of the age class.

The growth parameters L_∞ and *k* of the Von Bertalanffy equation for the 66 populations showed an ample range of values: L_∞ varied between 29.15 cm and 116 cm, and *k* varied between 0.05 and 0.41 g year^{-1} (Table 1). The results for the mean specific growth rate (*G*) confirm the wide range of data (Table 1). Figure 2 shows the evolution of *G* in the brown trout populations by age class, being higher in young individuals and decreasing with age. The index of the growth

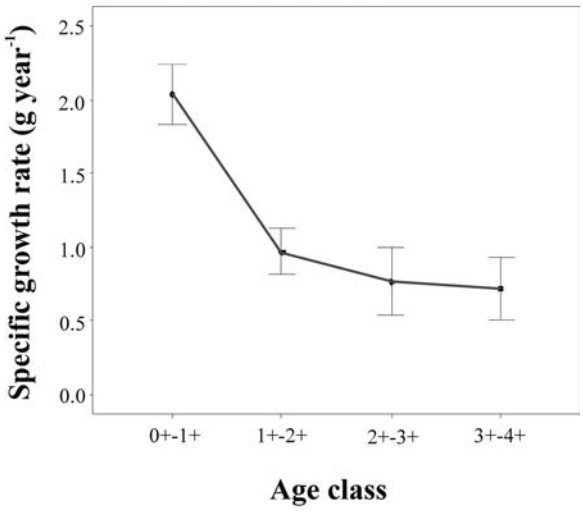

Figure 2. Specific growth rate (g year^{-1}) in the brown trout populations of the Cantabrian-Atlantic siliceous rivers of Galicia by age class. Error bars represent 95 % confidence intervals. *Tasa de crecimiento específica (g año^{-1}) en poblaciones de trucha común de ríos silíceos Cantábrico-Atlánticos de Galicia por clase de edad. Las barras de error representan intervalos de confianza del 95 %.*

Table 2. Results of Kruskal-Wallis tests among the sections with different angling regulations. The *CF* (condition factor), L_∞ and *k* (growth parameters calculated using FISAT II software package), specific growth rate (*G*), index of growth performance phi-prime (Φ′) and *b*–values of the weight–length relationship. *Significance <0.05. *Resultados de la prueba Kruskal–Wallis entre secciones con diferente tipo de regulación de pesca deportiva.* CF *(factor de condición),* L_∞ *y* k *(parámetros de crecimiento calculados usando el software FISAT II), tasa de crecimiento específica (*G*), índice de crecimiento estándar phi prima (Φ′) y* b*-valores de la relación peso-longitud. *Significación <0.05.*

	Kruskal–Wallis test			Kruskal–Wallis test	
	H	*p*		*H*	*p*
Brown trout performance			Density 1+ (trout m^{-2})	3.09	0.213
CF	0.81	0.666	Biomass 1+ (g m^{-2})	5.93	0.052
Growth parameters			Density 2+ (trout m^{-2})	4.49	0.106
k (g $year^{-1}$)	1.40	0.498	Biomass 2+ (g m^{-2})	3.57	0.167
L∞ (cm)	1.02	0.602	Density 3+ (trout m^{-2})	2.43	0.296
G_{0+-1+} (g $year^{-1}$)	2.80	0.247	Biomass 3+ (g m^{-2})	6.00	0.050
G_{1+-2+} (g $year^{-1}$)	1.11	0.573	Density 4+ (trout m^{-2})	0.84	0.657
G_{2+-3+} (g $year^{-1}$)	0.91	0.634	Biomass 4+ (g m^{-2})	2.27	0.321
G_{3+-4+} (g $year^{-1}$)	1.63	0.443	Density juveniles (trout m^{-2})	2.46	0.292
Mean *G*(g $year^{-1}$)	2.51	0.285	Biomass juveniles (g m^{-2})	6.57	0.037*
Φ′	6.52	0.038*	Density adults (trout m^{-2})	3.71	0.156
b–values	0.79	0.675	Biomass adults (g m^{-2})	5.41	0.067
Population parameters			Production (g m^{-2} per year)	8.00	0.018*
Total density (trout m^{-2})	4.02	0.134	Survival (*S*)	1.27	0.529
Total biomass (g m^{-2})	14.79	0.001*	Mortality (*Z*)	1.20	0.942
Density 0+ (trout m^{-2})	0.70	0.703	P/B (per year)	0.88	0.644
Biomass 0+ (g m^{-2})	0.32	0.851			

performance phi-prime (Φ′) varied between 2.27 and 2.94 (Table 1). Statistically significant differences were found among the sections with different types of angling regulation (Kruskal-Wallis test; $H = 6.52$, $p = 0.038$), with the index higher being in unexploited versus exploited-open sections (Mann-Whitney U test; $p = 0.014$). However, no differences were observed between the unexploited and exploited-regulated sections (Mann-Whitney U test; $p = 0.374$) or between the exploited-regulated and exploited-open sections (Mann-Whitney U test; $p = 0.226$).

Regarding the weight–length relationship, all of the estimated *b*-values are within the range 2.83–3.21, but the growth of *S. trutta* was not strictly isometric (t-test, $df = 65$, $t = 2.059$, $p = 0.044$). For each regulated angling section, the brown trout populations of the unexploited and exploited-regulated sections showed isometric growth (t-test, $df = 10$, $t = 0.137$, $p = 0.894$ and t-test, $df = 10$, $t = 0.127$, $p = 0.901$, respectively), with only the exploited-open sections showing no isometric growth (t-test, $df = 43$, $t = 2.477$, $p = 0.017$). Table 1 reports the descriptive statistics and reference categories of the growth parameters.

The population parameters also showed spatial and temporal fluctuations (Table 4); for example, the percentage of juveniles in terms of density varied between 33.35 and 100 % and the biomass between 7.17 and 100 %. The reference categories of the population parameters are given in Table 4.

Effects of fishery management on population parameters

Concerning the effects of angling exploitation on the population parameters, the differences in the biomass, biomass of juveniles and production among the different angling-regulation sections were statistically significant (Table 2 and Fig. 3). The biomass was higher in the unexploited than in the exploited-regulated (Mann-Whitney U test; $p = 0.008$) or exploited-open sections

Table 3. Size and weight data for each age class. *Only one individual was found. *Estadísticos de talla y peso para cada clase de edad*. **Sólo capturado un ejemplar.*

	Statistics					Statistics			
	Mean	SE	Min	Max		Mean	SE	Min	Max
0+					4+				
Size (cm)	6.9	0.02	2.3	11	Size (cm)	32.9	1.37	27	49
Weight (g)	4.3	0.04	1	17	Weight (g)	435.0	74.55	208	1422
1+					5+*				
Size (cm)	13.6	0.04	8.2	21.6	Size (cm)	47	—	—	—
Weight (g)	33.0	0.31	3	121.6	Weight (g)	1323	—	—	—
2+					6+*				
Size (cm)	19.1	0.10	14.1	26.5	Size (cm)	50.6	—	—	—
Weight (g)	89.2	1.47	34	222	Weight (g)	2192	—	—	—
3+					7+*				
Size (cm)	25.9	0.35	19	40.5	Size (cm)	58	—	—	—
Weight (g)	210.7	9.22	82	732	Weight (g)	2513	—	—	—

Table 4. Statistics and reference categories of population parameters. Specific survival rate (*S*), instantaneous mortality rate (*Z*) and production/biomass (P/B per year). Standard error (SE) and minimum (Min) and maximum (Max). *Only one individual was found. *Estadísticas y categorías de referencia de los parámetros poblacionales. Tasa de supervivencia específica (*S*), tasa instantánea de mortalidad (Z), producción/biomasa (P/B por año). Error estándar (SE), mínimo (Min) y máximo (Max). * Sólo capturado un ejemplar.*

	Statistics				Reference categories				
	Mean	SE	Min	Max	Very poor	Poor	Normal	High	Very high
Total density (trout m^{-2})	0.3	0.026	0.04	0.97	<0.07	0.07–0.17	0.17–0.35	0.35–0.56	> 0.56
Total biomass (g m^{-2})	8.62	0.891	1.04	36.74	<2.72	2.72–4.53	4.53–9.69	9.69–16.13	> 16.13
Density 0+ (trout m^{-2})	0.14	0.021	0	0.803	<0.01	0.01–0.04	0.04–0.14	0.14–0.41	> 0.41
Biomass 0+ (g m^{-2})	0.61	0.093	0	3.83	<0.05	0.05–0.12	0.12–0.58	0.58–1.81	> 1.81
Density 1+ (trout m^{-2})	0.12	0.013	0	0.52	<0.02	0.02-0.05	0.05-0.16	0.16-0.29	> 0.29
Biomass 1+ (g m^{-2})	3.88	0.458	0.11	23.13	<0.93	0.93-1.91	1.91-4.67	4.67-8.13	> 8.13
Density 2+ (trout m^{-2})	0.03	0.004	0	0.15	<0.004	0.004-0.01	0.01-0.04	0.04-0.06	> 0.06
Biomass 2+ (g m^{-2})	2.69	0.343	0.2	14.86	<0.48	0.48-1.0	1.0-3.43	3.43-5.49	> 5.49
Density 3+ (trout m^{-2})	0.01	0.002	0.001	0.048	<0.003	0.003-0.004	0.004-0.013	0.013-0.033	> 0.033
Biomass 3+ (g m^{-2})	2.12	0.449	0.03	13.81	<0.41	0.41-0.72	0.72-2.30	2.30-4.33	> 4.33
Density 4+ (trout m^{-2})	0.004	0.0007	0.0001	0.009	<0.007	0.007-0.002	0.002-0.004	0.004-0.008	> 0.008
Biomass 4+ (g m^{-2})	1.53	0.324	0.22	3.17	<0.24	0.24-0.53	0.53-2.59	2.59-3.02	> 3.02
Density 5+ (trout m^{-2})*	0.004	—	—	—	—	—	—	—	—
Biomass 5+ (g m^{-2})*	5.6	—	—	—	—	—	—	—	—
Density 6+ (trout m^{-2})*	0.001	—	—	—	—	—	—	—	—
Biomass 6+ (g m^{-2})*	0.47	—	—	—	—	—	—	—	—
Density 7+ (trout m^{-2})*	0.004	—	—	—	—	—	—	—	—
Biomass 7+ (g m^{-2})*	10.65	—	—	—	—	—	—	—	—
Density juveniles (trout m^{-2})	0.26	0.026	0.03	0.91	<0.06	0.06–0.13	0.13–0.29	0.29–0.53	> 0.53
Biomass juveniles (g m^{-2})	4.42	0.47	0.9	24.53	<1.19	1.19–2.26	2.26–5.34	5.34–8.59	> 8.59
Density adults (trout m^{-2})	0.04	0.005	0	0.18	<0.003	0.003–0.01	0.01–0.04	0.04–0.08	> 0.08
Biomass adults (g m^{-2})	4.2	0.696	0	29.51	<0.44	0.44–1.17	1.17–4.29	4.29–7.91	> 7.91
Production (g m^{-2} per year)	13.28	1.319	1.25	59.52	<4.39	4.39–6.41	6.41–15.79	15.79–27.19	> 27.19
Survival (*S*)	1.33	0.193	0	7.01	<0.18	0.18–0.38	0.38–1.47	1.47–3.01	> 3.01
Mortality (*Z*)	-0.66	0.1	-2.07	1.89	<-1.60	-1.60 and -1.09	-1.09 and -0.30	-0.30–0.20	> 0.20
P/B (per year)	1.62	0.06	0.43	2.59	<1	1–1.28	1.28–1.85	1.85–2.29	> 2.29

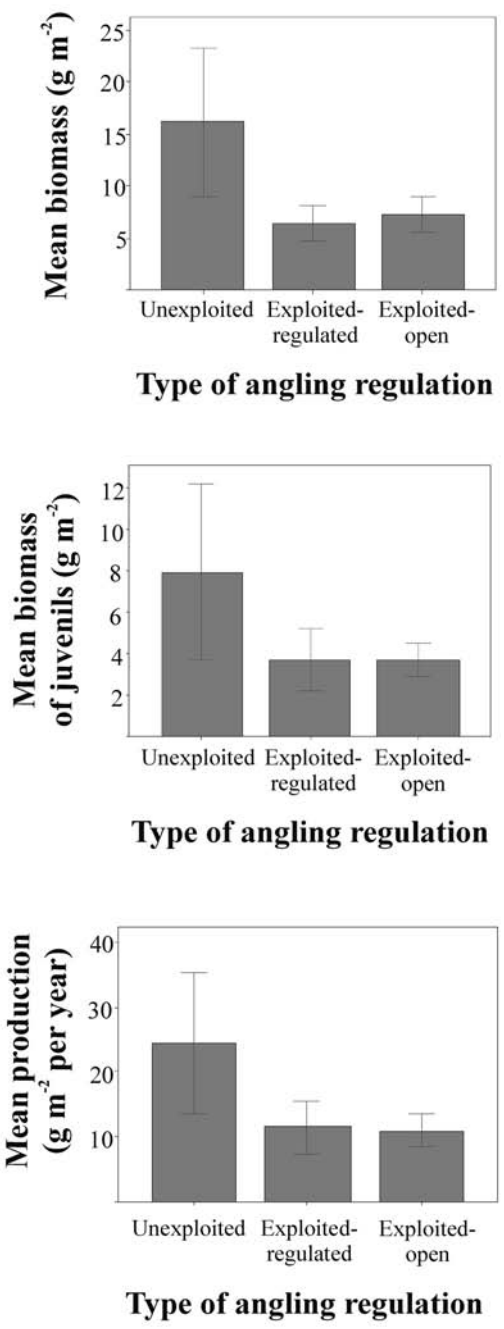

Figure 3. Mean total biomass (g m^{-2}), mean biomass of juveniles (g m^{-2}) and mean production (g m^{-2} per year) in the brown trout populations of the Cantabrian-Atlantic siliceous rivers of Galicia by type of angling regulation. Error bars represent 95 % confidence intervals. *Biomasa total media (g m^{-2}), biomasa de juveniles media (g m^{-2}) y producción media (g m^{-2} por año) en poblaciones de trucha común de ríos silíceos Cantábrico-Atlánticos de Galicia para cada tipo de regulación de pesca deportiva. Las barras de error representan intervalos de confianza del 95 %.*

(Mann-Whitney U test; $p < 0.002$). Similarly, the biomass of juveniles and production were higher in the unexploited than in the exploited-regulated (Mann-Whitney U test; $p = 0.02$ and Mann-Whitney U test; $p = 0.039$, respectively) or exploited-open sections (Mann-Whitney U test; $p = 0.012$ and Mann-Whitney U test; $p = 0.007$, respectively). Table 5 shows the values of the biomass, biomass of juveniles and production for each type of angling regulation.

DISCUSSION

Percentiles have frequently been used for the establishment of reference categories in different freshwater subjects, such as the use of ecological indicator values of freshwater diatoms (Van Dam *et al*., 1994), to test a eutrophication assessment method (Ferreira *et al*., 2007) or growth standards of fish populations (Jackson *et al*., 2008; Pedicillo *et al*., 2010). Within this context, several researchers have recently employed different fish metrics and biotic indices to assess the ecological status of Mediterranean trout-type streams (e.g., Benejam *et al*., 2008; Ayllón *et al*., 2012). However, the establishment of reference categories for the brown trout growth and population parameters is essential before meaningful comparisons can be made among rivers, as the evaluation of the characteristics of a fish population often involves making comparisons with standard reference conditions or among different localities (Pedicillo *et al*., 2010).

For example, the range of growth parameters reported in this study reveals a considerable variability in growth among the 66 sampling sites studied. This variation is normal because growth rates depend on the combination of several factors, such as the water temperature (e.g., Elliott, 1994; Parra *et al*., 2009; 2012), food intake (e.g., Elliott, 1994; Mambrini *et al*., 2006), genetic factors (e.g., Jensen, 1985; McDowall, 1994), social interactions (e.g., Metcalfe, 1994; Lobón-Cerviá, 2007), latitude and altitude (Parra *et al*., 2009) or even alkalinity, with growth being faster in rivers with a high calcium content (Kennedy & Fitzmaurice, 1971). Although our

Table 5. Total biomass, biomass of juveniles, production and index of growth performance phi-prime (Φ′). Data are presented for each angling regulation type. Standard error (SE) minimum (Min), maximum (Max) and sample size (*n*). *Biomasa total, biomasa de juveniles, producción e índice de crecimiento estándar phi-prima (Φ′). Los datos se presentan para cada tipo de regulación de pesca deportiva. Error estándar (SE), mínimo (Min), máximo (Max) y tamaño de la muestra (*n*).*

		Unexploited	**Exploited-regulated**	**Exploited-open**
Biomass (g m^{-2})	Min	1.04	2.6	1.7
	Max	37.74	10.06	35.72
	Mean	16.2 ± 3.19	6.5 ± 0.76	7.2 ± 0.87
	n	11	11	44
Biomass juveniles (g m^{-2})	Min	1.0	1.08	0.90
	Max	24.5	8.50	13.06
	Mean	7.96 ± 1.935	3.70 ± 0.665	3.71 ± 0.411
	n	11	11	44
Production (g m^{-2} per year)	Min	2.5	5.1	1.25
	Max	59.5	22.0	41.2
	Mean	24.3 ± 4.91	11.5 ± 1.81	10.9 ± 1.22
	n	10	11	41
Index of growth performance phi-prime (Φ′)	Min	2.42	2.43	2.27
	Max	2.86	2.89	2.94
	Mean	2.70 ± 0.038	2.64 ± 0.047	2.58 ± 0.023
	n	11	11	44

results for the Von Bertalanffy growth parameters (L_∞ and k) appear to be similar to those previously described in other regions of the Iberian Peninsula (e.g., García de Jalón *et al*., 1986; 1990; Lobón-Cerviá *et al*., 1986; Martínez & García de Jalón, 1988; Maia & Valente, 1999), the lack of information about reference categories for growth parameters makes it difficult to determine whether the growth is high or low. In fact, concerning the growth performance phi-prime index, Pedicillo *et al*. (2010) classified the growth rates of *S. trutta* in Central Italy according to the standard growth curves of the Von Bertalanffy equations into five categories (very poor, poor, normal, good and very good). These authors found that the index of growth performance ranged from 2.45 as "very poor" to 2.66 as "very good". Our results are similar to those of Pedicillo *et al*. (2010), except for the last category for which we attained higher values (> 2.81).

The population age structure in *S. trutta* shows within-site variation (Maia & Valente, 1999), with a maximum longevity between 6 and 9 years and a clear dominance of age groups 0+ to 3+ (Maia & Valente, 1999; Parra *et al*., 2009). In this study, the brown trout populations were dominated by groups 0+, 1+ and 2+, a result that was similar to Rodrigues *et al*. (1994) and Nicola & Almodóvar (2002).

Alcaraz-Hernández *et al*. (2007) found that the most relevant variables that explain the density and biomass of brown trout populations in Mediterranean trout-type streams were the stream width and percentage of cobbles. Within this context, the population parameters may also vary substantially within a geographical area (e.g., Joyce *et al*., 1990; Elliott, 1994; Stanfield *et al*., 2006) and are well documented in the Iberian Peninsula (e.g., Lobón-Cerviá & Penczak, 1984; García de Jalón *et al*., 1986; Lobón-Cerviá *et al*., 1986; 2011; Martínez & García de Jalón, 1988; Maia & Valente, 1999; Alonso-González & García de Jalón, 2001, Almodóvar & Nicola, 2004; Alonso-González *et al*., 2008; 2011), with the exception of the NW area. Thus, the scarcely reported densities and biomasses for the rivers of Galicia range from 0.008 trout m^{-2} and 0.026 g m^{-2} in the River Ulla (Garcia de Jalón *et al*., 1990) to 0.864 trout m^{-2} and 17.61 g m^{-2} in the River Miñor (Hervella & Caballero,

1999). More recently, Sánchez-Hernández *et al*. (2011) found that *S. trutta* dominated the fish community in the River Ladra, with a density of 0.077 trout m^{-2}. Using the data of the present work (Table 4), the reported densities would correspond to the very poor category in the River Ulla (Garcia de Jalón *et al*., 1990), poor category in the River Ladra (Sánchez-Hernández *et al*., 2011) and very high category in the River Miñor (Hervella & Caballero, 1999).

Production is the best indicator of the quantitative performance of a fish population in any type of habitat (Jones *et al*., 1996; Minns *et al*., 1996), and production varies in salmonids according to different parameters, such as the angling regulation, benthos production or environmental factors (Waters 1988; Kwak & Waters, 1997; Almodóvar & Nicola, 2004; Almodóvar *et al*., 2006). In rivers, the annual production of brown trout usually ranges from 0.14 to 54.70 g m^{-2} per year (Elliott, 1994 and references therein). The published values of this parameter in the Iberian Peninsula vary greatly (Lobón-Cerviá & Penczak, 1984; García de Jalón *et al*., 1986; 1990; Martínez & García de Jalón, 1988; Lobón-Cerviá *et al*., 1986; 2011; Lobón-Cerviá, 2003), with extreme values of 46.1 g m^{-2} per year obtained for the River Ucero (Lobón-Cerviá *et al*., 1986) and 0.8 for the River Jarama (Lobón-Cerviá & Penczak, 1984), both in Central Spain. The only published data we could find for Galician watercourses was that of García de Jalón *et al*. (1990) who found that production ranged from 0.9 g m^{-2} per year in the River Ulla to 29.7 g m^{-2} per year in an affluent, the River Deza. Our range of production values is similar to these, but the normal category we propose is different, as shown in Table 4.

The turnover (P/B) ratio for fish populations is usually below 1 (Cowx, 2003), and the P/B (per year) ratio indicates how quickly the biomass is potentially changing (Randall & Minns, 2000). Moreover, the P/B ratio varies inversely with the fish size-at-maturity and longevity, and it is, therefore, specific for species and populations (Randall & Minns, 2000). For the brown trout populations in the Iberian Peninsula, most of the P/B ratios vary between 0.6 and 3.8 (Lobón-Cerviá & Penczak, 1984; Martínez & García de Jalón, 1988; García de Jalón *et al*., 1990; Alonso-González & García de Jalón, 2001; Almodóvar & Nicola, 2004; Lobón-Cerviá *et al*., 2011). Interestingly, the turnover ratios obtained in this study were within this range, but the P/B (per year) ratios for the high and very high categories were above 2, indicating that there were few old individuals, as shown in Table 4.

Different authors have demonstrated that angling exploitation reduces the mean age, age diversity and number of fish exceeding the minimum size in exploited sections (e.g., Braña *et al*., 1992; Scott *et al*., 1999; Almodóvar & Nicola, 2004; Jennings & Blanchard, 2004; Hsieh *et al*., 2006; 2010). Our results are consistent with those obtained in previous works (Coble, 1988; Almodóvar & Nicola, 1998; 2004; Jennings & Blanchard, 2004), as the population parameters (biomass and production) were higher in the unexploited than in the two exploited sections. Moreover, in this study, the density and turnover (P/B) ratio did not seem to be affected by the angling regulation, as had been observed by Almodóvar & Nicola (2004).

The study of the growth of fish populations has been considered to be an important tool in fisheries assessment (e.g., Arslan *et al*., 2004; Oscoz *et al*., 2005; Nowak *et al*., 2009). However, although most researchers agree that the different exploitation status of salmonid populations can affect the growth patterns (Donald & Alger, 1989; Braña *et al*., 1992; Jenkins, 2003), the exact mechanism is not well understood. For example, Braña *et al*. (1992) stated that, despite the fact that the growth rates were not absolutely consistent, brown trout exhibited faster growth in some exploited sections of rivers. Donald & Alger (1989) found that the growth of *Salvelinus fontinalis* increased when the density of the older cohort of fish was reduced, thus growth was favoured by harvest; however, Jenkins (2003) showed negative effects of catch-and-release angling on the growth of *Oncorhynchus mykiss*. Almodóvar & Nicola (2004) found no differences in the brown trout growth parameters between differently regulated angling sections, but these researchers demonstrated that the

fast-growing populations were more susceptible to angling harvest than the slow-growing ones. In our case, we found almost no differences in the growth parameters among the angling-regulation sections, but the index of growth performance phi-prime (Φ') was higher for the unexploited versus the exploited-open sections, suggesting that differences in growth can occur at different angling regulations, as previously found by Braña *et al*. (1992). According to this index, the brown trout of the Galician rivers showed faster growth in the unexploited sections.

The reported decline of many stocks of *S. trutta* in the Iberian Peninsula has generated a great deal of interest in developing conservation and management plans to protect the brown trout populations. These plans require a deep knowledge of the habitat-specific requirements, distribution and population parameters of the species, as management actions might include habitat restoration or even the restocking of populations. However, this type of information has not been systematically recorded and published, and there is a need of reference values to provide stakeholders with clear guidelines for the design of management plans. We hope our work will trigger further investigations on this subject.

ACKNOWLEDGEMENTS

A portion of this work was performed in the laboratories of the Station of Hydrobiology of USC "Encoro do Con" at Vilagarcía de Arousa. This work was partially supported by the project 10PXIB2111059PR of the Xunta de Galicia and the project MIGRANET of the Interreg IV B SUDOE (South-West Europe) Territorial Cooperation Programme (SOE2/P2/E288). The authors are also grateful to one anonymous reviewer for comments that have improved the manuscript.

REFERENCES

AAS, O., W. HAIDER & L. HUNT. 2000. Angler responses to potential harvest regulations in a Norwegian sport fishery: a conjoint-based choice modeling approach. *North American Journal of Fisheries Management*, 20: 940–950.

ALCARAZ-HERNÁNDEZ, J. D., F. MARTÍNEZ CAPEL, M. PEREDO & A. B. HERNÁNDEZ-MASCARELL. 2007. Relación entre densidades y biomasas de *Salmo trutta fario* y mediciones del mesohábitat en tramos trucheros de la Comunidad Valenciana. *Limnetica*, 26: 159–168.

ALLEN, K. R. 1971. Relation between production and biomass. *Journal of the Fisheries Research Board of Canada*, 28: 1573–1581.

ALMODÓVAR, A. & G. G. NICOLA. 1998. Assessment of a brown trout *Salmo trutta* population in the River Gallo (central Spain): angling effects and management implications. *Italian Journal of Zoology*, 65: 539–543.

ALMODÓVAR, A. & G. G. NICOLA. 2004. Angling impact on conservation of Spanish stream-dwelling brown trout *Salmo trutta*. *Fisheries Management and Ecology*, 11: 173–182.

ALMODÓVAR, A., G. G. NICOLA & B. ELVIRA. 2006. Spatial variation of brown trout production: the role of environmental factors. *Transactions of the American Fisheries Society*, 135: 1348–1360.

ALONSO-GONZÁLEZ, C. & D. GARCÍA DE JALÓN. 2001. Bases para la ordenación de la pesca en la cuenca del Alto Tormes (Ávila). *Limnetica*, 20: 293–304.

ALONSO-GONZÁLEZ, C., J. GORTÁZAR, D. BAEZA SANZ & D. GARCÍA DE JALÓN. 2008. Dam function rules based on brown trout flow requirements: design of environmental flow regimes in regulated streams. *Hydrobiologia*, 609: 253–262.

ALONSO, C., D. GARCÍA DE JALÓN, J. ÁLVAREZ & J. GORTÁZAR. 2011. A large-scale approach can help detect general processes driving the dynamics of brown trout populations in extensive areas. *Ecology of Freshwater Fish*, 20: 449–460.

ARSLAN, M., A. YILDIRIM & S. BEKTA. 2004. Length-Weight Relationship of Brown Trout, *Salmo trutta* L., Inhabiting Kan Stream, Çoruh Basin, North-Eastern Turkey. *Turkish Journal of Fisheries and Aquatic Sciences*, 4: 45–48.

AYLLÓN, D., A. ALMODÓVAR, G. G. NICOLA, I. PARRA & B. ELVIRA. 2012. A new biological indicator to assess the ecological status of Mediterranean trout type streams. *Ecological Indicators*, 20: 295–303.

BAGENAL, T. B. & F. W. TESCH. 1978. Age and growth. In: *Methods for assessment of fish produc-*

tion in fresh waters. T. B. Bagenal (ed.): 101–136. Blackwell Science Publications, Oxford.

BENEJAM, L., E. APARICIO, M. J. VARGAS, A. VILA-GISPERT & E. GARCÍA-BERTHOU. 2008. Assessing fish metrics and biotic indices in a Mediterranean stream: effects of uncertain native status of fish. *Hydrobiologia*, 603: 197–210.

BRAÑA, F., A. G. NICIEZA & M. M. TOLEDO. 1992. Effects of angling on population structure of brown trout, *Salmo trutta* L., in mountain streams of Northern Spain. *Hydrobiologia*, 237: 61–66.

BUTLER, J. R. A., A. RADFORD, G. RIDDINGTON & R. LAUGHTON. 2009. Evaluating an ecosystem service provided by Atlantic salmon, sea trout and other fish species in the River Spey, Scotland: the economic impact of recreational rod fisheries. *Fisheries Research*, 96: 259–266.

COBLE, D. W. 1988. Effects of angling on bluegill populations: management implications. *North American Journal of Fisheries Management*, 8: 277–283.

COWX, I. G. (ed.) 2003. *Interactions between Fish and Birds: Implications for Management*. Fishing News Books, Blackwell Science, Ltd., London. 376 pp.

COWX, I. G. & P. A. FREAR. 2004. Assessment of year class strength in freshwater recreational fish populations. *Fisheries Management and Ecology*, 11: 117–123.

DONALD, D. B. & D. J. ALGER. 1989. Evaluation of exploitation as a means of improving growth in a stunted population of brook trout. *North American Journal of Fisheries Management*, 9: 177–183.

ELLIOTT, J. M. 1994. *Quantitative ecology and the brown trout*. University Press, Oxford. 286 pp.

FERREIRA, J. G., S. B. BRICKER & T. C. SIMAS. 2007. Application and sensitivity testing of an eutrophication assessment method on coastal systems in the United States and European Union. *Journal of Environmental Management*, 82: 433–445.

FILIPE, A. F., M. B. ARAÚJO, I. DOADRIO, P. L. ANGERMEIER & M. J. COLLARES-PEREIRA. 2009. Biogeography of Iberian freshwater fishes revisited: the roles of historical versus contemporary constraints. *Journal of Biogeography*, 36: 2096–2110.

GARCÍA DE JALÓN, D., E. TOLOSANA-ESTEBAN & F. RODRÍGUEZ-ALCALDE. 1986. Estimación de algunos parámetros poblacionales de la trucha común (*Salmo trutta fario*) en los ríos pirenaicos. *Boletín de la Estación Central de Ecología*, 29: 51–58.

GARCÍA DE JALÓN, D., M. MAYO, F. HERVELLA, E. BARCELÓ & C. VILLETA. 1990. *Pesca fluvial en Galicia. Bases limnológicas para su gestión*. Xunta de Galicia. Santiago de Compostela, 145 pp.

GARCÍA DE JALÓN, D., M. MAYO, F. HERVELLA, E. BARCELÓ & T. FERNÁNDEZ. 1993. *Principios y técnicas de gestión de la pesca en aguas continentales*. Mundi-Prensa, Madrid. 247 pp.

GAYANILO, F. C. J., P. SPARRE & D. PAULY. 2005. *FAO-ICLARM stock assessment tools II (FISAT II), revised version. User's guide*. FAO, Rome. 168 pp.

GONZÁLEZ DEL TÁNAGO, M. & D. GARCÍA DE JALÓN. 2006. Caracterización jerárquica de los ríos españoles. Propuesta de tipología de tramos fluviales para su clasificación atendiendo a la directiva marco del agua. *Limnetica*, 25: 81–98.

GRANADO-LORENCIO, C. 1996. *Ecología de peces*. Universidad de Sevilla, Sevilla. 353 pp.

HERNANDO, J. A. & M. C. SORIGUER. 1992. Biogeography of the freshwater fish of the Iberian Peninsula. *Limnetica*, 8: 243–253.

HERVELLA, F. & P. CABALLERO. 1999. *Inventariación piscícola de los ríos Gallegos*. Xunta de Galicia. Santiago de Compostela. 124 pp.

HSIEH, C. H., C. S. REISS, J. R. HUNTER, J. R. BEDDINGTON, R. M. MAY & G. SUGIHARA. 2006. Fishing elevates variability in the abundance of exploited species. *Nature*, 443: 859–862

HSIEH, C. H., A. YAMAUCHI, T. NAKAZAWA & W. F. WANG. 2010. Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences*, 72: 165–178.

JACKSON, Z. J., M. C. QUIST & J. G. LARSCHEID. 2008. Growth standards for nine North American fish species. *Fisheries Management and Ecology*, 15: 107–118.

JENKINS, T. M. 2003. Evaluating recent innovations in bait fishing tackle and technique for catch-and-release of rainbow trout. *North American Journal of Fisheries Management*, 23: 1098–1107.

JENNINGS, S. & J. L. BLANCHARD. 2004. Fish abundance with no fishing: predictions based on macroecological theory. *Journal of Animal Ecology*, 73: 632–642.

JENSEN, J. W. 1985. The potential growth of salmonids. *Aquaculture*, 48: 223–231.

JENSEN, J. W., T. NØST & I. P. MUNIZ. 1997. The ecology of brown trout and Arctic charr in two lakes in Høylandet. *Hydrobiologia*, 348: 127–143.

JONES, M. L., R. G. RANDALL, D. HAYES, W. DUNLOP, J. IMHOF, G. LACROIX & N. J. R. WARD. 1996. Assessing the ecological effects of habitat change: moving beyond productive capacity. *Canadian Journal of Fisheries and Aquatic Sciences*, 53: 446–457.

JOYCE, L. A., C. H. FLATHER, P. A. FLEBBE, T. W. HOEKSTRA & S. J. URSIC. 1990. Integrating forage, wildlife, water, and fish projections with timber projections at the regional level: A case study in southern United States. *Environmental Management*, 14: 489–500.

KENNEDY, M. & P. FITZMAURICE. 1971. Growth and food of brown trout *Salmo trutta* (L.) in Irish Waters. *Proceedings of the Royal Irish Academy*, 71: 269–352.

KLEMETSEN, A., P.-A. AMUNDSEN, J. B. DEMPSON, B. JONSSON, N. JONSSON, M. F. O'CONNELL & E. MORTENSEN. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish*, 12: 1–59.

KWAK, T. J. & T. F. WATERS. 1997. Trout production dynamics and water quality in Minnesota streams. *Transactions of the American Fisheries Society*, 126: 35–48.

LOBÓN-CERVIÁ, J. 2003. Spatiotemporal dynamics of brown trout production in a Cantabrian stream: effects of density and habitat quality. *Transactions of the American Fisheries Society*, 132: 621–637.

LOBÓN-CERVIÁ, J. 2007. Density-dependent growth in stream-living brown trout *Salmo trutta* L. *Functional Ecology*, 21: 117–124.

LOBÓN-CERVIÁ, J. 2010. Density dependence constrains mean growth rate while enhancing individual size variation in stream salmonids. *Oecologia*, 164: 109–115.

LOBÓN-CERVIÁ, J. & T. PENCZAK. 1984. Fish production in the Jarama River, central Spain. *Holarctic Ecology*, 7: 128–137.

LOBÓN-CERVIÁ, J., A. DE SOSTOA & C. MONTAÑÉS. 1986. Fish production and its relation with the community structure in an aquifer-fed stream of Old Castile (Spain). *Polskie Archiwum Hydrobiologii*, 33: 333–343.

LOBÓN-CERVIÁ, J., G. GONZÁLEZ & P. BUDY. 2011. Factors driving spatial and temporal variation in production and production/biomass ratio of stream-resident brown trout (*Salmo trutta*) in Cantabrian streams. *Freshwater Biology*, 56: 2272–2287.

MAIA, C. F. Q. & A. C. N. VALENTE. 1999. The brown trout *Salmo trutta* L. populations in the river Lima catchment. *Limnetica*, 17: 119–126.

MAMBRINI, M., L. LABBÉ, F. RANDRIAMANANTSOA & T. BOUJARD. 2006. Response of growth-selected brown trout (*Salmo trutta*) to challenging feeding conditions. *Aquaculture*, 252: 429–440.

MARTÍNEZ, J. & D. GARCÍA DE JALÓN. 1988. Estudio de las poblaciones trucheras del río Tormes. *Ecología*, 2: 303–313.

MARTÍNEZ-ANSEMIL, E. & P. MEMBIELA. 1992. The low mineralized and fast turnover watercourses of Galicia. *Limnetica*, 8: 125–130.

MCDOWALL, R. M. 1994. On size and growth in freshwater fish. *Ecology of Freshwater Fish*, 3: 67–79.

MEMBIELA, P., C. MONTES & E. MARTÍNEZ-ANSEMIL. 1991. Características hidroquímicas de los ríos de Galicia, NW de la Península Ibérica. *Limnetica*, 7: 163–174.

METCALFE, N. B. 1994. The role of behaviour in determining salmon growth and development. *Aquaculture and Fisheries Management*, 25: 67–76.

MINNS, C. K., J. R. M. KELSO & R. G. RANDALL. 1996. Detecting the response of fish to habitat alterations in freshwater ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, 53: 403–414.

MOURA, P., M. B. GASPAR & C. M. MONTEIRO. 2009. Age determination and growth rate of a *Callista chione* population from the southwestern coast of Portugal. *Aquatic Biology*, 5: 97–106.

NICOLA, G. G. & A. ALMODÓVAR. 2002. Reproductive traits of stream-dwelling brown trout *Salmo trutta* in contrasting neighbouring rivers of central Spain. *Freshwater Biology*, 47: 1353–1365.

NICOLA, G. G. & A. ALMODÓVAR. 2004. Growth pattern of stream-dwelling brown trout under contrasting thermal conditions. *Transactions of the American Fisheries Society*, 133: 66–78.

NIEMELÄ, E. 2004. *Variation in the yearly and seasonal abundance of juvenile Atlantic salmon in a long-term monitoring programme. Methodology, status of stocks and reference points*. Ph.D. Thesis.

University of Oulu. Oulu (Finland). 54 pp.

NOWAK, M., W. POPEK, W. JAGUSIAK, S. DEPTUŁA, J. POPEK, K. TATOJ, K. KLĘCZAR & P. EPLER. 2009. Weight-length relationships for three fishes (*Leuciscus leuciscus*, *Phoxinus phoxinus*, *Salmo trutta*) from the Strwiąż River (Dniester River drainage). *Archives of Polish Fisheries*, 17: 313–316.

OSCOZ, J., F. CAMPOS & M. C. ESCALA. 2005. Weight–length relationships of some fish species of the Iberian Peninsula. *Journal of Applied Ichthyology*, 21: 73–74.

PARRA, I., A. ALMODÓVAR, G. G. NICOLA & B. ELVIRA. 2009. Latitudinal and altitudinal growth patterns of brown trout *Salmo trutta* at different spatial scales. *Journal of Fish Biology*, 74: 2355–2373.

PARRA, I., A. ALMODÓVAR, D. AYLLÓN, G. G. NICOLA & B. ELVIRA. 2012. Unravelling the effects of water temperature and density dependence on the spatial variation of brown trout body size. *Canadian Journal of Fisheries and Aquatic Sciences*, 69: 1–12.

PAULY, D. & J. L. MUNRO. 1984. Once more on comparison of growth in fish and invertebrates. *ICLARM Fishbyte*, 1: 21–22.

PEDICILLO, G., A. CAROSI, L. GHETTI & M. LORENZONI. 2010. Population size structure indices and growth standards for *Salmo (trutta) trutta* Linnaeus, 1758 in Central Italy. *Knowledge and Management of Aquatic Ecosystems*, 399: 8–22.

RANDALL, R. G. & C. K. MINNS. 2000. Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 1657–1667.

RICKER, W. E. 1975. *Computation and interpretation of biological statistics of fish populations*. Bulletin of the Fisheries Research Board of Canada. Canada. 382 pp.

RODRIGUES, L. S. B., R. CORTÉS & A. MONZÓN. 1994. Utilización del hábitat por *Salmo trutta* L. *Limnetica*, 10: 129–135.

SÁNCHEZ-HERNÁNDEZ, J., R. VIEIRA-LANERO, M. J. SERVIA & F. COBO. 2011. Feeding habits of four sympatric fish species in the Iberian Peninsula: keys to understanding coexistence using prey trais. *Hydrobiologia*, 667: 119–132.

SCOTT, B., G. MARTEINSDÓTTIR & P. WRIGHT. 1999. Potential effects of maternal factors on spawning stock-recruitment relationships under varying fishing pressure. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 1882–1890.

STANFIELD, L. W., S. F. GIBSON & J. A. BORWICK. 2006. Using a landscape approach to identify the distribution and density patterns of salmonids in Lake Ontario tributaries. *American Fisheries Society Symposium*, 48: 601–621.

VAN DAM, H., A. MERTENS & J. SINKELDAM. 1994. A coded checklist and ecological indicator values of freshwater diatoms from The Netherlands. *Netherlands Journal of Aquatic Ecology*, 28: 117–133.

VON BERTALANFFY, L. 1938. A quantitative theory of organic growth (Inquiries on growth laws. II). *Human Biology*, 10: 181–213.

WATERS, T. F. 1988. Fish production-benthos production relationships in trout streams. *Polskie Archiwum Hydrobiologii*, 35: 545–561.

ZAMORA, L., A. VILA & J. NASPLEDA 2009. La biota de los ríos: los peces. In: *Conceptos y técnicas en ecología fluvial*. A. Elosegi & S. Sabater (cords.): 271–291. Fundación BBVA. Bilbao.

ZIPPIN, C. 1958. The removal method population and estimation. *Journal of Wildlife Management*, 22: 82–90.

Appendix 1. Date, location, weight–length relationship and angling regulation of the sampling sites. Weight–length relationship (*b*), coefficient of determination (r^2) and sample size (*n*). *Significance <0.05. *Fecha, localización, relación peso-longitud y tipo de regulación de pesca deportiva de las estaciones de muestreo. Coeficiente de determinación (r^2) y tamaño de la muestra (n). *Significación <0.05.*

River	Year	UTM (29T)	Weight–length	r^2	*n*	Angling regulation
Anllóns	2007	509070 4785516	y=2.9605x–1.8817	0.978*	117	Exploited-open
Furelos	2007	580203 4747203	y=3.0964x–2.0543	0.966*	672	Exploited-open
Lengüelle	2007	544138 4762713	y=3.157x–2.1012	0.954*	837	Exploited-open
Tambre	2007	556103 4760391	y=3.1543x–2.0935	0.939*	561	Exploited-open
Umia	2008	528604 4716565	y=2.9863x–1.9128	0.972*	252	Unexploited
Umia	2008	535734 4693212	y=2.9366x–1.8337	0.979*	73	Exploited-open
Umia	2008	540959 4693487	y=3.0405x–1.9404	0.994*	45	Exploited-open
Umia	2008	553395 4696434	y=2.9949x–1.9485	0.991*	101	Exploited-open
Umia	2008	526463 4714746	y=3.0607x–1.9685	0.970*	46	Exploited-open
Umia	2008	522558 4710954	y=3.0226x–1.9458	0.984*	44	Exploited-regulated
Umia	2008	520384 4709255	y=3.0878x–2.0357	0.977*	50	Exploited-regulated
Umia	2008	531419 4717433	y=3.0867x–2.0197	0.969*	115	Exploited-open
Barcés	2009	554535 4786009	y=3.0503x–1.9788	0.990*	106	Exploited-open
Barcés	2009	548212 4781329	y=3.1219x–2.0692	0.961*	122	Exploited-open
Illade	2009	591752 4790431	y=3.064x–1.9918	0.986*	24	Exploited-open
Illade	2009	592122 4791360	y=3.2192x–2.186	0.991*	45	Exploited-open
Illade	2009	593095 4792543	y=2.966x–1.8931	0.987*	31	Exploited-open
Maciñeira	2009	586307 5112862	y=3.2194x–2.1652	0.969*	33	Exploited-open
Maciñeira	2009	587404 4785539	y=2.914x–1.8212	0.991*	63	Exploited-open
Mandeo	2009	578798 4788281	y=2.9845x–1.8845	0.996*	128	Exploited-regulated
Mandeo	2009	567947 4790635	y=2.9453x–1.837	0.996*	98	Exploited-regulated
Mandeo	2009	574451 4789363	y=2.9477x–1.8577	0.995*	197	Exploited-open
Mandeo	2009	580276 4776490	y=3.0308x–1.9552	0.989*	241	Exploited-open
Mandeo	2009	584866 4766623	y=3.0952x–2.0494	0.984*	32	Exploited-open
Mandeo	2009	580338 4786209	y=2.9986x–1.911	0.993*	99	Exploited-open
Mandeo	2009	581904 4780107	y=3.0225x–1.9415	0.991*	111	Exploited-open
Meidelo	2009	580107 5456593	y=2.9601x–1.8748	0.993*	43	Exploited-open
Mendo	2009	567487 4781963	y=3.0698x–1.9806	0.996*	155	Exploited-open
Mendo	2009	565128 4790698	y=3.0185x–1.9237	0.993*	135	Exploited-open
Barxas	2010	567040 4665194	y=3.0392x–1.9552	0.993*	38	Exploited-open
Caselas	2010	537273 4657707	y=2.9662x–1.8666	0.998*	20	Exploited-open
Deva	2010	558660 4667951	y=3.071x–1.9956	0.996*	79	Exploited-regulated
Deva	2010	558230 4663221	y=3.1222x–2.0244	0.997*	11	Unexploited
Deza	2010	562892 4733043	y=2.9649x–1.8851	0.996*	28	Exploited-open
Deza	2010	559186 4735036	y=3.0782x–1.9994	0.994*	32	Exploited-open
Furnia	2010	525576 4649970	y=3.0926x–2.0393	0.997*	21	Exploited-open
Furnia	2010	525328 4652650	y=2.9349x–1.8903	0.966*	62	Exploited-open
Hospital	2010	523227 4648114	y=2.8949x–1.8061	0.994*	10	Exploited-open
Hospital	2010	522505 4650632	y=2.9783x–1.8735	0.979*	35	Exploited-open
Landro	2010	611063 4815914	y=3.1027x–2.0282	0.988*	355	Unexploited
Louro	2010	531881 4670265	y=3.0742x–1.9832	0.977*	91	Exploited-regulated
Pego	2010	520274 4647306	y=3.0188x–1.9151	0.987*	80	Exploited-open
Ribadil	2010	562880 4666272	y=3.1176x–2.0347	0.991*	46	Exploited-open
Tamuxe	2010	515039 4647179	y=3.1357x–2.0824	0.984*	35	Exploited-open
Tamuxe	2010	514098 4642207	y=3.0711x–2.0389	0.993*	9	Exploited-open
Termes	2010	550390 4660358	y=3.0567x–1.9822	0.996*	68	Unexploited

continued

Appendix 1. (continued) Date, location, weight–length relationship and angling regulation of the sampling sites. Weight–length relationship (*b*), coefficient of determination (r^2) and sample size (*n*). *Significance <0.05. *Fecha, localización, relación peso-longitud y tipo de regulación de pesca deportiva de las estaciones de muestreo. Coeficiente de determinación* (r^2) *y tamaño de la muestra (*n*). *Significación <0.05.*

River	Year	UTM (29T)	Weight–length	r^2	*n*	Angling regulation
Tripes	2010	527546 4656519	y=2.9723x–1.9236	0.987*	28	Exploited-open
Tripes	2010	529282 4654682	y=2.8654x–1.812	0.913*	41	Exploited-open
Vilameá	2010	574105 4636335	y=3.0281x–1.9825	0.998*	155	Exploited-open
Barral	2011	525115 4715631	y=3.0434x–1.986	0.996*	142	Exploited-open
Deva	2011	558660 4667951	y=3.0104x–1.9238	0.997*	65	Exploited-regulated
Deva	2011	558230 4663221	y=2.8355x–1.7334	0.968*	39	Unexploited
Hospital	2011	522505 4650632	y=3.0152x–1.9549	0.991*	52	Exploited-open
Liñares	2011	543143 4732294	y=2.9962x–1.8791	0.997*	53	Unexploited
Moreda	2011	598524 4728101	y=2.9334x–1.8683	0.979*	54	Unexploited
Moreda	2011	600704 4728715	y=3.0567x–2.0211	0.998*	125	Unexploited
Moreda	2011	601813 4728654	y=3.0315x–1.9979	0.997*	89	Unexploited
Sar	2011	527961 4735192	y=3.02x–1.943	0.995*	50	Exploited-open
Sar	2011	527618 4734039	y=3.0935x–2.062	0.993*	43	Exploited-regulated
Sar	2011	527871 4732466	y=2.8303x–1.7255	0.985*	13	Exploited-regulated
Tamuxe	2011	514098 4642207	y=3.1796x–2.1372	0.984*	32	Exploited-open
Té	2011	515629 4724811	y=3.0157x–1.9281	0.956*	140	Exploited-open
Ulla	2011	554283 4738221	y=3.0323x–1.9313	0.991*	126	Unexploited
Umia	2011	528353 4716218	y=3.1023x–1.9917	0.993*	66	Exploited-regulated
Verdugo	2011	536634 4688658	y=2.878x–1.7799	0.996*	24	Unexploited
Xubia	2011	568821 4819350	y=2.8579x–1.7793	0.986*	23	Exploited-regulated

Limnetica, 31 (2): 289-304 (2012)

Temporal variation of phytoplankton in two neighbouring Mediterranean shallow lakes in Doñana National Park (Spain)

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Received: 28/7/11 Accepted: 17/5/12

ABSTRACT

Temporal variation of phytoplankton in two neighbouring Mediterranean shallow lakes in Doñana National Park (Spain)

This study was aimed at describing the phytoplankton dynamics and structure of two eutrophic to hypereutrophic Mediterranean shallow lakes (Santa Olalla and Dulce). The two systems are close together and can function as one water body at times of heavy rainfall, but once separated, they evolve differently. The Shannon diversity index was low for both shallow lakes (average values of 1.11 in Santa Olalla and 1.79 in Dulce). The average phytoplankton Chl *a* concentrations and primary production rates were very high, although slightly higher in Santa Olalla (365.2 mg m^{-3} and 1.29 g C m^{-3} h^{-1}, respectively) than in Dulce (230 mg m^{-3} and 0.88 g C m^{-3} h^{-1}). Phytoplankton variation in the lakes was related to shifts in the physical and chemical features of lake water as well as hydrological conditions, a finding that is corroborated by the canonical correspondence analysis results, which showed a different pattern of evolution in each system. Eight functional groups were found in Santa Olalla (D, H_1, J, K, M, S_1, W_2 and Y), although the D, W_2 and Y groups were only predominant during the first four months of the study. For the rest of the period, the system was particularly dominated by the H_1, K and S_1 groups. Dulce exhibited a more complex distribution of phytoplankton functional groups over time. Ten functional groups were observed in this system (D, H_1, J, K, M, P, S_1, S_2, W_2 and Y). Some characteristics of these systems, such as rapid water volume fluctuations, low light penetration and low concentration of inorganic nutrients, are stressful conditions for phytoplankton, which may account for the low phytoplankton diversity and the equilibrium phases recorded for many months in both wetlands.

Key words: Phytoplankton dynamics, hypereutrophic shallow Mediterranean lakes, phytoplankton diversity, functional groups.

RESUMEN

Variación temporal del fitoplancton de dos lagunas someras mediterráneas contiguas del Parque Nacional de Doñana (España)

El presente estudio tiene como objetivo describir la dinámica y estructura del fitoplancton en dos lagunas eutróficas a hipereutróficas Mediterráneas (Santa Olalla y Dulce, España). Ambos sistemas están muy próximos y se unen superficialmente en periodos de fuertes lluvias, sin embargo, cuando el nivel desciende, evolucionan de forma separada. El índice de diversidad de Shannon fue bajo para ambos sistemas (valores promedio de 1.11 en Santa Olalla y 1.79 en Dulce). La concentración media de Chl a *y las tasas de producción primaria del fitoplancton fueron muy altas, aunque ligeramente superior en Santa Olalla (365.2 mg m^{-3} y 1.29 g C m^{-3} h^{-1}, respectivamente) con respecto a Dulce (230 mg m^{-3} y 0.88 g C m^{-3} h^{-1}). Las variaciones del fitoplancton están relacionadas con cambios en las características físicas y químicas del agua, así como con las condiciones hidrológicas, lo que es corroborado por el Análisis de Correspondencia Canónica (CCA), que muestra un patrón de evolución diferente en ambos sistemas. En Santa Olalla fueron observados ocho grupos funcionales (D, H_1, J, K, M, S_1, W_2 y Y), si bien los grupos D, W_2 y Y sólo predominaron en los primeros cuatro meses de estudio. El resto del tiempo, el sistema estuvo dominado sobre todo por los grupos H_1, K y S_1. Dulce mostró una distribución más compleja de grupos*

funcionales a lo largo del tiempo, observándose diez grupos (D, H_1, J, K, M, P, S_1, S_2, W_2 y Y). Algunas de las características de ambos sistemas, como la rápida fluctuación en el volumen de agua, la baja penetración de la luz o la escasa concentración de nutrientes inorgánicos, son condiciones de estrés para el fitoplancton, lo que puede explicar su baja diversidad y las fases de equilibrio registradas durante muchos meses en ambos humedales.

Palabras clave: *Dinámica fitoplanctónica, lagunas hipertróficas mediterráneas, diversidad del fitoplancton, grupos funcionales.*

INTRODUCTION

Very shallow lakes (Z_{max} < 5 m) are common wetland types in the Mediterranean region, particularly in Spain. Most of these shallow lakes are small (usually less than 10 ha) (Casado & Montes, 1995), isolated and highly interesting, both ecologically and in terms of biodiversity (Beklioglu *et al.*, 2007). During the last three decades, most of these small aquatic systems have been damaged due to human pressure. The deterioration of many northern temperate shallow lakes has been the focus of many studies, which have contributed greatly to a general understanding of the functioning of these ecosystems and the restoration of some of them (Perrow *et al*., 1997; Jeppesen *et al*., 2007; Søndergaard *et al*., 2008). Comparable information for Mediterranean shallow lakes is limited (Beklioglu *et al*., 2007), and the establishment of reference sites becomes necessary, although difficult given the intensive anthropogenic alteration of water bodies (Moss, 2007). Nevertheless, some Mediterranean shallow lakes located in protected areas appear to have remained unchanged. This is the case for Santa Olalla and Dulce, both located in Doñana National Park (Spain). Both wetlands are natural eutrophic to hypereutrophic systems, and their study could contribute to a better understanding of the behaviour of Mediterranean shallow lakes.

Phytoplankton, like other major components of aquatic systems, has been a preferred target for taxonomic study in shallow lakes, but despite the growing number of recent works on the forces that drive special and temporal phytoplankton patterns, our knowledge of phytoplankton ecology comes primarily from moderate-sized or large lakes (Padisák *et al*., 2003).

This work examines the monthly succession of phytoplankton during a two years study conducted in two mixed hypereutrophic shallow lakes in a south temperate area based on their algal functional groups (Reynolds *et al*., 2002; Padisák *et al*., 2003; Padisák *et al*., 2009), which are related to multidimensional features of the environment. A canonical correspondence analysis was used to ascertain the primary environmental variables driving phytoplankton community dynamics. This study was intended to contribute to the knowledge of phytoplankton dynamics in two unmodified shallow lakes from the Mediterranean region and evaluate the possibility of considering Santa Olalla and Dulce as reference systems in the area.

MATERIALS AND METHODS

Study Sites

The study was conducted in two shallow lakes, Santa Olalla and Dulce, over a period of 2 years, during which monthly measurements were taken from February 1998 to February 2000. Both wetlands are located on the south-western Atlantic coast of Spain (Fig. 1) in Doñana National Park. The climate of the area is predominantly Mediterranean, with dry and hot summers and little rainfall in the winters. Santa Olalla and Dulce are hypogenic shallow lakes where the main input into the systems is superficial waters from regional and local discharge flows (Manzano, 2001). Santa Olalla is larger than Dulce

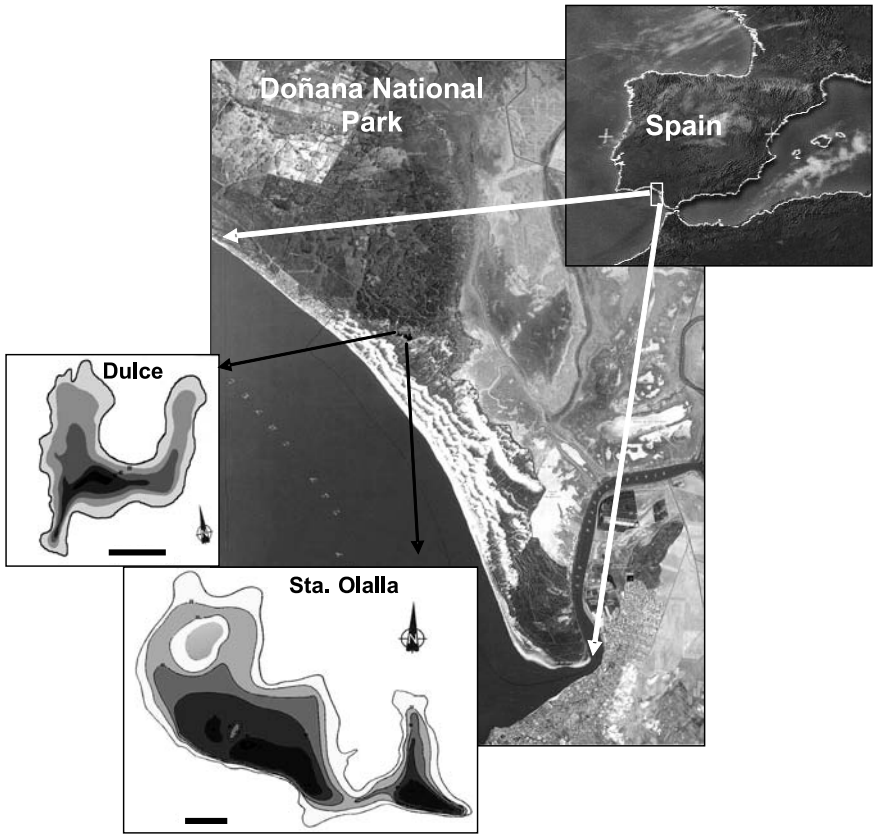

Figure 1. Location of the Santa Olalla and Dulce shallow lakes on the southwest coast of Spain. Shape and orientation of the lake basins. Bar 100 m. *Situación de las lagunas de Santa Olalla y Dulce en la costa suroeste de España. Orientación y forma de las cubetas de las lagunas. Barra 100 m.*

(Table 1), and both lakes are shallow systems with gentle slopes. The wind is strong over both shallow lakes, and vertical water mixing was observed during sampling. Santa Olalla and Dulce are only a few metres apart, and during seasons of high precipitation, they work as a single system (Toja *et al*., 1991, Álvarez *et al*., 2001). This behaviour was confirmed during the first months of the study, as there was very abundant precipitation early in the 1997-1998 hydrological cycle. The maximum values of water volume were registered during the initial part of the study period in both shallow lakes.

Physical and chemical parameters

Water conductivity and temperature were measured *in situ* using a WTW-LF 330/SET conductivimeter; pH and redox potential were determined using a 323 A WTW pH-meter, whereas dissolved oxygen (DO) concentrations were estimated with a WTW 340-B oxymeter. Measurements were taken 5-10 cm below the water surface at a location where the depth of the water column was approximately 0.5 m. Nutrient concentrations (NO_3, NO_2, NH_4^+, total N (TN), total P (TP) and soluble reactive phosphorus, SRP) were determined in the laboratory following standard methods (APHA 1989). Organic N was estimated by subtracting inorganic nitrogen (IN) from TN (IN = sum of NO_3, NO_2 and NH_4^+) and organic P by subtracting SRP from TP. The concentration of polyphenolic compounds was estimated according to Box's procedure (1983). The euphotic zone (Z_{eu}) was calculated as 2.7 times the Secchi depth (Cole, 1983).

Table 1. Physical and chemical variables and morphological features of the water columns of Santa Olalla (SO) and Dulce (D). (PAR) photosynthetically active radiation; (Water transp.) water transparency; (TA) total alkalinity; (PC) polyphenolic compounds; (TP) total phosphorous; (SRP) soluble reactive phosphorous; (TN) total nitrogen; (IN) inorganic nitrogen. *Características morfológicas y variables físico-químicas de la columna de agua en Santa Olalla (SO) y Dulce (D). (PAR) Radiación fotosintéticamente activa; (Water transp.) Transparencia del agua; (TA) Alcalinidad total; (PC) Compuestos polifenólicos; (TP) Fósforo total; (SRP) Fósforo reactivo soluble; (TN) Nitrógeno total; (IN) Nitrógeno inorgánico.*

	Volume (m^3)		Depth (m)		Water T (mean of 24 h) (°C)		PAR ($\mu E\ m^{-2}\ s^{-1}$)		pH		Water transp. (m)		O_2 midday (%)	
	SO	D	SO	D	SO	D	SO	D	SO	D	SO	D	SO	D
Mean	165315	34867	1.28	0.93	18.68	16.01	522.3	549.7	9.52	8.76	0.14	0.24	156.7	131.6
SD	253650	39885	0.52	0.42	4.96	5.47	142.5	287.1	0.88	0.93	0.08	0.22	65.7	47.5
Max	796776	141497	2.34	1.77	25.7	25.7	737	942.5	10.77	10.2	0.33	0.90	331	217
Min	290	3	0.44	0.0	10.8	8.39	315	65.9	7.33	6.77	0.05	0.04	28.5	45
n	23	23	23	23	15	11	15	11	24	23	24	23	24	23

	Conductivity ($\mu S\ cm^{-1}$)		TA ($meq\ L^{-1}$)		PC ($meq\ L^{-1}$ Tanic acid)		TP ($mg\ L^{-1}$)		SRP ($\mu g\text{-at}\ P\ L^{-1}$)		TN ($mg\ L^{-1}$)		IN ($\mu g\text{-at}\ N\ L^{-1}$)	
	SO	D	SO	D	SO	D	SO	D	SO	D	SO	D	SO	D
Mean	2692	1997	2.89	1.79	2.21	4.32	0.664	0.567	3.10	17.29	13.34	11.26	110.1	318.48
SD	2573	3373	1.28	0.79	1.93	5.56	0.367	0.521	5.00	24.54	20.72	20.67	49.1	571.01
Max	11600	16580	6.18	4.11	8.13	22.87	1.450	1.830	18.5	82.28	80.89	100.8	228.0	2445.0
Min	532	312	0.87	0.69	0.28	0.45	0.110	0.050	0.00	0.00	1.98	0.9	40.0	5.00
n	24	23	22	22	24	23	24	23	21	22	24	23	21	22

	IN/SRP		NO_2^- ($\mu g\text{-at}\ N\ L^{-1}$)		NH_4 ($\mu g\text{-at}\ N\ L^{-1}$)		Chl *a* ($mg\ m^{-3}$)		Rate of $PP^{14}C$ ($g\ C\ m^{-3}\ h^{-1}$)		Diversity Index (*H'*)		Total algae ($cells\ ml^{-1}$)	
	SO	D	SO	D	SO	D	SO	D	SO	D	SO	D	SO	D
Mean	51.98	68.92	1.2	108.43	108.9	210.04	365.18	230.00	1.29	0.88	1.11	1.79	$2.29{\cdot}10^7$	$4.64{\cdot}10^6$
SD	58.52	77.43	3.6	337.77	50.2	286.02	304.86	284.38	1.11	2.92	0.91	0.79	$4.69{\cdot}10^7$	$7.61{\cdot}10^6$
Max	215.71	307.27	13.0	1318.0	228.0	1427.0	1094.40	1324.0	3.61	2.92	3.16	3.67	$2.03{\cdot}10^8$	$2.28{\cdot}10^7$
Min	71	8.7	0.0	0.00	40.0	5.00	24.40	4.01	0.098	bdl[1]	0.04	0.12	1382	171
n	21	22	21	22	21	22	24	23	24	23	24	23	24	23

[1] Bellow the detection limit.

[1] Por debajo del límite de detección.

Carlson's index (TSI) (Carlson, 1977) was used to determine the trophic status of the lakes using Secchi depth, Chl *a* and TP.

Biological parameters

Phytoplanktonic chlorophyll-*a* (Chl *a*) concentrations were estimated monthly from triplicate samples. Water samples were filtered through Whatman GF/F glass microfibre filters (0.7 μm) *in situ* and placed in 5 ml of a 90 % acetone solution for extraction over 24 h at 4º C in darkness. Chl *a* was measured using a spectrophotometer (Cary/1C/ UV-Visible spectrophotometer Varian), and its concentration was calculated using the Jeffrey & Humphrey (1975) trichromatic method. The primary productivity of phytoplankton ($PP^{14}C$) was determined using the ^{14}C method according to Goldman *et al.* (1974). Photosynthesis was measured *in situ* by suspending one dark and two light polycarbonate bottles (®Nunclon, InterMed) 15 cm below the surface

for an incubation period of 2.5 h at midday. The optimal incubation time was determined in a preliminary experiment in which 10 light bottles and 5 dark bottles were incubated simultaneously. After the first hour, 2 light bottles and a dark one were removed every 30 min. The production rate was the highest 2.5 hours from the beginning of the experiment and then declined.

Samples collected to estimate phytoplankton abundance, biovolume and diversity were fixed with formaldehyde (4 % V/V) *in situ*. Species identifications as well as phytoplankton abundance and biovolume estimations were performed with an inverted optical microscope with epifluorescence (Olympus IX50). Individual phytoplankton cells were counted after filtering 0.1 ml (or different dilutions, depending on the samples) through black Isopore membrane filters GTBP with a 0.2 μm pore size and washing the cells with citrate buffer (pH 6). Each filter was examined for the autofluorescence of cell pigments at 1000X. The measurements were made under microscope according to the method described by Fry (1990). Biomass was calculated by measuring at least 30 individuals of each species and using simple geometric approximations (Rott, 1981). Species abundance was then converted into biovolume. The dominant phytoplankton species were considered to be those representing 10 % or more of the total sample biovolume. Dominant taxa were classified into functional groups according to Reynolds *et al*. (2002), Padisák *et al*. (2003) and Padisák *et al*. (2009).

Numerical analyses

The diversity of each sample was based on the Shannon index: $H' = -\Sigma\, p_i \cdot \log_2 p_i$ where p_i is the proportion of the biovolume represented by species *i* in the sample. The Bray-Curtis dissimilarity, calculated from biovolume data between pairs of chronologically contiguous samples, was used as an estimate of the differentiation of the community along the complex environmental gradient (Bloom, 1981; Salmaso, 1996).

The relationships among the measured variables were explored using correlation coefficients (Pearson for parametric and Spearman for non-parametric variables). Normality was examined by means of the Kolmogorov-Smirnov test. Canonical correspondence analysis (CCA) was performed using XLSTAT version 3.01 (Addinsoft 1995-2008) to elucidate the relationships between the phytoplankton and the environmental variables over the study period, using all data from both shallow lakes. To satisfy the assumptions of normality and homogeneity of variance of the data, all data were logarithmically transformed before the analyses.

RESULTS

Evolution of physical and chemical parameters

The mean values of the physical, chemical and morphological variables of Santa Olalla and Dulce are summarised in Table 1. Both systems exhibited large variations in water volume. Maximum values were recorded in the beginning of the investigation period (February 1998). Santa Olalla had a maximum depth of 2.34 m and Dulce 1.77 m. In September 1999, both shallow lakes reached their lowest water volume for the study period (0.44 m for Santa Olalla, dry for Dulce), with a gradual increase in volume during the following months. Santa Olalla exhibited higher average pH, water temperature, oxygen concentration, conductivity, total alkalinity, total P and total N values, whereas Dulce exhibited higher values for water transparency, polyphenolic compounds, SRP and inorganic N. N-NO_3^- was not found in Santa Olalla during the study period and N-NO_2^- was measurable in only 4 months (March, April, October and November 1999). In Dulce Lake, the measured value for N-NO_3^- was 0 in most months except for June 1999 and February 2000, whereas N-NO_2^- was present from March–May and July–August. Inorganic nitrogen in both systems is mainly in the reduced form of ammonia. The variations in SRP and IN over the months of the study period are illustrated in Figure 2A. It should be noted that no stratification of the water column occurred in either of the two systems. The euphotic zone was

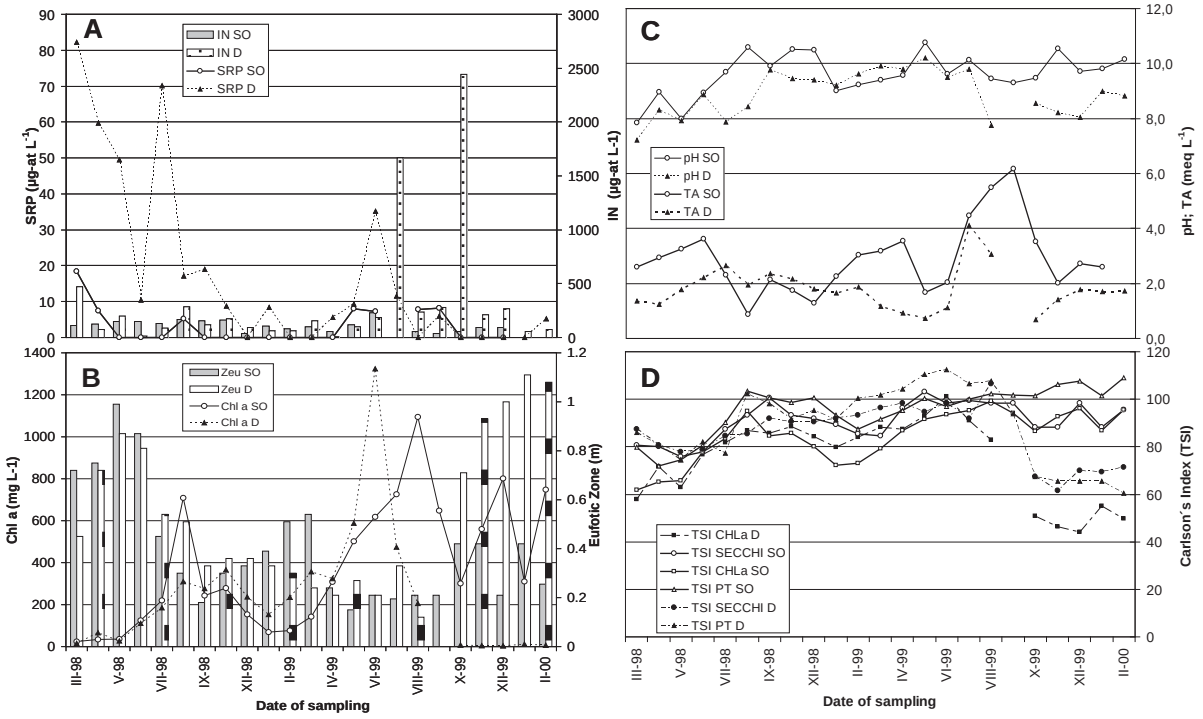

Figure 2. Changes over time in Santa Olalla and Dulce in the following variables: values of SRP and inorganic nitrogen (IN) (2A); concentration of Chl *a* and depth of the euphotic zone (2B); pH and total alkalinity (TA) (2C); Carlson's index values (calculated based on Secchi depth, TP and the concentration of Chl *a*) showing the trophic status in both systems (2D). *Cambios a lo largo del tiempo en Santa Olalla y Dulce en: los valores de SRP y nitrógeno inorgánico (IN) (2A); concentración de Chl* a *y profundidad de la zona eufótica (2B); pH y alcalinidad total (2C); valores del índice de Carlson (calculados a partir de los valores del disco de Secchi, fósforo total y concentración de Chl* a*) mostrando el estado trófico de ambos sistemas (2D).*

shallow in both wetlands (Fig. 2B), primarily due to the abundance of phytoplankton and the concentration of polyphenolic compounds.

The Carlson's index values based on Secchi depth, TP and the concentration of Chl *a* (Fig. 2D) were higher than 60 for both lakes, except for Chl *a* in September 1999 when Dulce dried up. The index tends to increase towards the hypereutrophic condition in both lakes over time. Only Dulce, after drying, showed lower index values, but in general these values remained within the range of eutrophy (Fig. 2D).

Chl *a*, primary production rates and phytoplankton abundance, biovolume and diversity

The average phytoplankton Chl *a* concentration was higher in Santa Olalla than in Dulce (Table 1). Maximum and minimum values were observed in Dulce in June 1999 (1324 mg Chl *a* m^{-3}) and in December 1999 (4 mg Chl *a* m^{-3}), respectively (Fig. 2B). In Santa Olalla, maximum phytoplankton production ($PP^{14}C$) was recorded in September 1999 (3.61 g C m^{-3} h^{-1}) and the minimum in May 1998 (0.098 g C m^{-3} h^{-1}). In Dulce, the highest primary production rate was recorded in August 1998 (2.92 g C m^{-3} h^{-1}), whereas the lowest value (below the detection limit of the scintillation counter apparatus) was recorded between October 1999 and February 2000, just after Dulce's dry period.

Eight functional groups were recorded in Santa Olalla: D, H_1, J, K, M, S_1, W_2 and Y codons (Table 2). The D (represented by *Cyclotella* spp. of small-cell size), W_2 (represented by *Trachelomonas volvocina*) and Y (*Cryptomonas phaseolus*) groups only appeared during

the first study period (February to May 1998), followed by S_1 (represented by *Planktothrix agardhii*) and H_1 (represented by nitrogen-fixing cyanobacteria species like *Anabaena spiroides* and *Anabaenopsis circularis*) groups in June and July of 1998. In July, H_1 was accompanied by the M (*Microcystis aeruginosa*) group. From August 1998 to January 1999, the system was dominated by the K group of small-celled non-vacuolate cyanobacteria types (*Aphanothece clathrata* and *Chroococcus dispersus*, which represented more than 80 % of the total phytoplankton biovolume in those months). From February to April 1999, the K group appeared together with the H_1 group (*A. circularis*) and, to a lesser extent, non-gelatinous and non-motile Chlorococcales (J group–*Tetraedron minimum*). From May 1999 until October of the same year, the S_1 group (this time with *Leptolyngbya* sp. and *Limnothrix amphigranulata*) predominated again, but the J codon (*Pediastrum boryanum* and *Tetraedron minimum*) was also present from August onwards. From November to December, the K group, accompanied by the S_1 codon, dominated once again. From January to February 2000, the K group appeared together with the H_1 group.

Dulce Lake exhibited a more complex distribution of phytoplankton functional groups over time. Ten functional groups were observed during the study period (Table 3). During the first four months (February to May 1998), the J group (*Pediastrum boryanum*, *Scenedesmus opoliensis* and *S. ovalternus*) appeared together with the W_2 (*Trachelomonas volvocina*), D (*Cyclotella*

Table 2. Dominant phytoplankton species in Santa Olalla. In parentheses: % of the biomass of species in each month. Only takes into account the % of species with a biomass equal to or greater than 10 %. The durations of the phases are taken in accordance with the results of the correspondence analysis (Fig. 4). *Especies fitoplanctónicas dominantes en Santa Olalla. En paréntesis % de biomasa de cada especie. Sólo se ha tenido en cuenta aquellas especies con un % de biomasa igual o superior al 10 %. La duración de cada fase es establecida de acuerdo con los resultados del Análisis de Correspondencia (Fig. 4).*

Santa Olalla	1st dominant specie	2nd dominant specie	3rd dominant specie	Functional groups	Phases	*H′*
February 98	*Trachelomonas volvocina* (35 %)	*Cryptomonas phaseolus* (28 %)	*Cyclotella* sp. (13 %)	W_2-Y-D	P1SO	2.96
March 98	*Trachelomonas volvocina* (81 %)	*Cryptomonas phaseolus* (10 %)		W_2-Y		3.16
April 98	*Cyclotella* sp. (74 %)	*Trachelomonas volvocina* (20 %)		D- W_2		1.62
May 98	*Cyclotella* sp. (52 %)	*Trachelomonas volvocina* (11 %)		D- W_2		1.12
June 98	*Anabaena spiroides* (28 %)	*Planktothrix agardhii* (28 %)	*Cryptomonas phaseolus* (28.3 %) *Trachelomonas volvocina* (13 %)	H_1-S_1-Y- W_2		0.93
July 98	*Anabaenopsis circularis* (77 %)	*Microcystis aeruginosa* (12 %)		H_1-M	P2SO	2.37
August 98	*Chroococcus dispersus* (86 %)	*Aphanothece clathrata* (10 %)		K		0.44
September 98	*Aphanothece clathrata* (84 %)	*Chroococcus dispersus* (15 %)		K		0.04
October 98	*Chroococcus dispersus* (86 %)	*Aphanothece clathrata* (12 %)		K		0.41
December 98	*Chroococcus dispersus* (60 %)	*Aphanothece clathrata* (39 %)		K		0.1
January 99	*Chroococcus dispersus* (79 %)	*Anabaenopsis circularis* (11 %)		K- H_1		0.71
February 99	*Anabaenopsis circularis* (55 %)	*Pediastrum boryanum* (25 %)	*Chroococcus dispersus* (10 %)	H_1-J-K		0.59
March 99	*Anabaenopsis circularis* (55 %)	*Chroococcus dispersus* (20 %)		H_1-K		0.51
April 99	*Chroococcus dispersus* (20 %)	*Aphanothece clathrata* (18 %) *Tetraedron minimum* (18 %)	*Chlorella* sp. (17 %) *Microcystis aeruginosa* (11 %)	K-J-M		0.91
May 99	*Leptolyngbya* sp. (44 %)	*Microcystis aeruginosa* (17 %)		S_1-M	P3SO	2.53
June 99	*Leptolyngbya* sp. (89 %)			S_1		1.53
July 99	*Limnothrix amphigranulata* (70 %)	*Microcystis aeruginosa* (10 %)		S_1-M		1.63
August 99	*Limnothrix amphigranulata* (58 %)	*Monoraphidium griffithii* (18 %)		S_1-J		2.1
September 99	*Limnothrix amphigranulata* (44 %)	*Leptolyngbya* sp. (20 %) *Pediastrum boryanum* (20 %)		S_1-J		1.8
October 99	*Leptolyngbya* sp. (34 %)	*Limnothrix amphigranulata* (27 %)	*Tetraedron minimum* (18 %)	S_1-J		2.38
November 99	*Aphanothece clathrata* (34 %)	*Limnothrix amphigranulata* (28 %)	*Scenedesmus acuminatus* (21 %)	K- S_1-J	P2SO	0.32
December 99	*Aphanothece clathrata* (39 %)	*Scenedesmus acuminatus* (22 %)	*Limnothrix amphigranulata* (18 %)	K-J- S_1		0.29
January 00	*Anabaenopsis circularis* (47 %)	*Aphanothece clathrata* (28 %)	*Scenedesmus acuminatus* (23 %)	H_1-K		0.42
February 00	*Anabaenopsis circularis* (49 %)	*Aphanothece clathrata* (32 %)	*Scenedesmus acuminatus* (13 %)	H_1-K		0.26

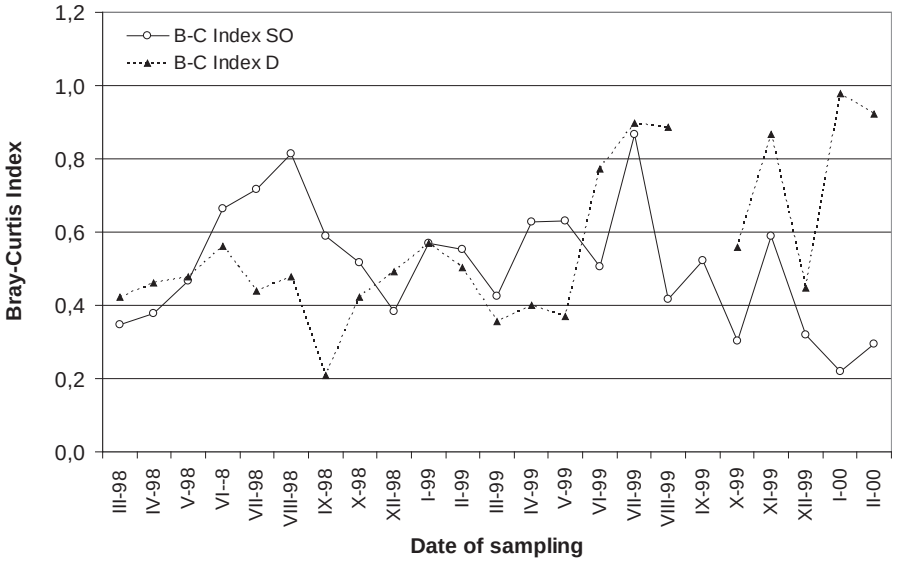

Figure 3. Rates of community change in Santa Olalla and Dulce estimated by the Bray-Curtis index, calculated from biovolume data for the chronologically contiguous phytoplankton samples. *Tasa de cambio de la comunidad fitoplanctónica en Santa Olalla y Dulce estimada mediante el cálculo del índice de Bray-Curtis a partir de los datos del biovolumen en muestras cronológicamente consecutivas.*

sp.) or P (*Aulacoseria* sp.) groups, depending on the month. From June to September 1998, the P-M groups (*Microcystis aeruginosa*) co-dominated with W_2 or several groups belonging to cyanobacteria (H_1 –*Anabaena spiroides*, S_1–*Planktothrix agardhii*, S_2–*Arthrospira platensis* or K–*Chroococcus dispersus*). In October 1998, the Y group (*Cryptomonas phaseolus*) co-dominated with the J group. From December 1998 to May 1999, the H_1 group appeared together with the J codon almost every month. In June 1999, the J and M groups predominated, whereas the Y group did so in July. In August, before its dry period, Dulce was strongly dominated by *Arthrospira platensis* (group S_2). After drying up (October 1999 to February 2000), Dulce was dominated by *Cyclotella* sp. and other small-sized diatoms (D group) except in January, where the predominant group was Y.

Figure 3 illustrates an estimate of the community change rate (Bray-Curtis Index) (Bloom, 1981). The values are normally very dependent on the time interval used. Values tend to be low for samples collected during short time intervals and show maximum values for samples collected in different seasons (Salmaso, 2003). In this study, four week intervals were used to observe the variation of the phytoplankton community. The community change rate for Santa Olalla increases gradually in the first study period (from March to August 1998), after which changes are smaller, except in July 1999, where the change rate once again had a high value. The Bray-Curtis index exhibited low values during Dulce's first hydrological cycle and increased during the second cycle, between May and June 1999, and especially just after Dulce's dry period, between November 1999 and February 2000.

Low Shannon index values (H') were obtained for both shallow lakes, with an average of 1.11 for Santa Olalla and 1.79 for Dulce (Table 1). In Santa Olalla, the highest biodiversity ($H' = 3.16$) was observed at the beginning of the study (February and March 1998). Afterwards, biodiversity decreased continuously until the winter of 1998 (though it had a peak in July 1998), when it recovered slightly only to decrease once again in the winter of 1999-2000. It is interesting to note that in September 1998 Santa Olalla was completely dominated by cyanobacteria and had a very low H' value (0.04) (Table 2). Dulce had greater biodiversity than Santa Olalla most

Table 3. Dominant phytoplankton species in Dulce. In parentheses: % of the biomass of species in each month. Only takes into account the % of species with a biomass equal to or greater than 10 %. The duration of the phases are taken in accordance with the results of the correspondence analysis (Fig. 4). *Especies fitoplanctónicas dominantes en Dulce. En paréntesis % de biomasa de cada especie. Sólo se ha tenido en cuenta aquellas especies con un % de biomasa igual o superior al 10 %. La duración de cada fase es establecida de acuerdo con los resultados del Análisis de Correspondencia (Fig. 4).*

Dulce	1st dominant specie	2nd dominant specie	3rd dominant specie	Functional groups	Phases	H'
February 98	*Scenedesmus ovalternus* (44 %)	*Scenedesmus opoliensis* (12 %)	*Cryptomonas phaseolus* (10 %) *Trachelomonas volvocina* (10 %)	J-Y- W_2	P1D	1.46
March 98	*Trachelomonas volvocina* (62 %)	*Scenedesmus opoliensis* (22 %) *Pediastrum boryanum* (22 %)		W_2-J		1.07
April 98	*Cyclotella* sp. (47 %)	*Pediastrum boryanum* (15 %)	*Trachelomonas volvocina* (13 %) *Scenedesmus opoliensis* (12 %)	D-J- W_2		2.3
May 98	*Trachelomonas volvocina* (29 %)	*Scenedesmus opoliensis* (21 %)	*Aulacoseira* sp. (13 %)	W_2-J-P		1.64
June 98	*Microcystis aeruginosa* (23 %)	*Aulacoseira* sp. (20 %)	*Anabaena spiroides* (15 %) *Trachelomonas volvocina* (11 %)	M-P-H_1-W_2		2.25
July 98	*Planktothrix agardhii* (40 %)	*Microcystis aeruginosa* (21 %)	*Aulacoseira* sp. (17 %)	S_1-M-P		1.64
August 98	*Aulacoseira* sp. (25 %)	*Arthrospira platensis* (23 %)	*Microcystis aeruginosa* (10 %)	P-S_2-M		1.61
September 98	*Arthrospira platensis* (23 %)	*Chroococcus dispersus* (19 %)	*Aulacoseira* sp. (16 %) *Anabaena spiroides* (15 %)	S_2-K-P- H_1	P2D	1.82
October 98	*Scenedesmus quadricauda* (22 %)	*Cryptomonas phaseolus* (18 %)		J-Y		3.67
December 98	*Anabaena spiroides* (47 %)	*Pediastrum boryanum* (13 %)		H_1-J		1.92
January 99	*Anabaena spiroides* (53 %)	*Monoraphidium contortum* (15 %)		H_1-J	P3D	1.195
February 99	*Anabaena spiroides* (48 %)	*Pediastrum boryanum* (42 %)		H_1-J		1.13
March 99	*Anabaenopsis circularis* (44 %)	*Pediastrum boryanum* (20 %)	*Anabaena spiroides* (17 %)	H_1-J		1.99
April 99	*Anabaena spiroides* (36 %)	*Anabaenopsis circularis* (23 %)	*Microcystis aeruginosa* (12 %)	H_1-M		2.17
May 99	*Anabaenopsis circularis* (25 %)	*Scenedesmus quadricauda* (23 %)	*Scenedesmus opoliensis* (17 %) *Anabaena spiroides* (15 %)	H_1-J		1.95
June 99	*Microcystis aeruginosa* (47 %)	*Scenedesmus quadricauda* (37 %)		M-J	P2D	0.55
July 99	*Cryptomonas phaseolus* (81 %)			Y	P4D	3.06
August 99	*Arthrospira platensis* (83 %)	*Cyclotella* sp. (13 %)		S_2-D		0.12
September 99*						
October 99	*Others small-cell diatoms* (89 %)			D		2.39
November 99	*Others small-cell diatoms* (69 %)			D	P2D	2.5
December 99	*Others small-cell diatoms* (69 %)	*Euglena gracilis* (20 %)		D- W_2		2.47
January 00	*Cryptomonas phaseolus* (81 %)	*Monoraphidium contortum* (10 %)		Y-J		1.17
February 00	*Others small-cell diatoms* (71 %)	*Monoraphidium arcuatum* (15 %)		D-J		0.85

* Dulce remained dry during September 1999.

of the time. The H' values for Dulce exhibited two peaks: October 1998 ($H' = 3.67$, maximum value) and July 1999 ($H' = 3.06$). The minimum value was observed in August 1999 ($H' = 0.12$) shortly before Dulce dried up (Table 3).

The canonical correspondence analysis (CCA) showed a significant value ($p < 0.0001$) for the permutation probe. The first two axes together explained 46.36 % of the total variability in the data. The first CCA axis separated the two shallow lakes except for the first four months of the study in Santa Olalla, which are placed next to Dulce's months (Fig. 4) since both lakes were in superficial contact over that period. Santa Olalla appears to the right, influenced by higher TN and TP concentrations, pH, conductivity and higher biovolumes of cyanobacteria (particularly *Aphanothece clathrata*, *Limnothrix amphigranulata* and *Leptolyngbya* sp.) and chlorophytes (*Scenedesmus acuminata* and *Tetraedron minimum*) (Fig. 5). Dulce is located on the left of the diagram, influenced by higher values for inorganic nitrogen (IN), phosphorous (SRP), the depth of the euphotic zone and higher total biovolumes of Bacillariophyta (*Aulacoseria* sp.), Euglenophyta (especially *Trachelomonas volvocina*) and Cryptophyta (*Cryptomonas phaseolus*). The second CCA axis indicated a grad-

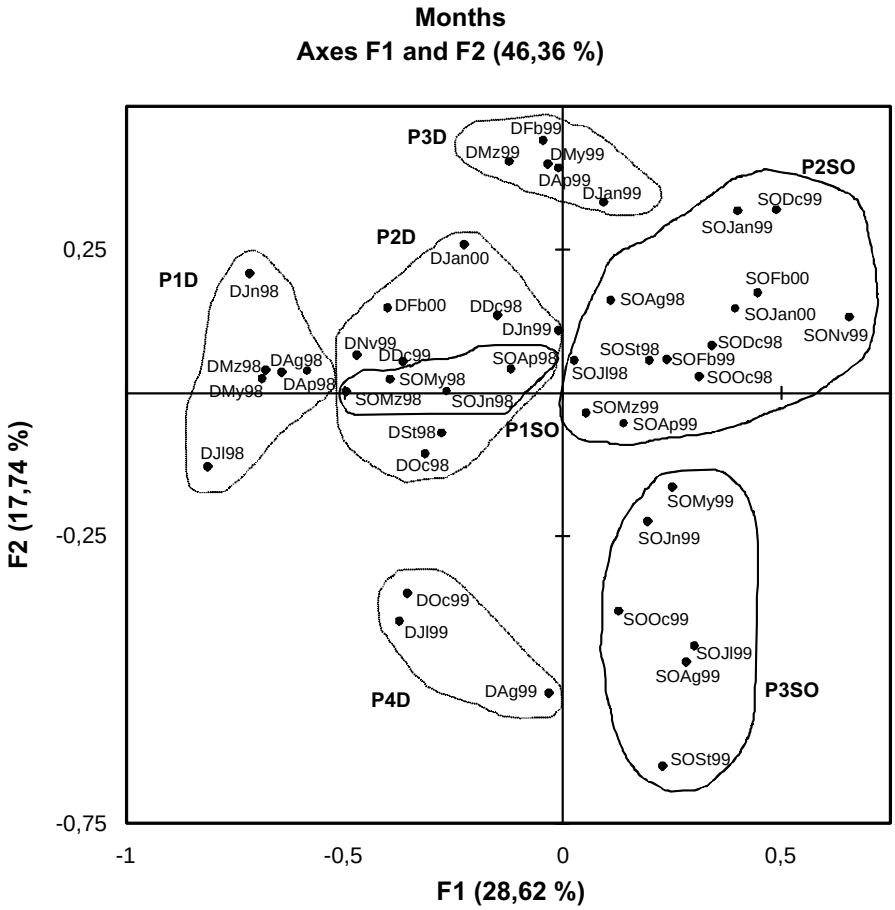

Figure 4. Score dispersion of samples along the first two CCA axes. Samples were grouped into phases over time. P1SO, P2SO and P3SO: different phases in Santa Olalla. P1D, P2D, P3D and P4D: different phases in Dulce. *Dispersión de las muestras en los dos primeros ejes del CCA. Las muestras se agrupan en fases a lo largo del tiempo. P1SO, P2SO y P3SO: Diferentes fases de Santa Olalla. P1D, P2D, P3D y P4D: Diferentes fases de Dulce.*

ual move towards hypereutrophication in both systems over the study period. There is a maximum in summer 1999 (Fig. 4), determined by high values of TN, the TN:TP ratio, conductivity, total alkalinity and temperature and low water volumes in the lakes (Fig. 5). The lakes revert to a more moderate eutrophic state in the autumn and winter of 1999-2000.

DISCUSSION

Santa Olalla and Dulce are two natural eutrophic/hypereutrophic shallow lakes with very high TN, TP and Chl *a* concentrations, phytoplanktonic biomass and, especially, primary production, along with low diversity (Table 1). Cyanobacteria dominated most of the study period in both shallow lakes , particularly in Santa Olalla, which exhibited a more eutrophic state, especially during the final months of the study (Fig. 2D).

In both Santa Olalla and Dulce, N and P are predominantly in organic form, inorganic nutrients are in very low concentrations most of the time (Fig. 2A), and the N/P ratio (Table 1) indicates a deficiency in P for most of the months in both shallow lakes (Coleto, 2003). Given the high primary production in both systems, this deficiency does not appear to be limiting phytoplankton growth. In addition, high rates of de-

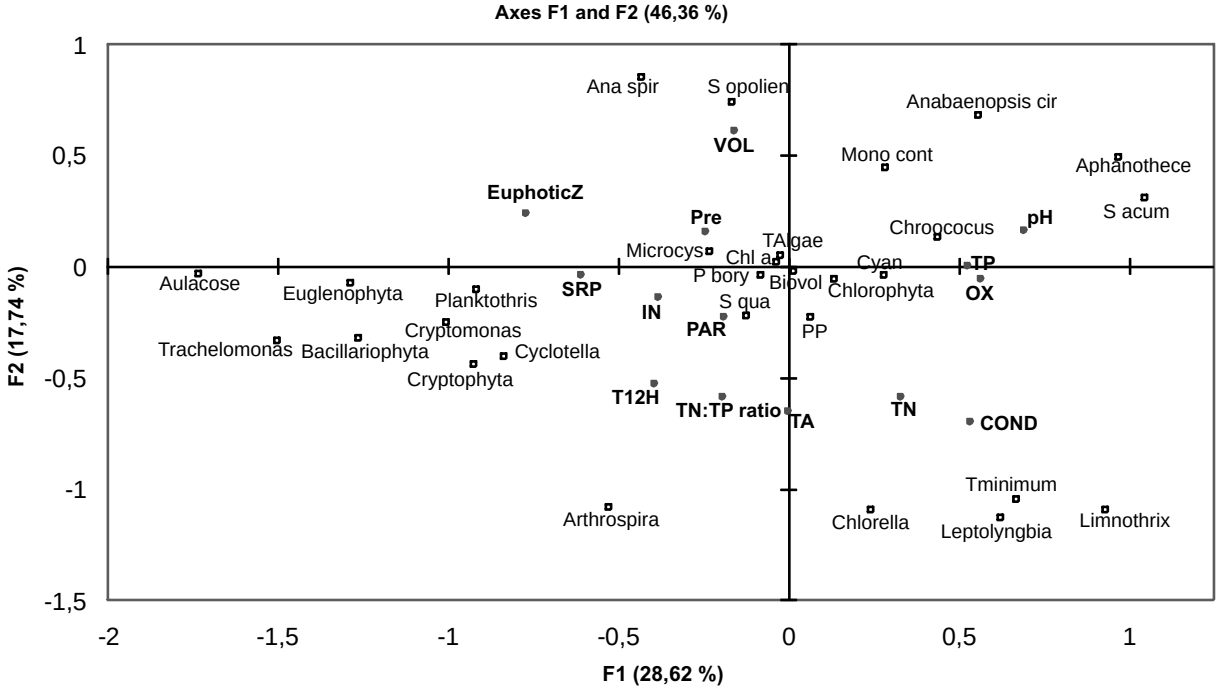

Figure 5. Scores of phytoplankton species biovolume and abiotic variables according to the correspondence analysis using all data from both shallow lakes. (Ana spir) *Anabaena spiroides*; (Anabaenopsis cir) *Anabaenopsis circularis*; (Aphanothece) *Aphanothece clathrata*; (Arthrospira); *Arthrospira platensis*; (Aulacose) *Aulacoseria* sp.; (Cyclotella) *Cyclotella* sp.; (Chlorella) *Chorella* sp.; (Chroococcus) *Chroococcus dispersus*; (Cryptomonas) *Cryptomonas phaseolus*; (Leptolyngbya) *Leptolyngbya* sp.; (Limnothrix) *Limnothrix amphigranulata*; (Microcy) *Microcystis aeruginosa*; (Mono cont) *Monoraphidium contortum*; (P bory) *Pediastrum boryanum*; (Planktothrix) *Planktothrix agardhii*; (S acum) *Scenedesmus acuminatus*; (S opolien) *Scenedesmus opoliensis*; (S qua) *Scenedesmus quadricauda*; (T minimum) *Tetraedron minimum*; (Trachelomonas) *Trachelomonas volvocina*; (Bacillariophyta) total biovolume of Bacillariophyta; (Biovol) total biovolume of phytoplankton; (Chl *a*) total Chlorophyll *a*; (Chlorophyta) total biovolume of Chlorophyta; (Cryptophyta) total biovolume of Cryptophyta; (Cyan) total biovolume of cyanobacteria; (Euglenophyta) total biovolume of Euglenophyta; (PP) primary production rate; (TAlgae) total number of phytoplankton cells; (COND) electrical conductivity; (Euphotic Z) euphotic zone depth; (OX) dissolved oxygen; (IN) inorganic nitrogen concentration; (PAR) photosyntetically active radiation; (Pre) rain precipitation; (SRP) soluble reactive phosphorus; (TA) total alkalinity; (T12H) temperature at midday; (TN) total nitrogen; (TN:TP ratio) ratio of total nitrogen: total phosphorus rate; (TP) total phosphorus; (VOL) water volume of the shallow lakes. *Situación de las variables abióticas y de las especies de fitoplancton según su biovolumen, conforme al Análisis de Correspondencia, usando los datos de ambas lagunas. (Ana spir)* Anabaena spiroides*; (Anabaenopsis cir)* Anabaenopsis circularis*; (Aphanothece)* Aphanothece clathrata*; (Arthrospira)* Arthrospira platensis*; (Aulacose)* Aulacoseria sp.*; (Cyclotella)* Cyclotella *sp.; (Chlorella)* Chorella *sp.; (Chroococcus)* Chroococcus dispersus*; (Cryptomonas)* Cryptomonas phaseolus*; (Leptolyngbya)* Leptolyngbya *sp.; (Limnothrix)* Limnothrix amphigranulata*; (Microcy)* Microcystis aeruginosa*; (Mono cont)* Monoraphidium contortum*; (P bory)* Pediastrum boryanum*; (Planktothrix)* Planktothrix agardhii*; (S acum)* Scenedesmus acuminatus*; (S opolien)* Scenedesmus opoliensis*; (S qua)* Scenedesmus quadricauda*; (T minimum)* Tetraedron minimum*; (Trachelomonas)* Trachelomonas volvocina*; (Bacillariophyta) Biovolumen total de Bacillariofitas; (Biovol) Biovolumen total del fitoplancton; (Chl* a*) Clorofila* a *total; (Chlorophyta) Biovolumen total de Clorofitas; (Cryptophyta) Biovolumen total de Cryptofitas; (Cyan)) Biovolumen total de Cianobacterias; (Euglenophyta)) Biovolumen total de Euglenofitas; (PP) Tasa de producción primaria; (TAlgae) Número total de células fitoplanctónicas; (COND) Conductividad; (Euphotic Z) Profundidad de la zona eufótica; (OX) Oxígeno disuelto; (IN) Concentración de N inorgánico; (PAR) Radiación fotosintéticamente activa; (Pre) Precipitaciones; (SRP) Fósforo reactivo soluble; (TA) Alcalinidad total; (T12H) Temperatura del agua al medio día; (TN) Nitrógeno total; (TN:TP ratio) relación Nitrógeno total: fósforo total; (TP) Fósforo total; (VOL) Volumen de agua en las lagunas.*

composition were observed in both Santa Olalla and Dulce (Álvarez *et al*., 2001), which indicates a rapid mineralisation of organic matter and suggests that primary producers assimilate dissolved nutrients almost instantaneously after mineralisation (López-Archilla *et al*., 2004). Most of the decaying organic matter is found in the sediments of the lakes. Some of the P released may be re-

tained in the sediments, to be adsorbed primarily by Fe in these systems (Coleto, 2003). However, this fraction is readily bio-available to organisms depending on the pH and redox state of the sediment-water interface (Scheffer, 1998), especially when these areas become anoxic, which occurs in several months during the study period (data not shown). The low values of oxygen in the water column in Santa Olalla and Dulce appear to be linked to a slightly higher concentration of SRP and IN (Fig. 5), favouring the presence of a higher number of species (particularly bacillariophytes, cryptophytes, euglenophytes and some species of chlorophytes). However, these species appear for short periods before being replaced by species of cyanobacteria and chlorophytes when the inorganic nutrient concentrations became even lower. These species are strongly dominant in the phytoplanktonic community, and their presence suggests that they have the ability to rapidly capture the inorganic nutrients released through decomposition and that they compete more successfully for such inorganic nutrients than cryptophytes, bacillariophytes or euglenophytes. This capacity may be related to their relatively smaller cell size (*Aphanothece clathrata, C. dispersus, T. minimum*) or their filamentous shape with small diameter (*Limnothrix amphigranulata* and *Leptolyngbya* sp.) and the consequent increase in their surface area/volume ratio.

Despite the facts that Santa Olalla and Dulce have similar physical and chemical features, are in close proximity to each other and are hydrologically connected, their phytoplankton dynamics are markedly different, which appears to be due to small environmental differences between the lakes and especially the different hydrological regimes, as shown by the CCA analysis (Figures 4 and 5). This analysis discriminates between the Santa Olalla and Dulce samples and shows a different evolution pattern in each shallow lake. Three different phases related to the increase of the trophic level could be observed in Santa Olalla (phase 1 from March 1998 to June 1998; phase 2 from July 1998 to April 1999, phase 3 from May 1999 to October 1999 and phase 2 again from November 1999 to February 2000) (Fig. 4), whereas Dulce presented a more complex pattern of four different phases: phase 1 from March 1998 to August 1998; phase 2 from September 1998 to December 1998 and phase 3 from January to May 1999; in June 1999, Dulce returned to phase 2 and entered into phase 4 from July 1999 until October 1999. From November 1999 to February 2000, the system returned to phase 2 once again (Fig. 4).

Phase 1 in Santa Olalla (Fig. 4), at the beginning of the study, is located between phases 1 and 2 of Dulce. In this period, both lakes were very similar and the phytoplankton assemblage was dominated by the D, Y and W_2 functional groups in both lakes, although the J group was also important in Dulce during this period. The D-Y-J groups are a common element in shallow enriched systems (Reynolds *et al*., 2002; Romo and Villena, 2005), whereas the W_2 group (represented by *Trachelomonas volvocina*) is found in aerated lakes (Reynolds *et al*., 2002). According to Padisák *et al*. (2003), the relationships of this functional codon with other groups and with environmental patterns that enhance its occurrence have remained rather unclear. In this study, all of those functional groups are related to low conductivity, greater depth of the euphotic zone, maximum water volume of the lakes and the presence of inorganic nutrients, especially SRP (Fig. 5). Cyanobacteria appeared in Santa Olalla for the first time during the last month of phase 1 (June 1998). *A. spiroides* (H_1 group) and *Planktothrix agardhii* (S_1 group) jointly accounted for 56 % of the total biomass, but *Cryptomonas phaseolus* (Y) and *Trachelomonas volvocina* (W_2) together represented 27 % (Table 2). June 1998, together with the first month of phase 2 (July 1998), appeared to be a period of transition to a different state, where the predominance of cyanobacteria is practically absolute.

Functional group K appeared during the first appearance of phase 2 in Santa Olalla (Fig. 4 and Table 2) and was present almost every month during this phase. Reynolds *et al*. (2002) found that this group of small-celled colonial and non-vacuolate cyanobacteria survives well at a high pH, and Padisák *et al*. (2003) observed its presence in shallow, nutrient rich, turbid lakes. In

Santa Olalla, the appearance of this group is related to high conductivity and pH, low depth of the euphotic zone, low SRP concentration and a low TN:TP ratio (Fig. 5), a feature that is shared with *Anabaenopsis circularis* (H_1), which occurs during several months in this phase.

Phase 3 (Fig. 4) corresponds to higher temperatures, conductivity and total alkalinity, low water volume in the lake and a shallow depth of the euphotic zone (all features from late spring and early summer) (Fig. 5) and the appearance of the S_1 (*Limnothrix amphigranulata* and *Leptolyngbya* sp.) functional group, which may be accompanied by the M (*Microcystis aeruginosa*) or J (*P. boryanum* or *T. minimum*) codons. Reynolds *et al*. (2002) related group S_1 to shallow enriched lakes where light is increasingly the limiting constraint, as is the case here. In contrast with *L. amphigranulata*, another species of the same genus, *L. redekei*, is a typical phytoplankton species of turbid mixed layers of the lakes and lowland rivers of Central Europe (Meffert, 1988). *Limnothrix redekei* has also been observed, but in winter/spring, in some shallow lakes such as Lake Melangee (Germany) (Mischke, 2003) or Lake Kastoria (Greece), a shallow Mediterranean lake where this species made up 99 % of the phytoplankton biomass in the winter (Moustaka-Gouni *et al*., 2007). In Santa Olalla, *L. amphigranulata* appears in months when the water reaches its most turbid and hottest state, which might suggest that this species has requirements similar to those of *L. redekei* but prefers a higher temperature. *Planktothrix agardhii*, which appeared during the last month of phase 1 (June 1998), is another member of the S_1 functional group. Wiedner (1999) investigated the influence of mixing on the proportion of *Planktothrix* vs. *Limnothrix* and showed that *Planktothrix* exhibits faster uptake kinetics that *Limnothrix* when P is provided in pulses and at low concentration. This may be the reason why *Planktothrix* only appears in June 1998, when the turbidity of the water is high but there is still some SRP in the lake, whereas inorganic P is practically non-existent during phase 3.

After phase 3, the system returned to phase 2 (Fig. 4). The depth of the euphotic zone increased slightly, as did the water volume of the lake. There was a decrease in water temperature, but the rest of the environmental conditions were similar to those found during the first occurrence of phase 2. The K and H_1 functional groups were present again in this period. Villena & Romo (2003) found that small colonies of chroococcoid cyanobacteria replaced filamentous cyanobacteria, primarily in the summer, in Lake Albufera (Spain), a shallow Mediterranean lake similar to Santa Olalla in terms of the persistent dominance of cyanobacteria and shallow water (Romo & Miracle, 1994). In Santa Olalla, there is also a co-existence or alternation between chroococcoid and filamentous cyanobacteria. Villena & Romo (2003) found experimental evidence that under conditions of TP levels lower than 0.3 mg l^{-1}, water quiescence and low rates of zooplankton grazing, filamentous cyanobacteria were replaced by chroococcoid cyanobacteria in Lake Albufera. However, in Santa Olalla, the TP level was always greater than 0.8 mg l^{-1} during this second phase 2 in which such cyanobacteria were registered. The filamentous cyanobacterium *Anabaenopsis circularis* (H_1 group) was only negatively correlated with water temperature ($P = 0.008$), whereas the chroococcoid *Aphanothece* (K group) was negatively correlated with the number of hours of light ($p = 0.001$) and light intensity ($p = 0.019$). This suggests that in Santa Olalla, the predominance of one group over another is more related to day length than it is to TP concentration.

As before, Dulce exhibited a more complex pattern than Santa Olalla, and the stages are not related as clearly to the functional groups. The J, Y, W_2, D, P, M, H_1 and S_1 functional codons alternated randomly during phase 1 (Table 3 and Fig. 4). In the last three months of this period (June to August 1998), different cyanobacteria appeared and co-dominated with *Aulacoseria* sp. (P group). Reynolds *et al*. (2002) associated the P group with lakes of lower latitudes or temperate lakes in the summer when the epilimnion is continuously mixed, although this can also happen in shallow non-stratified lakes such as Dulce, which has a water column that is completely mixed due to wind and its gentle slopes (Álvarez *et al*., 2001). The P group is characteristically associated

with desmids (Reynolds *et al*., 2002). However, these kinds of associations with cyanobacteria are not often found in the literature. Phase 1 was characterised by a high depth of the euphotic zone, high precipitation, higher SRP and inorganic N concentrations and moderate pH values (Fig. 5).

Phase 2 was characterised by lower values for the euphotic zone depth, precipitation and SRP concentration compared to those of phase 1, whereas phase 3 appeared to be marked primarily by the volume of the water body and low TA, TN:TP ratio, temperature, TN and conductivity values (Fig. 4 and 5). Both phases were defined by the dominance of filamentous cyanobacteria with heterocytes (H_1 functional group: *A. spiroides* and *Anabaenopsis circularis*) accompanied by several chlorophytes of the J functional group (*P. boryanum*, *Monoraphidium contortum* or *Scenedesmus quadricauda*) except in October, when *S. quadricauda* together with *Cryptomonas phaseolus* dominated. *Anabaenopsis circularis* also appeared in phase 2 of Santa Olalla, but *A. spiroides*, which exhibited a particular predominance in phase 3 of Dulce, was unimportant in Santa Olalla during the study period. It is possible that *A. spiroides* is not able to withstand the high pH values that *Anabaenopsis circularis* can, which would explain why *A. spiroides* is not significant in Santa Olalla where pH values are very high.

Phase 4 integrated the months before and after Dulce dried up in September (Fig. 4). In this phase, the Y, S_2 (*Arthrospira platensis*) and D functional groups alternated (Table 3). *Arthrospira platensis* was the dominant species before Dulce dried up. This is the first time that this species has been described in Dulce. Its dominance appears to be associated with a high evaporation rate (rapid loss of water), very high conductivity and a high temperature (Fig. 5). After phase 4, the system returned to phase 2 (Fig. 4). The abiotic conditions were similar to those of the previous phase 2; however, the biological variables were very different (low phytoplankton biomass, number of cells and concentration of chlorophyll *a* and a predominance of small bacillariophytes of the D group: *Nitzschia* spp. and *Synedra* sp. or *Cryptomonas phaseolus*, Y group).

Sommer *et al*. (1993) defined three criteria for the identification of equilibrium states in phytoplankton seasonal succession: (i) a maximum of three species of algae contribute more than 80 % of the total biomass, (ii) their dominance persists for more than 1-2 weeks and (iii) during that period, the total biomass does not increase significantly. Because this study is based on one sampling per month, that duration of equilibrium cannot be considered. In addition, both of the studied shallow lakes have, like many Mediterranean aquatic systems, rapid loss of water by evaporation, which increases the number of cells per volume of water and, therefore, the concentration of algal biomass. Having taken these considerations into account, we can affirm that equilibrium phases in phytoplankton assemblages are relatively frequent in Dulce and especially in Santa Olalla (Tables 2 and 3). Padisák *et al*. (2003) found that equilibrium phases are rare in 80 studied Hungarian lakes. However, lakes that experience stress conditions such as salinity or nutrient deficiencies are more likely to support phytoplankton communities in equilibrium. According to Padisák *et al*. (2003), competitive interactions are of secondary importance in stressed systems such as the above, and the primary factor of selection is the evolutionary adaptation to such stress conditions. In Santa Olalla and Dulce, high water level fluctuations, low inorganic nutrient concentrations and the low light penetration can be considered permanent stress factors for phytoplankton, and only a few species are adapted to these conditions. This could explain the low diversity and number of species found in both shallow lakes as well as the high frequency of recorded equilibrium phases.

In conclusion, Santa Olalla and Dulce are two Mediterranean shallow lakes with a natural tendency towards hypereutrophy. Cyanobacteria dominate the phytoplankton most of the time in Santa Olalla, whereas in Dulce they can co-dominate with small bacillariophytes and chlorophytes. Small differences in environmental and hydrological features between the two lakes produce differences in the characteristics and dynamics of their respective phytoplankton.

The stress that the phytoplankton in these lakes is subject to could explain the existence of a steady-state for many months. The study of these anthropologically unchanged systems can allow us a deeper understanding of the dynamics of Mediterranean shallow lakes.

ACKNOWLEDGEMENTS

We would like to thank Sergio Álvarez, Fernando Barajas and Raquel Jimenez for their field and laboratory assistance, and especially the Doñana Biological Station team. This work was supported by Comisión Interministerial de Ciencia y Tecnología project CICYT HID 97-0321-CO2.

REFERENCES

ÁLVAREZ, S., E. RICO, E., M. C. GUERRERO, M. C. & C. C. MONTES. 2001. Decomposition of *Juncus maritimus* in two shallow lakes of Doñana National Park. VII. Decomposition Organic Matter in Standing Waters. *International Review of Hydrobiology*, 86: 541–554.

APHA-AWWA-WPCF (1989). *Standard Methods for the Examination of Water and Wastewater*. S. Clesceri, A. E. Greenberg & R. Trussell (eds). 17th Edn. L. American Public Health Association: Washington, USA.

BEKLIOGLU, M., S. ROMO, I. KAGALOU, X. QUINTANA & E. BECARES. 2007. State of the art in the functioning of shallow Mediterranean lakes: workshop conclusions. *Hydrobiologia*, 584: 317–326.

BLOOM, S. A. 1981. Similarity Indices in community studies: Potential pitfalls. *Marine Ecology*, 5: 125-128.

BOX, J. D. 1983. Investigation of the Folin-Ciocalteau phenol reagent for the determination of polyphenolic substrates in natural waters. *Water Research*, 17: 511–525.

CARLSON, E. 1977. A trophic index for lakes. *Limnology and Oceanography*, 22: 361–369.

CASADO, S. & C. MONTES, 1995. *Guía de los lagos y humedales de España*. Reyero, J.M. (Ed.) Madrid. 154 pp.

COLE, G. 1983. *Textbook of Limnology*, 3rd edn. London: The C.V. Mosby Co. 256 pp.

COLETO, M. C. 2003. *Funciones hidrológicas y biogeoquímicas e las formaciones palustres hipogénicas de los Mantos Eólicos de El Abalario-Doñana (Huelva).* PhD. Thesis. Autónoma de Madrid University. 461 pp.

FRY, J. C. 1990. Direct methods and biomass estimation. *Methods in Microbiology*, 122: 41–85.

GOLDMAN, C. R., E. STEEMANN-NIELSEN, R. A. VOLLENWEIDER, & R. G. AND WELTZEL, 1974. Methods for measuring production rates: measurements (*in situ*) on isolated samples of natural comnmunities. The ^{14}C light and dark bottle technique. In: *A Manual on Methods for Measuring Primary Production in Aquatic Environments:* 88–92. IBP Handbook Nº 12. Blackwell Scientific Publications.

JEFFREY, S., W. & G. F. HUMPHREY, 1975. New spectrophotometric equations for determining chlorophylls *a*, *b*, c_1 and c_2 in higher plants, algae and natural phytoplankton. *Biochemie und Physiologie der Pflanzen*, 167: 191–194.

JEPPESEN, E., M. SØNDERGAARD, M. MEERHOFF, T. L. LAURIDSEN & J. P. JENSEN. 2007. Shallow lake restoration by nutrient loading reduction-some recent findings and challenges ahead. *Hydrobiologia*, 584: 239–252.

LÓPEZ-ARCHILLA, A.I, S. MOLLA, MªC. COLETO, MªC. GUERRERO & C. MONTES. 2004. Microbial Ecosystem metabolism in a eutrophic Mediterranean dune wetland (The Santa Olalla Shallow lake, Doñana National Park, SW Spain). *Wetlands*, 24: 848–858.

MANZANO, M. 2001. Clasificación de los humedales de Doñana atendiendo a su funcionamiento hidrológico. *Hidrogeología y Recursos Hidráulicos* XXIV, 24: 57–75.

MEFFERT, M. E. 1988. Planktic unshealthed filaments (Cyanophyceae) with polar and central gas-vacuoles. II Biology, population dynamics and biotopes of Limnothrix redekei (Van Goor) Meffert. *Archiv für Hydrobiolgie*, 116: 257–282.

MISCHKE, U. 2003. Cyanobacteria associations in shallow polytrophic lakes: influence of environmental factors. *Acta Oecologica*, 24: S11–S23.

MOSS, B. 2007. Shallow lakes, the water framework directive and life: What should it all be about? *Hydrobiologia*, 584: 381–394.

MOUSTAKA-GOUNI, M., E. VARDAKA & E. TRYFON, 2007. Phytoplankton species succession in a shallow lakes (L. Kastoria. Greece): steady-

state dominance of *Limnothrix redekei*, *Microcystis aeruginosa* and *Cylindrospermosis raciboskii*. *Hydrobiologia*, 575: 129–140.

PADISÁK, J., G. BORICS, G. FEHÉR, I. GRIGORSZKY, I. OLDAL, A. SCHMIDT, & Z. ZÁMBÓNÉ-DOMA. 2003. Dominant species, functional assemblages and frequency of equilibrium phases in later summer phytoplankton assemblages in Hungarian small shallow lakes. *Hydrobiologia*, 502: 157–168.

PADISÁK, J., L. O. CROSSETTI & L. NASELLI-FLORES. 2009. Use and misuse in the application of the phytoplankton functional classification: a critical review with updates. *Hydrobiologia*, 621: 1–19.

PERROW, M. R., M. L. MEIJER, P. DAWIDOWICZ & H. COOPS. 1997. Biomanipulation in shallow lakes: state of the art. *Hydrobiologia*, 342/343: 355–365.

REYNOLDS, C. S., V. L. M. HUSZAR, C. KRUK, L. NASELLI-FLORES & S. MELO. 2002. Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research*, 24: 417–428.

ROMO, S. & R. MIRACLE. 1994. Long-term phytoplankton changes in a shallow hypertrophic lake, Albufera of Valencia (Spain). *Hydrobiologia*, 275/276: 153–164.

ROMO, S. & M. J. VILLENA. 2005. Phytoplankton strategies and diversity under different nutrient levels and planktivorous fish densities in a shallow lake. *Journal of Phytoplankton Research*, 27: 1273–1286.

ROTT, E., 1981. Some results from phytoplankton counting intercalibrations. *Schweizerische Zeitschrift für Hydrologie*, 43: 35.

SALMASO, N. 1996. Factors affecting the seasonality and distribution of cyanobacteria and chlorophytes: a case study from the large lakes south of the Alps, with special reference to Lake Garda. *Hydrobiologia*, 438: 43–63.

SALMASO, N. 2003. Life strategies, dominance patterns and mechanisms promoting species coexistence in phytoplankton communities along complex environmental gradients. *Hydrobiologia*, 502: 13–36.

SCHEFFER, M. 1998. *Ecology of shallow lakes*. Ed. Chapman & Hall. Population and Biology Series 22. 357 pp.

SOMMER, U., J. PADISÁK, C. S. REYNOLDS & P. JUHÁSZ-NAGY. 1993. Hutchinson's heritage: the diversity-disturbance relationship in phytoplankton. *Hydrobiologia*, 249: 1–7.

SØNDERGAARD, M., L. LIBORIUSSEN, A. R. PEDERSEN & E. JEPPENSEN. 2008. Lake restoration by fish removal: Short- and long-term effects in 36 Danish lakes. *Ecosystems*, 11: 1291–1305.

TOJA, J., T. LÓPEZ, & N. GABELLONE. 1991. Successional changes in two dune ponds (Doñana National Park). *Verhandlungen der Internationalen Vereinigung für Limnologie*, 24: 1556–1559.

VILLENA, M. J. & S. ROMO. 2003. Phytoplankton changes in a shallow Mediterranean lake (Albufera of Valencia, Spain) after sewage diversion. *Hydrobiologia*, 506/509: 281–287.

WIEDNER, C. 1999. *Toxische und nicht-toxische Cyanobakterien in Gewässern der Scharmützelseeregion: ihr Vorkommen in Gewässern unterschiedlicher Trophie und Morphometrie und Steuermechanismen ihrer Dynamik in polymiktischen Flachseen*. Diss., BTU Cottbus, Fakultät für Umwelt und Verfahenswissenschaten. 131 pp.

Limnetica, 31 (2): 305-322 (2012)
 ISSN: 0213-8409

Factors controlling phytoplankton in tropical high-mountain drinking-water reservoirs

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Received: 30/9/11 Accepted: 3/7/12

ABSTRACT

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Hydraulic dynamics is one of the primary factors determining the structural and temporal changes in phytoplankton communities in reservoirs. There is little information on the factors that explain the temporal changes in biotic communities in the high-mountain reservoirs that provide water to the city of Bogotá (Colombia). Our objective was to identify the environmental factors controlling the biomass and composition of algal communities in four tropical high-mountain reservoirs. We hypothesised that hydraulic dynamics is the major determining factor in temporal changes in phytoplankton communities in tropical mountain reservoirs regardless of the nutrient concentration in the system. We studied the temporal changes in phytoplankton over five years in four reservoirs that exhibit different nutrient concentrations and hydraulic management regimes. The phytoplankton in all of the reservoirs were characterised by the dominance of Dinophyceae. Canonical correspondence analyses and Pearson's correlations showed that the water renewal rate primarily explains the phytoplankton composition, followed by total nitrogen, total phosphorous and silicates. The effect of the water renewal rate was different depending on the particular conditions in each system; thus, in reservoirs with greater hydraulic dynamics, the water renewal rate explained the selection of secondary species and dominant species adapted to a broad range of environmental conditions. In the reservoir with a higher physical stability, eventual changes in the water renewal rate shifted the dominant species, reduced diversity and altered phytoplankton succession. In the reservoir with the largest volume and lowest nutrient concentration, phytoplankton species were selected primarily based on chemical and physical variables related to climatic seasonality. Our results suggest that the model for hydraulic management of the reservoirs plays an important role: in highly dynamic reservoirs, there is a direct causal relationship between phytoplankton and physical variables such as stability and water renewal rate; in less dynamic environments, phytoplankton species growth responds primarily to water chemistry.

Key words: Diversity, phytoplankton composition, thermal stability, water renewal rate.

RESUMEN

Factores que controlan el fitoplancton en embalses tropicales de alta montaña destinados al consumo humano

La dinámica hidráulica es uno de los principales factores que determinan la estructura y los cambios temporales de las comunidades fitoplanctónicas en embalses. Información de los factores que explican los cambios temporales de las comunidades biológicas en los embalses de alta montaña que proveen de agua la ciudad de Bogotá es escasa. El objetivo de este trabajo fue identificar los factores ambientales que controlan la biomasa y la composición de las comunidades algales en cuatro embalses tropicales de alta montaña. La hipótesis de trabajo fue que la dinámica hidráulica es el factor que principalmente determina los cambios temporales en la comunidad fitoplanctónica, con respecto a la concentración de nutrientes del sistema. Durante cinco años se estudiaron los cambios temporales del fitoplancton en cuatro embalses que se caracterizan por presentar diferentes concentraciones de nutrientes y diferente manejo hidráulico. El fitoplancton de todos los embalses se caracterizó por la dominancia de Dinophyceae. Análisis de Correspondencia Canónica y correlaciones de

Pearson mostraron que la tasa de renovación hídrica explicó primariamente el fitoplancton seguida por el nitrógeno total, el fósforo total y los silicatos. El efecto de la tasa de renovación hídrica sobre el fitoplancton fue diferente dependiendo de las condiciones particulares de cada sistema; así, en embalses con una alta dinámica hidráulica, la tasa de renovación explicó las especies secundarias y seleccionó especies dominantes adaptadas a un amplio rango de condiciones ambientales. En el embalse con alta estabilidad física, cambios eventuales en la tasa de renovación cambiaron las especies dominantes, redujeron la diversidad y modificaron la sucesión del fitoplancton. En el embalse de mayor volumen y más baja concentración de nutrientes, el fitoplancton es seleccionado principalmente por otras variables físicas y químicas relacionadas con la estacionalidad climática. Los resultados sugieren que el modelo de manejo hidráulico de los embalses juega un papel importante en embalses más dinámicos, al determinar una relación causal directa entre el fitoplancton y variables físicas como la estabilidad y la tasa de renovación hídrica, mientras en embalses menos dinámicos, el crecimiento de las especies respondió principalmente a la química del agua.

Palabras clave: *Diversidad, composición del fitoplancton, estabilidad térmica, tasa de renovación del agua.*

INTRODUCTION

Compositional and temporal changes in phytoplankton communities are explained by complex interactions among physical, chemical, and biological factors (Margalef, 1983; Pannard *et al.*, 2008; Padisak *et al.*, 2010). The effects of chemical parameters on phytoplankton have been widely studied, and a smaller number of studies have considered the role of physical environmental factors in algal communities (Zohary *et al.*, 2010). Factors such as light availability and the physical stability of the water column may be determinants for the selection of phytoplankton species in natural systems that are exposed to high hydraulic variability or in man-made lakes with intensive management (Bouvy *et al.*, 2003; Naselli-Flores & Barone, 2005; Tolotti *et al.*, 2010).

The physical factors of the environment related to the thermal stability of the water column are important in determining the size and shape of phytoplankton (Naselli-Flores *et al.*, 2007). Physical variables such as water column stability affect the phytoplankton directly by selecting shapes depending on the intensity of the turbulence and indirectly by modifying nutrient availability (Becker *et al.*, 2008). Interactions among these factors causes a response in the algal community by selecting species according to the C-S-R primary adaptive strategies (Reynolds, 1984; Reynolds, 1997). C-species dominate in stratified waters with high nutrient concentrations, S-species dominate in oligotrophic environments and are able to self-regulate vertical movement, and R-species are either tolerant of or dependent on turbulence and prefer high nutrient concentrations.

Consequently, the phytoplankton community of a lake or reservoir will be dominated by functional groups of organisms with adaptations to the environmental conditions of the ecosystem (Borges *et al.*, 2008; Pacheco *et al.*, 2010). Variables related to hydraulic management, such as variation in the water level, the water renewal rate, and the water discharge frequency, have important consequences for the organisation of algal communities in man-made lakes (Mac Donagh *et al.*, 2009; Seeligmann & Tracanna, 2009; Gaytan-Herrera *et al.*, 2011).

Tropical aquatic systems generally have a constant temperature during the entire year, with a monomictic thermal regime and a long period of stratification in deep water bodies (Lewis, 2000). Constant temperatures and more incident radiation favour rapid stratification after holomixis (Lewis, 1973), with the subsequent development of an algal succession that frequently culminates in domination by a few species for long periods of time (Soares *et al.*, 2009). Factors that reduce the thermal stability of the water column, such as wind and increases in the water renewal rate, may provoke changes in the system's physical and chemical conditions and thus modify the community structure (Chellappa *et al.*, 2009). These aspects have

been widely studied in tropical lowland water bodies (Gomes & Miranda, 2001; Bouvy *et al.*, 2003; Gaytan-Herrera *et al.*, 2011), but studies in tropical mountain areas are scarce.

Our objective was to identify the environmental factors controlling the biomass and composition of algal communities in these tropical high-mountain reservoirs. Understanding the responses of algal communities to the physical and chemical characteristics of these environments will provide basic information for decision-making on issues related to reservoir operation and management. Mountainous aquatic systems in Colombia are of great importance because 70 % of the population lives in the Andean area and depends primarily on the water supply from high-mountain areas; hence, reservoirs such as those supplying water to the city of Bogotá have been constructed to ensure adequate coverage of the people's needs. We hypothesised that hydrological dynamics are the major determining factor in temporal changes in the phytoplankton communities of tropical mountain reservoirs, regardless of the nutrient concentration in the system.

MATERIALS AND METHODS

Study area

The present study was conducted as part of the monitoring that the *Empresa de Acueducto y Alcantarillado de Bogotá E.S.P.* (Aqueduct and Sewage Company of Bogotá) is currently performing in the reservoirs that provide drinking water to Bogotá (Fig. 1). Bogotá is located in the Eastern Cordillera of Colombia at 2600 m.a.s.l. and has a population surpassing eight million inhabitants. To meet the daily water demand, the city is provided with water from the Chuza, San Rafael, La Regadera, and Chisacá reservoirs in addition to water from several nearby streams.

The studied reservoirs exhibit differences in bathymetry, reservoir volumes and nutrient concentrations (Table 1). Chisacá, La Regadera, and San Rafael have annual rainfalls varying from 900 to 1200 mm and two rainy seasons, one from April-June and another from September-November. Chuza has an annual rainfall near 3000 mm with a single but prolonged rainy season from May to August. Overall, the basins

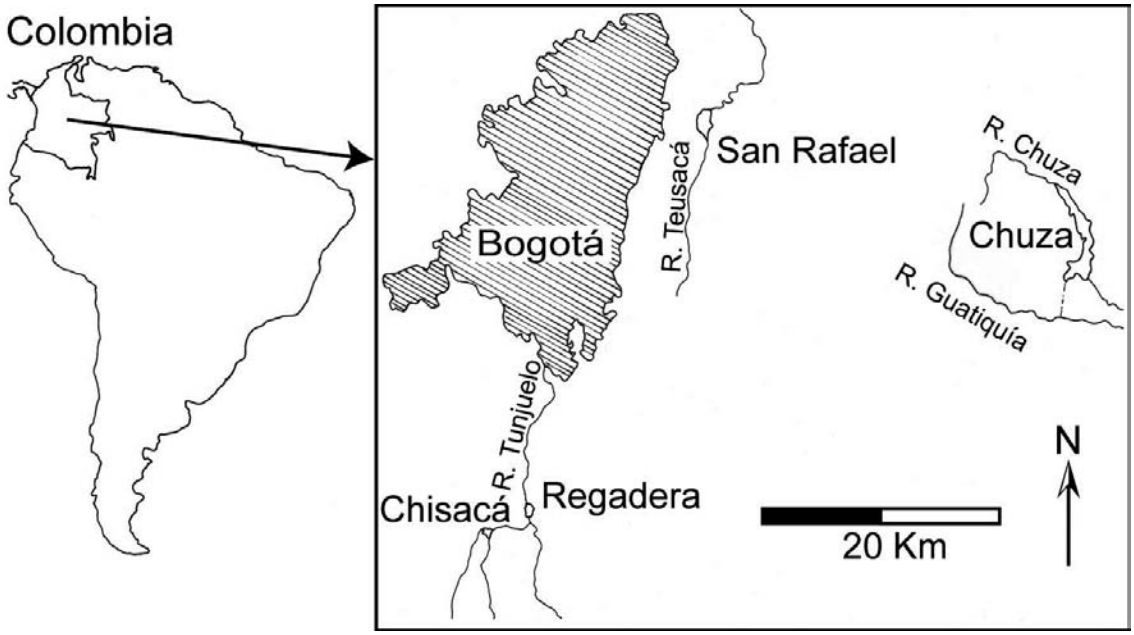


Figure 1. Geographic locations of the four reservoirs studied. *Ubicación geográfica de los cuatro embalses estudiados.*

of all of the reservoirs flow in areas with highly organic and deep soils and benefit from different levels of protection. The Chuza basin lies within a national natural park with dominant herbaceous and shrubby vegetation typical of *páramo* ecosystems. The Chisacá, La Regadera and San Rafael basins are poorly protected with extensive crop fields and human settlements nearby.

The detection of a two-month period with a high density of *Dolichospermum solitarium* (Klebahn) Wacklin, Hoffmann & Komárek (formerly *Anabaena solitaria* Klebahn) in La Regadera at

Table 1. Summary of the geographic and morphometric data and median values of the physical and chemical characteristics studied in the four reservoirs. Data within brackets indicate the range of values. *Resumen de las características geográficas y morfométrica y mediana de las variables físicas y químicas estudiadas. Valores en paréntesis indican el rango de la variable.*

	Chisacá	La Regadera	San Rafael	Chuza
Coordinates	4° 23′ 47.7″ N 74° 8′ 32.4″ W	4° 23′ 4.9″ N 74° 10′ 11.9″ W	4° 42′ 10.2″ N 73° 59′ 14.6″ W	4° 34′ 22.7″ N 73° 42′ 16.8″ W
Altitude (m.a.s.l.)	3146	2997	2777	2990
Maximum volume (m^3)	7 072 183	4 000 000	50 000 000	250 000 000
Area (ha)	53	41	371	580
Maximum depth (m)	24	26	50	85
Relative depth (%)	2.9	3.6	2.3	3.1
Water renewal rate (d^{-1})	0.009 (0-0.061)	0.042 (0-0.25)	0.002 (0.003-0.024)	0.007 (0.001-0.015)
Conductivity (μS/cm)	27.0 (10-38)	24.0 (11-61.5)	58.0 (6-89)	33.4 (5-49)
Total organic carbon (μg/l)	4700 (2500-10 700)	4800 (2300-11 200)	3600 (600-113 600)	2600 (250-10 300)
Total phosphorus (μg/l)	40 (< 10-2140)	70 (< 10-750)	20 (< 10-1330)	20 (< 10-2190)
Total Kjedahl nitrogen (μg/l)	700 (< 100-3800)	700 (< 100-3000)	600 (< 100-12 000)	400 (< 100-3800)
Soluble reactive phosphorus SRP (μg/l)	20 (< 10-1063)	20 (< 10-40)	10 (< 10-50)	10 (10-50)
$N\text{-}N0_3^-$ (μg/l)	130 (< 10-610)	170 (< 10-1143)	100 (< 10-490)	70 (< 10-350)
$N\text{-}N0_2^-$ (μg/l)	3.0 (< 1.0-10)	3.0 (< 1.0-10)	2.0 (< 1.0-13)	2.0 (< 1.0-15)
$N\text{-}NH_4^+$ (μg/l)	200 (< 100-1000)	200 (< 100-700)	200 (< 100-1500)	180 (< 100-439)
SRSi (μg/l)	3210 (673-14 574)	2980 (1004-13 661)	1710 (406-9929)	1000 (164-2806)
pH	6.82 (5.04-8.8)	6.90 (6.02-8.75)	7.00 (6.02-7.9)	7.34 (6.1-7.87)
Total solids (mg/l)	42.5 (10-221)	40.0 (20-135)	46.0 (4.7-115)	28.5 (14-103)
Water temperature (°C)	13.2 (11.1-18.7)	14.1 (11.7-18.3)	15.3 (13.5-18.7)	13.2 (11.5-17.8)
Secchi disk (m)	1.2 (0.4-3.7)	1.0 (0.12-1.85)	2.5 (1.5-4.4)	4.0 (0.3-6.4)
Temperature gradient (°C)	6.1 (1.9-8.1)	5.3 (0.5-8.6)	6.5 (1.1-8.8)	3.0 (0.3-7.9)
Mixing zone (m)	4.0 (2-14)	3.0 (1-6)	7.5 (1-30)	8.0 (1-56)
Euphotic zone: mixing zone	1.01 (0.19-2.5)	1.08 (0.32-2.16)	0.92 (0.29-8.91)	1.20 (0.09-10.34)

the end of 2004 highlighted the necessity of increasing the thermal instability of the lakes to prevent similar events in the future. For this reason, short and sporadic openings of the bottom valves of Chisacá and La Regadera have been conducted since mid-2005 to allow the rapid mixing of the water column. The frequency and intensity of this procedure are variable, ranging from weekly to monthly, and dependent on the water availability in the basin.

Sample collection and analysis

Samplings were performed between January 2004 and March 2009 with a frequency varying between monthly and quarterly depending on the reservoir. In the case of Chisacá and La Regadera, the monitoring of plankton and the thermal structure of the water column was performed monthly, whereas water samples for the chemical analyses were collected quarterly, both starting in mid-2005.

There was only one sampling point for each basin in Chisacá and La Regadera and four sampling points each in San Rafael and Chuza. At each of the sampling points, we collected 3-litre samples of water at half the transparency value of the Secchi disk (SD) using a van Dorn bottle. Samples were carefully homogenised, and then smaller volumes were taken for the chemical analyses and the study of phytoplankton. Samples for the analysis of phytoplankton were preserved in Lugol's solution.

Temperature and oxygen profiles were produced using a multiparameter probe (YSI 52) collecting measurements at one-meter intervals starting from the surface and moving down to the bottom. Water transparency was estimated using a Secchi disk. Conductivity and pH were measured *in situ* at every sampling point with a HACH probe.

The following parameters were analysed following the APHA *et al.* (2005) methods: alkalinity (H_2SO_4 titration), hardness (2320–B titration), turbidity (nephelometric), silicates (SRSi, colorimetric-molybdosilicate), total phosphorus (TP, colorimetric-stannous chloride 4500–P), soluble reactive phosphorus (SRP, 4500–P), total Kjeldahl nitrogen (TKN, H_2SO_4 titration), N–NH_4^+ (4500–NH_4–C), N–NO_3^- (4500–NO_3–B), N–NO_2^- (4500–NO_2-B), total iron (TFe, IC-Plasma 3500–Fe–C), and total organic carbon (TOC, combustion-infrared 5310–B).

Phytoplankton were quantified using sedimentation chambers (Utermöhl, 1958) and by counting at least 200 individuals of the most frequent taxon under a Bausch & Lomb inverted microscope at 800×.

Data analysis

Three approaches were used to describe the physical stability of the water column: the surface-bottom temperature gradient, Schmidt's stability and the rate of water renewal for the reservoir. Schmidt's thermal stability (Wetzel & Likens, 2000) was calculated in relation to the water column at the sampling point. The rate of water retention was analysed as the average daily values for the 15 days before the sampling.

The euphotic zone of the water column was estimated using a factor of 2.7 times the Secchi disk depth (Cole, 1994). The mixing zone (z_{mix}) was estimated from the temperature and dissolved oxygen profiles (Becker *et al.*, 2008). The ratio between the euphotic zone and the depth of the mixing layer ($z_{eu}:z_{mix}$) was calculated to estimate the availability of light in the water column (Jensen *et al.*, 1994). Data on phytoplankton were transformed to biovolume values by measuring the cells of each species and approximating them to geometric shapes (Sun & Liu, 2003). The assignment of each species to the strategies C, S, and R was performed based on morphological traits (Reynolds, 1997).

Dissolved nutrients (SRP, N–NH_4^+, N–NO_3^- and N–NO_2^-) represented a high percentage of data that fell below the detection limit of the analytical methods used in our study but maintained the same tendencies observed for TP and TKN. We found that TP was significantly correlated to SRP ($r = 0.89$, $p < 0.001$, $n = 65$) and NKT to N–NH4$^+$ ($r = 0.37$, $p < 0.001$, $n = 70$) and DIN ($r = 0.32$, $p < 0.001$, $n = 82$). Therefore, we used NKT and TP in the statistical analyses to understand the relationships between phytoplankton and nutrients. NTK and TP data below

the detection limit (< 5 % of data) were estimated as an average between zero and the value of the detection limit in the statistical analyses.

The relationship between phytoplankton and the environment was analysed with a canonical correspondence analysis–CCA (Jongman *et al.*, 1995). Data from Chisacá and La Regadera were analysed together due to the low number of samples of chemical data and the connectivity between the two basins.

First, data were analysed with a CCA with the forward selection (full model) procedure, including physical, chemical and hydrological variables that showed a low correlation coefficient (inflation <10 %). In the final CCA (minimum model), we excluded non-significant variables, as well as species with a low biovolume and a frequency lower than 5 % of the total sample. A Monte Carlo test (999 permutations, $\alpha = 0.05$) was used to find the significance of the axes of species and of the relationship between species and environment.

A CCA was used to find the species that are more strongly related to the environmental variables and the species in which the more significant environmental variables were added one by one. Species accounting for more than 10 % of the variance in each variable were considered to be selected by this variable.

With the aim of analysing changes in the structure of phytoplankton communities, we calculated Pearson's correlations between the main environmental variables and the ecological diversity (species richness and Shannon index) and community turnover rate. The community turnover rate per sample was calculated from the Shannon beta diversity according to Jost (2007).

RESULTS

Physical and chemical characteristics of the reservoirs

The four reservoirs showed a tendency for thermal stratification during most of the year and presented a temperature gradient between the surface and bottom that was always less than 7 °C (Fig. 2). Thermal stratification induced a strong chemical gradient in the water column that is reflected in the hypoxic conditions of the hypolimnion. In Chisacá and La Regadera, the low water renewal rate in 2004 caused the maintenance of a thermally and chemically stratified water column for 17 months (Fig. 3). Afterwards, more intense hydraulic management caused strong stratifications lasting for short periods of time (less than 5 months) and deep mixed layers lasting for prolonged periods of time. The high variation in the water renewal rate determined the high variability in the thermal stability of the two reservoirs, resulting in periods with more stability during the dry seasons.

In San Rafael, there was also a thermal and chemical stratification during three consecutive years (2006 to 2008) caused by a low water renewal rate. Periods with low thermal stability in the water column were caused by decreases in water retention in the reservoir. Chuza presented a thermal stratification regime that is driven by climate seasonality, in which the rainy seasons and high wind speeds drive the partial mixing of the water column and the dry seasons cause a thermal stratification that lasts seven months.

The ratio $z_{eu} : z_{mix}$ exhibited a median > 1 in Chisacá, La Regadera and Chuza. The four reservoirs tended to have higher values of $z_{eu} : z_{mix}$ when a period of low thermal stability changed to a high relative stability period. La Regadera presented values < 1 before the intensification of the hydraulic management of the reservoir, whereas in Chisacá, no temporal pattern was detected. During the period of prolonged stratification, San Rafael presented values that were almost always < 1 with a lower degree of variability, suggesting light limitations for phytoplankton growth. Chuza showed variation in the ratio values that was related to climatic seasonality (Fig. 3; Table 1).

All of the reservoirs exhibited chemical stratification, with high nutrient values in the hypolimnion. There were chemical differences among the reservoirs: Chisacá and La Regadera showed the highest TP and TKN concentrations and the lowest Secchi disk values; San Rafael presented the lowest TP concentrations; and Chuza showed the lowest TKN concentration

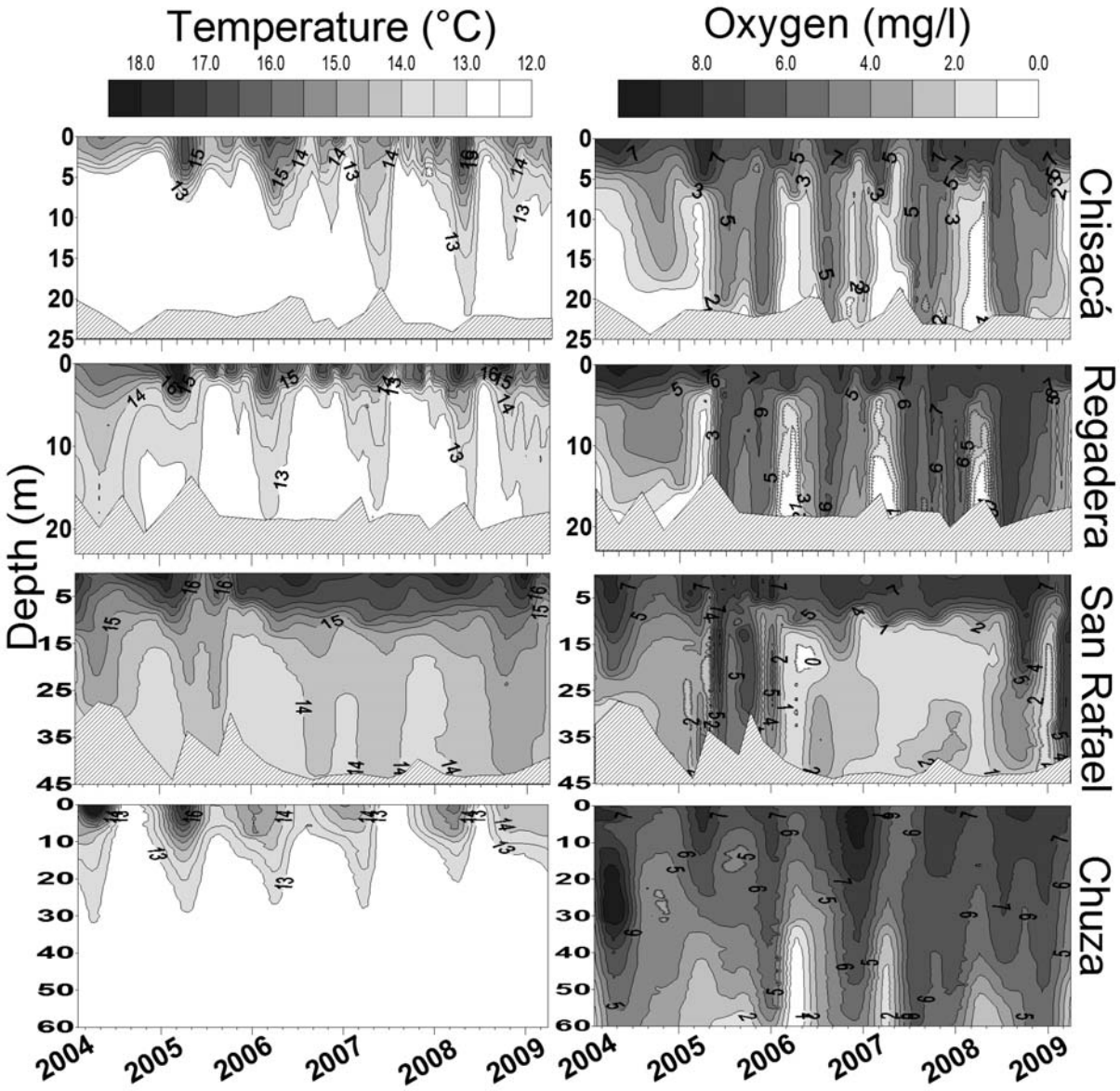


Figure 2. Temporal behaviour of water temperature and oxygen in the Chisacá, La Regadera, San Rafael, and Chuza reservoirs. The striped area represents the water column depth. *Comportamiento temporal de la temperatura y el oxígeno del agua en los embalses Chisacá, La Regadera, San Rafael y Chuza. El área reticulada representa la profundidad de la columna de agua.*

and the highest Secchi disk values (Table 1). The chemical characteristics of the reservoirs showed complex variations on a temporal basis that were not directly explained by the hydrological climatic seasonality; however, the chemical characteristics indicate that during the stratification periods, Chisacá, La Regadera and San Rafael tended to present higher concentrations of TKN, TP and TOC.

Temporal patterns of phytoplankton

Algal biovolumes in the different reservoirs were consistent with the nutrient concentrations. In

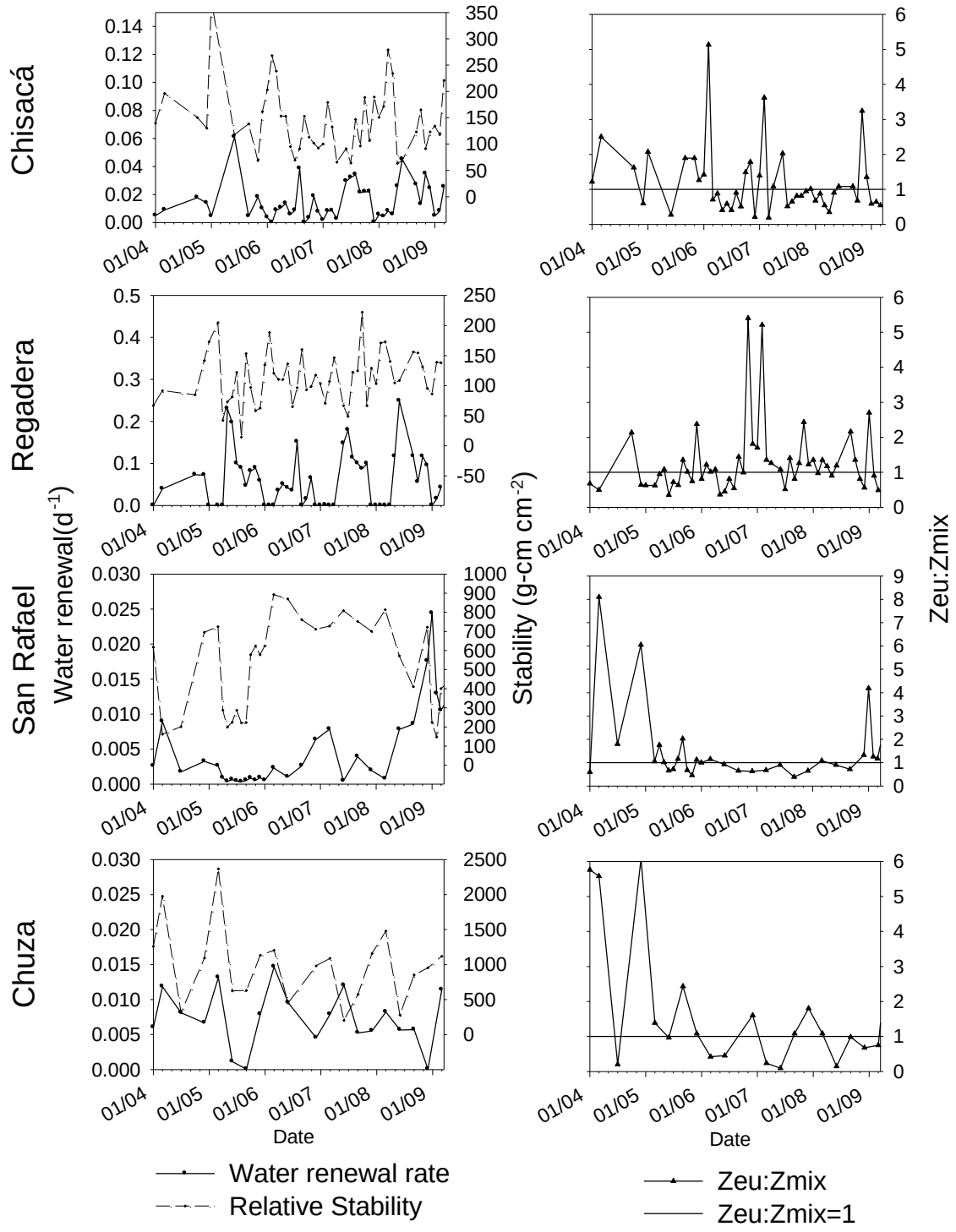


Figure 3. Temporal variation of the water renewal rate, Schmidt's thermal stability and the $z_{eu} : z_{mix}$ ratio. Notice that the axis scales are different. *Variación temporal de la tasa de renovación del agua, la estabilidad térmica de Schmidt y la relación* $z_{eu} : z_{mix}$. *Note que las escalas de los ejes son diferentes para cada embalse.*

this way, the highest values were found in La Regadera (mean = 13 mm^3/l) and Chisacá (mean = 16 mm^3/l), whereas Chuza presented the lowest values (< 7 mm^3/l). Algae communities were different in every reservoir, but overall, there was more similarity between the communities of Chisacá and La Regadera, and between those of San Rafael and Chuza (Fig. 4). Dinophyceae was the group with more dominant species, and Desmidiaceae (Zygnemaphyceae) was the family with the highest diversification of species in all of the reservoirs.

During 2004, Chisacá presented a community dominated by *Peridinium* cf. *cinctum*, *Ceratium* cf. *hirundinella* and *Trachelomonas volvocina*. With the increase in hydraulic management activities in the reservoir since mid-2005, there was a period dominated by *P. cinctum*. During the stratification period at the beginning of 2006, there was a change in the community that resulted in a phase dominated by *C. hirundinella*. This pattern was maintained during the periods of mixing and stratification in 2007. During most of 2008, *C. hirundinella* comprised more than 80 % of the biovolume. In this reservoir, the algal community underwent prolonged periods with one dominant species.

La Regadera showed high variation in community structure, which varied between *C. hi-*

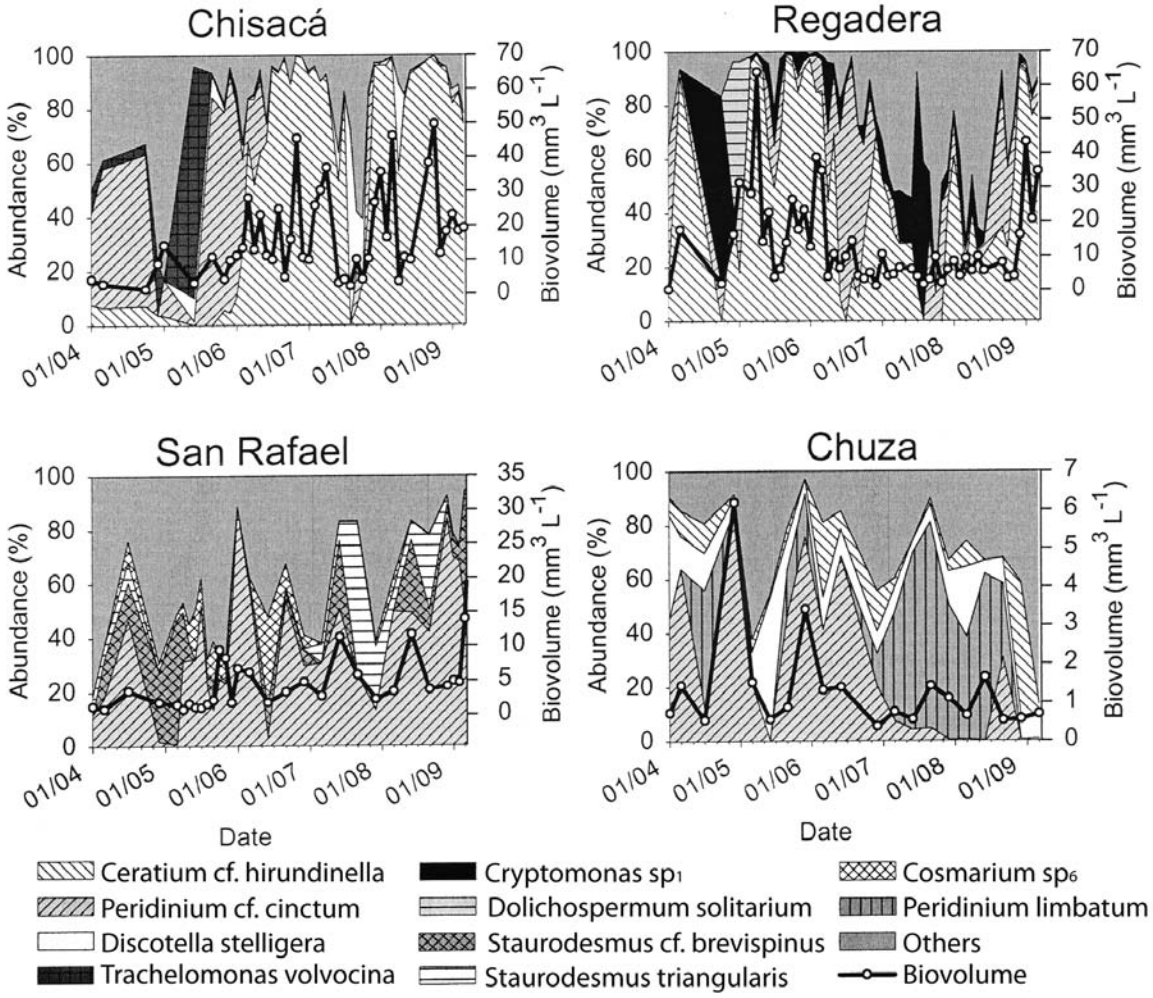


Figure 4. Temporal behaviour of the dominant phytoplankton species in the four reservoirs studied. *Comportamiento temporal de las especies de fitoplancton dominantes en los cuatro embalses estudiados.*

rundinella, *Cryptomonas* sp_1, and *P. cinctum* as the dominant species. At the end of 2004, there was a bloom of *Dolichospermum solitarium* (> 20 000 cells/ml) followed by the rapid growth of *C. hirundinella*. During most of 2006, the basin was dominated by *C. hirundinella*.

San Rafael revealed a more diverse community in which *C. hirundinella* was the species with the largest biovolume, but this community had a high variation in the dominant species and sporadic events with three or fewer species accounting for 80 % of the biovolume. During the two prolonged periods of stratification, small- (*Staurodesmus triangularis* and *Cosmarium* $sp._6$) and medium-sized (*Staurodesmus* cf. *brevispinus*) Desmidiaceae species were dominant or codominant. In Chuza, there was a reduced algal biovolume with dominance shifting from one species to another among *P. cinctum*, *Discotella stelligera*, *Peridinium limbatum*, and *C. hirundinella*.

The CCA models significantly explained 13.3 % of Chisacá and La Regadera species variability, 17.3 % of San Rafael species variability and 12.5 % of Chuza species variability (Table 2). The water renewal rate significantly explained the temporal variation in the phytoplankton communities in all of the reservoirs, with a higher fraction of variance explained for Chisacá, La Regadera and San Rafael (Fig. 5).

The CCA model for Chisacá and La Regadera suggests an inverse relationship between the water renewal rate and the temperature, explaining most of the temporal variability in phytoplankton; TP and TFe explained a second gradient of phytoplankton species variability. The CCA model for San Rafael shows that the phytoplankton species variability was accounted for TOC, water renewal rate, SRSi, and the ratio $z_{eu} : z_{mix}$. According to the CCA model for Chuza, TKN, SRSi, pH, and SD were the most important variables for phytoplankton.

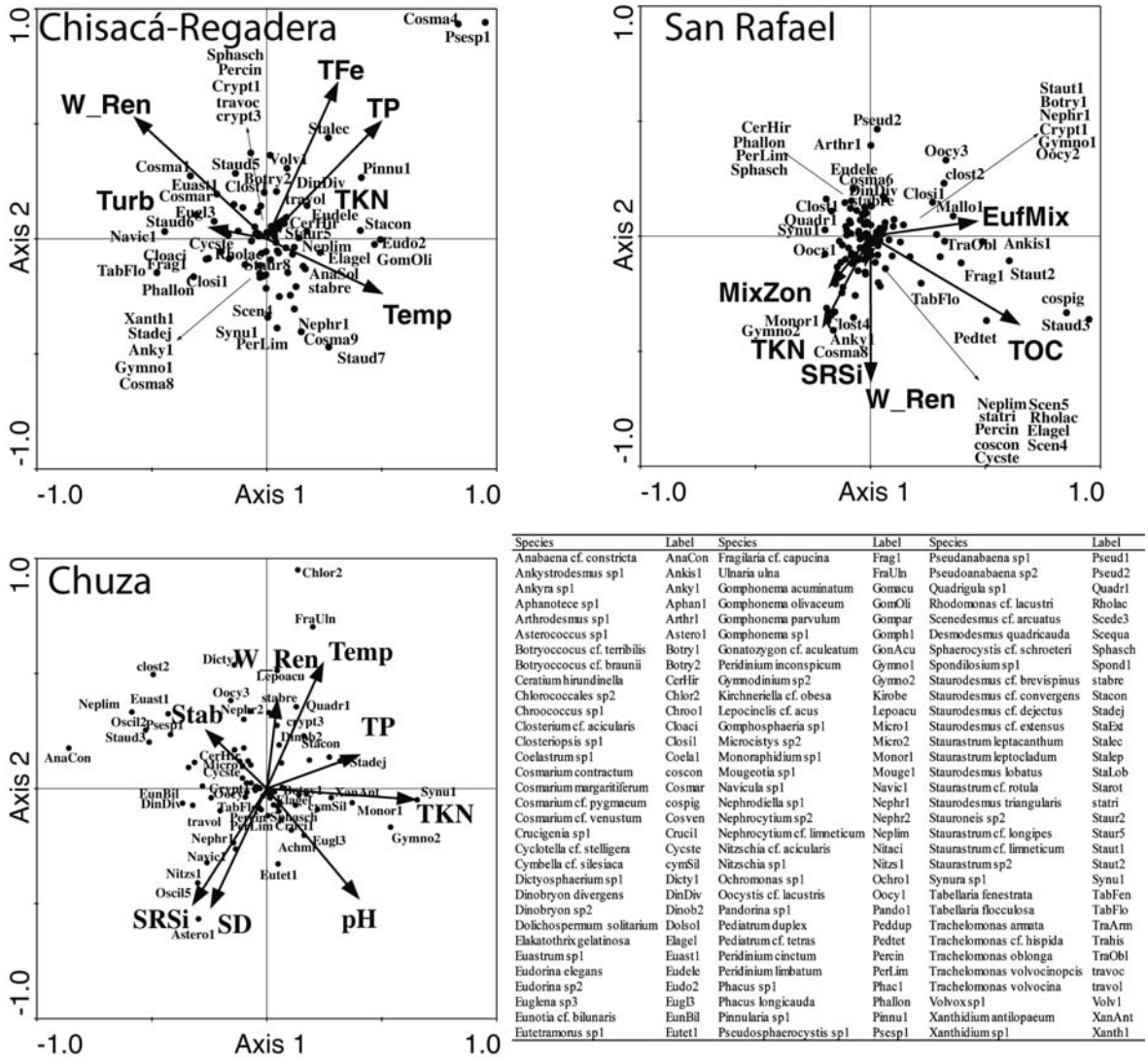
The CCA models suggest that periods with low and intermediate water renewal rates in Chisacá and La Regadera selected some species

Table 2. Summary of the canonical correspondence analyses and the variances of species explained by the environmental variables. *Resumen de los Análisis de Correspondencia Canónica y varianza explicada por las variables ambientales.*

Chisacá and La Regadera (n = 46)			San Rafael (n = 84)			Chuza (n = 78)		
λ first 3 axes		0.21	λ first 3 axes		0.20	λ first 3 axes		0.17
Total λ		1.55	Total λ		1.14	Total λ		1.39
Variance species data 3 axes (%):		13.3	Variance species data 3 axes (%):		17.3	Variance species 3 axes (%):		12.5
Variance species-environment (%):		62.9	Variance species-environment (%):		59.7	Variance species-environment (%):		52.5
				Conditional effects				
Variable	λ	P	Variable	λ	P	Variable	λ	P
W_Ren	0.07	0.008	W_Ren	0.05	0.001	TKN	0.05	0.001
TP	0.06	0.005	TOC	0.05	0.001	SRSi	0.04	0.001
TFe	0.05	0.022	SRSi	0.04	0.001	pH	0.04	0.001
Turb	0.05	0.019	EufMix	0.04	0.001	SD	0.04	0.001
TKN	0.05	0.048	TKN	0.03	0.001	Temp	0.03	0.001
Temp	0.05	0.036	MixZon	0.03	0.001	Stab	0.03	0.006
			SD	0.02	0.001	W_Ren	0.03	0.008
			Alca	0.02	0.005	Hardn	0.02	0.01
			TemGra	0.02	0.012	TP	0.03	0.02
			Hardn	0.01	0.027	TOC	0.02	0.043
			TFe	0.02	0.043			

λ: Eigenvalue, P: *p*-value, W_Ren: Water renewal rate, TP: Total phosphorus, TFe: Total Iron, Turb: Turbidity, TKN: Total Kjedahl nitrogen, Temp: Temperature, TOC: Total organic carbon, SRSi: Reactive Silica, EufMix: $z_{eu} : z_{mix}$, MixZon: Mixing zone, SD: Secchi disk, Alca: Alkalinity, TemGra: Gradient of temperature, Hardn: Hardness, Stab: thermal Stability.

of Desmidiaceae (*Staurodesmus dejectus*, *Staurodesmus* cf. *brevispinus*, *Staurastrum* sp.$_1$, *Staurastrum* cf. *limneticum*, *Staurodesmus* sp.$_6$) and Chlorophyceae (*Scenedesmus* spp.) with small and medium sizes and C strategies (Reynolds, 1997). Low and intermediate values of phosphorus selected for the colonial species *Sphaerocystis* cf. *schroeteri*, *Dinobryon divergens*, and *Eudorina elegans*, whereas high values selected for *Staurodesmus* cf. *brevispinus*. In San Rafael, high rates of water renewal selected *Gymnodinium* sp.$_2$, intermediate rates accounted



Species	Label	Species	Label	Species	Label
Anabaena cf. constricta	AnaCon	Fragilaria cf. capucina	Frag1	Pseudanabaena sp1	Pseud1
Ankystrodesmus sp1	Ankis1	Ulnaria ulna	FraUln	Pseudoanabaena sp2	Pseud2
Ankyra sp1	Anky1	Gomphonema acuminatum	Gomacu	Quadrigula sp1	Quadr1
Aphanotece sp1	Aphan1	Gomphonema olivaceum	GomOli	Rhodomonas cf. lacustri	Rholac
Arthrodesmus sp1	Arthr1	Gomphonema parvulum	Gompar	Scenedesmus cf. arcuatus	Scede3
Asterococcus sp1	Astero1	Gomphonema sp1	Gomph1	Desmodesmus quadricauda	Scequa
Botryococcus cf. terribilis	Botry1	Gonatozygon cf. aculeatum	GonAcu	Sphaerocystis cf. schroeteri	Sphasch
Botryoccocus cf. braunii	Botry2	Peridinium inconspicum	Gymno1	Spondilosium sp1	Spond1
Ceratium hirundinella	CerHir	Gymnodinium sp2	Gymno2	Staurodesmus cf. brevispinus	stabre
Chlorococcales sp2	Chlor2	Kirchneriella cf. obesa	Kirobe	Staurodesmus cf. convergens	Stacon
Chroococcus sp1	Chroo1	Lepocinclis cf. acus	Lepoacu	Staurodesmus cf. dejectus	Stadej
Closterium cf. acicularis	Cloaci	Gomphosphaeria sp1	Micro1	Staurodesmus cf. extensus	StaExt
Closteriopsis sp1	Closi1	Microcistys sp2	Micro2	Staurastrum leptacanthum	Stalec
Coelastrum sp1	Coela1	Monoraphidium sp1	Monor1	Staurastrum leptocladum	Stalep
Cosmarium contractum	coscon	Mougeotia sp1	Mouge1	Staurodesmus lobatus	StaLob
Cosmarium margaritiferum	Cosmar	Navicula sp1	Navic1	Staurastrum cf. rotula	Starot
Cosmarium cf. pygmaeum	cospig	Nephrodiella sp1	Nephr1	Staurodesmus triangularis	statri
Cosmarium cf. venustum	Cosven	Nephrocytium sp2	Nephr2	Stauroneis sp2	Staur2
Crucigenia sp1	Cruci1	Nephrocytium cf. limneticum	Neplim	Staurastrum cf. longipes	Staur5
Cyclotella cf. stelligera	Cycste	Nitzschia cf. acicularis	Nitaci	Staurastrum cf. limneticum	Staut1
Cymbella cf. silesiaca	cymSil	Nitzschia sp1	Nitzs1	Staurastrum sp2	Staut2
Dictyosphaerium sp1	Dicty1	Ochromonas sp1	Ochro1	Synura sp1	Synu1
Dinobryon divergens	DinDiv	Oocystis cf. lacustris	Oocy1	Tabellaria fenestrata	TabFen
Dinobryon sp2	Dinob2	Pandorina sp1	Pando1	Tabellaria flocculosa	TabFlo
Dolichospermum solitarium	Dolso1	Pediatrum duplex	Peddup	Trachelomonas amata	TraArm
Elakatothrix gelatinosa	Elagel	Pediatrum cf. tetras	Pedtet	Trachelomonas cf. hispida	Trahis
Euastrum sp1	Euast1	Peridinium cinctum	Percin	Trachelomonas oblonga	TraObl
Eudorina elegans	Eudele	Peridinium limbatum	PerLim	Trachelomonas volvocinopcis	travoc
Eudorina sp2	Eudo2	Phacus sp1	Phac1	Trachelomonas volvocina	travol
Euglena sp3	Eugl3	Phacus longicauda	Phallon	Volvox sp1	Volv1
Eunotia cf. bilunaris	EunBil	Pinnularia sp1	Pinnu1	Xanthidium antilopaeum	XanAnt
Eutetramorus sp1	Eutet1	Pseudosphaerocystis sp1	Psesp1	Xanthidium sp1	Xanth1

Figure 5. Representation of the first and second axes of the canonical correspondence analyses for the studied reservoirs (Environmental variables plotted with $\lambda > 0.03$). Labels of the representative species are shown in the figure. Label abbreviations of other species correspond to Clost: *Closterium*, Cosma: *Cosmarium*, Crypt: *Crytomonas*, Oocy: *Oocystis*, Mallo: *Mallomonas*, Oscil: *Oscillatoria*, Scene: *Desmodesmus*, Staud: *Staurodesmus*, and Stau: *Staurastrum*. Variable abbreviations are shown in Table 2. *Representación del primer y segundo eje de los Análisis de Correspondencia Canónica realizados para los embalses estudiados (se dibujan las variables ambientales con $\lambda > 0.03$). Los rótulos de las especies representativas se presentan en la figura. Rótulos de abreviaciones de otras especies son Clost:* Closterium, *Cosma:* Cosmarium, *Crypt:* Crytomonas, *Oocy:* Oocystis, *Mallo:* Mallomonas, *Oscil:* Oscillatoria, *Scene:* Desmodesmus, *Staud:* Staurodesmus *y Stau:* Staurastrum. *Las abreviaciones de las variables se presentan en la tabla 2.*

for *S. triangularis* and *Closterium* $sp._4$, and higher rates selected *Cosmarium* $sp._8$. TOC selected additional species, whereas intermediate values accounted for *Cosmarium* $sp._6$, *Oocystis* cf. *lacustris*, and *S. schroeteri* and high values selected *Staurodesmus* $sp._3$, *Cosmarium contractum*, and *Cosmarium* cf. *pygmaeum*. Low $z_{eu} : z_{mix}$ ratio values accounted for *Fragilaria* cf. *capucina*, *Closterium* $sp._1$ and *C. hirundinella*. In Chuza, low values of NTK selected *Oocystis* cf. *lacustris* and intermediate values of NTK selected *Gymnodinium* $sp._2$, *Monoraphidium* $sp._1$ and *Botryoccocus* cf. *terribilis*. Periods with low rates of water renewal selected *Elakatothrix gelatinosa*, *Asterococcus* $sp._1$, and *T. volvocina*.

Diversity and the turnover rate of phytoplankton

Species richness and Shannon diversity index values were highly variable in all of the reservoirs and did not show any significant correlation with physical, chemical or hydraulic variables. Species richness ranged between 6 and 49, with the lowest average in Chuza (19 species) and the highest average in San Rafael (33 species). The Shannon diversity index showed the lowest value in Chisacá (0.9) and the highest value in San Rafael (1.78).

The community turnover rate presented high temporal variability in all of the reservoirs and ranged between 0.01 and 0.91. La Regadera presented the highest average (0.72) and Chisacá the lowest average (0.27). No significant correlations were found between the community turnover rate and any of the chemical and physical variables of the Chisacá and La Regadera reservoirs. The community turnover rate was significantly correlated with the water renewal rate for San Rafael ($r = -0.35$, $p < 0.05$, $n = 80$) and Chuza ($r = -0.33$, $p < 0.05$, $n = 70$).

DISCUSSION

Phytoplankton growth is controlled primarily by light and nutrient availability (Naselli-Flores, 2000; Becker *et al.*, 2010). Changes in hydrology and climate can provoke the circulation of the water mass and affect the availability of light and nutrients for phytoplankton (Tundisi *et al.*, 2008). Physical factors such as the regulation of water inflow and outflow and the water retention time in reservoirs are important factors that can drive the temporal variation of phytoplankton communities (Soares *et al.*, 2008; Mac Donagh *et al.*, 2009).

In this sense, our results show a higher determination of the physical factors with respect to the water chemistry and phytoplankton composition of the studied reservoirs. According to the CCAs, the water renewal rate was the predominant factor that explained the temporal variations in the composition of the algal communities in Chisacá, La Regadera and San Rafael. In additional to seasonal variation, systems with complex hydrological dynamics tended to exhibit frequent species replacement and colonisation episodes (Reyes *et al.*, 2008). Hydrologic fluctuations and temporal variations in phosphorus levels in Chisacá and La Regadera provoked important changes in the secondary species in the system, whereas in San Rafael, the changes were related to the transition from a relatively short period of low thermal stability to a prolonged stratified period and, subsequently, to a final period of physical instability.

In Chuza, TKN, not the water renewal time, was the most important explanatory variable for the phytoplankton community. During some of the stratified periods in Chuza, there was an important reduction in the nitrogen concentration that may explain the great importance of this variable in the system. Chuza is a reservoir located in a protected basin, with low nutrient inputs from the basin during the rainy season. Because of this, small variations in the concentration of nitrogen may have an important impact on the temporal changes in phytoplankton.

Reservoirs with more complex hydrological dynamics presented broadly varied phytoplankton responses. In this sense, Chisacá and La Regadera, both reservoirs having a highly variable water renewal rate, exhibited phases when the relative abundances of one or two species constituted more than 80 % of the total biovolume

during the stratified and mixing periods, whereas in San Rafael and Chuza, these phases were less frequent, hence the communities were more diverse. Likewise, low nutrient concentrations in water bodies such as Chuza and San Rafael may promote the maintenance of more diverse communities (Interlandi & Kilham, 2001) in which there is a low probability of dominance by a few species.

In the case of Chisacá and La Regadera, during the period of thermal instability there was an initial phase with low variability in algal biomass that was followed by changes of up to 100 % of the biomass. Subsequently, a single species was dominant until 2006, followed by less frequent periods in 2007 and 2008 of dominance by a few species.

Greater physical stability has consequences for phytoplankton communities by provoking algal succession, where an eventual destabilisation of the water column may act as a disturbance (Sommer *et al.*, 1993). In San Rafael, the prolonged stratification time caused dominant species to be explained by the water renewal rate. Increases in the water renewal rate have a strong impact on the algal succession of this reservoir by reducing the equitability among species and the community turnover rate. Chisacá and La Regadera exhibited communities with a temporal succession that was not related to hydrology and was dominated by species adapted to a high degree of instability in the water column.

The smaller volume of La Regadera accounts for the higher impact of hydraulic movements on the renewal rate of this system in comparison with Chisacá. This is why *C. hirundinella* can dominate in conditions of low to moderate turbulence but not when the instability of the water column is too high. The perennial dominance of Dinophyceae species in a polymictic reservoir has been reported in subtropical reservoirs (Townsend & Luong-Van, 1998; Townsend, 2001), suggesting that species in this group can reach a stage where they are self-maintained and resist holomixis.

The maintenance of a permanent stratification, or a low ratio $z_{eu} : z_{mix}$, creates conditions in which phytoplankton are limited by nutrients and light. In these circumstances, species with strategies of tolerance to stress are favoured and dominate in the community (Reynolds, 2006). Regardless of the nutrient concentration and the thermal stability of the different reservoirs, the phytoplankton communities were dominated most of the time by Dinophyceae with S strategies, such as *C. hirundinella*, *P. cinctum*, and *P. limbatum*. *C. hirundinella* is a large Dinophyceae with a low growth rate that occurs preferentially in water bodies with a stable epilimnion and low nutrient concentrations (Harris, 1986; Reynolds, 1997; Kruk *et al.*, 2010). Its capacity to regulate its depth, locate itself in zones with adequate light intensities and move to areas with higher nutrient concentrations determines its dependence on low and moderate turbulence levels (Whittington *et al.*, 2000); however, it has also been associated with periods of instability or circulation with an increase in the phosphorus concentration (Hart & Wragg, 2009). The dominance of other large Dinophyceae species, such as *P. gatunense* and *C. furcoides*, has been explained by the resuspension of cysts from the sediment during mixing periods and the suitable conditions for excystation in a turbulent water column with high nutrient concentrations (Berman *et al.*, 1992; Matsumura-Tundisi *et al.*, 2010).

The dominance of *C. hirundinella* in the reservoirs of Chisacá and La Regadera during most of our study can be explained by the large size of this species and its high mobility during stratified periods and moderate turbulence. Generally, the hydraulic management of these reservoirs consists of rapid increases in the water renewal, followed by periods of one or two weeks with a low water renewal. During these short periods of time of high turbulence, *C. hirundinella* can sustain itself in an unstable water column and later become dominant in a water column that stratifies quickly. *P. cinctum* was dominant during stratified and mixing periods in San Rafael and Chuza. *P. cinctum* is a species with a relatively large size (47 μ m in its largest linear dimension), commonly found in artificial water bodies and occasionally forming blooms (Wynne *et al.*, 1982). This species has a high capacity for storing phosphorus; thus, in stratification periods, it can maintain important biomass, and during periods of thermal instability, it can profit from the increase in nutrients in the water column (Pollingher & Serruya, 1976).

Dinophyceae has species with different specific requirements but with a high plasticity when exposed to a broad range of environmental conditions (Lopes *et al.*, 2009; Cardoso *et al.*, 2010); therefore, these species are able to develop in different reservoir conditions. In the context of the water systems studied here, the physical stability of the water column did not explain the strategies of the dominant species but did explain some of the temporal turnovers among them.

In San Rafael, Desmidiaceae dominated or codominated in the periods of prolonged stratification, when the overall mixing zone showed variations in its amplitude. In tropical lakes, differences in temperature between day and night and wind provoke events of atelomixis that introduce slight variations in the conditions of the water column. These variations can explain the persistence of non-motile algae such as Desmidiaceae during stratified periods (Barbosa & Padisák, 2002) and the importance of changes of the water renewal rate on the phytoplankton of San Rafael. Small variations in the availability of nutrients and light can also restrain the development of phases of high dominances by a few species and stimulate a temporal turnover in the species of Desmidiaceae (Souza *et al.*, 2008).

In systems with a low tension due to exogenous conditions, factors intrinsic to the system such as seasonal variations in climate and hydrology (Martínez-Almeida & Tavera, 2005; Rivera *et al.*, 2005; Reyes *et al.*, 2008) and daily variations in radiation and thermal stability (Lewis, 1978; Esteves, 1998; Souza *et al.*, 2008) may regulate the temporal dynamics of plankton. Chuza is the only reservoir where the mixing periods were caused by the combined effects of wind and rain, as has been reported for tropical mountain lakes (Gunkel, 2000; Zapata-Anzola *et al.*, 2006; Donato, 2010); therefore, physical and chemical variables associated with climate seasonality explain an important fraction of the variability of phytoplankton in this system.

Our data show that variation in the water renewal rate is one of the primary factors driving the temporal changes in phytoplankton in the studied reservoirs; nonetheless, the relevance of this factor varied according to the particular conditions of the systems, such as the hydraulic management model, the nutrient concentrations, and the development of species that can readily adapt to fluctuating environmental conditions.

ACKNOWLEDGMENTS

We are grateful to all of the members of the project "*Seguimiento limnológico de las fuentes de agua captadas para el suministro realizado por la Empresa de Acueducto y Alcantarillado de Bogotá-E.S.P.*" carried out by the *Empresa de Acueducto y Alcantarillado de Bogotá-E.S.P.* and conducted by *Dirección de Ingeniería Especializada, Gerencia de Abastecimiento, Planta de Tratamiento Wiesner* and *Planta de Tratamiento El Dorado*. We are also grateful to *Laboratorio de Análisis de Aguas* for their contributions and support during all phases of the study. The data contained in this article belong to the *Empresa de Acueducto y Alcantarillado d*e Bogotá-ESP. We acknowledge the assistance of Sandra Constantino in translating and copy editing the manuscript.

REFERENCES

APHA, AWWA & WEF. 2005. *Standard Methods for the Examination of Water and Wastewater*. American Public Health Association. Washington D.C., USA. 1325 pp.

BARBOSA, F. A. R. & J. PADISÁK. 2002. The forgotten lake stratification pattern, and its ecological importance. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie*, 25: 1–11.

BECKER, V., L. CAPUTO, J. ORDONEZ, R. MARCE, J. ARMENGOL, L. O. CROSSETTI & V. L. M. HUSZAR. 2010. Driving factors of the phytoplankton functional groups in a deep Mediterranean reservoir. *Water Research*, 44: 3345–3354.

BECKER, V., V. L. M. HUSZAR, L. NASELLI-FLORES & J. PADISAK. 2008. Phytoplankton equilibrium phases during thermal stratification in a deep subtropical reservoir. *Freshwater Biology*, 53: 952–963.

BERMAN, T., Y. Z. YACOBI & U. POLLINGHER. 1992. Lake Kinneret phytoplankton: Stability

and variability during twenty years (1970-1989). *Aquatic Sciences*, 54: 104–127.

BORGES, P. A. F., S. TRAIN & L. C. RODRIGUES. 2008. Spatial and temporal variation of phytoplankton in two subtropical Brazilian reservoirs. *Hydrobiologia*, 607: 63–74.

BOUVY, M., S. M. NASCIMENTO, R. J. R. MOLICA, A. FERREIRA, V. HUSZAR & S. M. F. O. AZEVEDO. 2003. Limnological features in Tapacurá reservoir (northeast Brazil) during a severe drought. *Hydrobiologia*, 493: 115–130.

CARDOSO, L. D., P. B. FAGUNDES & V. BECKER. 2010. Spatial and temporal variations of Dinophyceae in subtropical reservoirs in southern Brazil. *Hydrobiologia*, 654: 205–214.

COLE, G. A. 1994. *Textbook of Limnology*. Waveland Press, Inc. Long Grove, USA. 412 pp.

CHELLAPPA, N. T., T. CHELLAPPA, F. R. A. CÂMARA, O. ROCHA & S. CHELLAPPA. 2009. Impact of stress and disturbance factors on the phytoplankton communities in Northeastern Brazil reservoir. *Limnologica*, 39: 273–282.

DONATO, J. 2010. *Phytoplankton of Andean Lakes in Northern South America (Colombia).* A. R. G. Gantner Verlag K. G. Ruggell, Liechtenstein. 419 pp.

ESTEVES, F. A. 1998. *Fundamentos de Limnologia*. Interciencia. Sao Pablo, Brazil. 602 pp.

GAYTAN-HERRERA, M. L., V. MARTINEZ-ALMEIDA, M. G. OLIVA-MARTINEZ, A. DURAN-DIAZ & P. RAMIREZ-GARCIA. 2011. Temporal variation of phytoplankton from the tropical reservoir Valle de Bravo, Mexico. *Journal of Environmental Biology*, 32: 117–126.

GOMES, L. C. & L. E. MIRANDA. 2001. Hydrologic and climatic regimes limit phytoplankton biomass in reservoirs of the Upper Paraná River Basin, Brazil. *Hydrobiologia*, 457: 205–214.

GUNKEL, G. 2000. Limnology of an Equatorial High Mountain Lake in Ecuador, Lago San Pablo. *Limnologica*, 30: 113–120.

HARRIS, G. P. 1986. *Phytoplankton Ecology. Structure Function and Fluctuation*. Chapman and Hall. London, UK. 384 pp.

HART, R. C. & P. D. WRAGG. 2009. Recent blooms of the dinoflagellate Ceratium in Albert Falls Dam (KZN): History, causes, spatial features and impacts on a reservoir ecosystem and its zooplankton. *Water SA*, 35: 455–468.

INTERLANDI, S. J. & S. S. KILHAM. 2001. Limiting resources and the regulation of diversity in phytoplankton communities. *Ecology*, 82: 1270–1282.

JENSEN, J. P., E. JEPPESEN, K. OLRIK & P. KRISTENSEN. 1994. Impact of nutrients and physical factors on the shift from cyanobacterial to chlorophyte dominance in shallow Danish lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 1692–1699.

JONGMAN, R. H. G., C. J. F. TER BRAAK & O. F. R. VAN TONGEREN (ed.). 1995. Data analysis in community and landscape ecology. Cambridge University Press. Cambridge, UK. 301.

JOST, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology*, 88: 2427–2439.

KRUK, C., V. L. M. HUSZAR, E. T. H. M. PEETERS, S. BONILLA, L. COSTA, M. LÜRLING, C. S. REYNOLDS & M. SCHEFFER. 2010. A morphological classification capturing functional variation in phytoplankton. *Freshwater Biology*, 55: 614–627.

LEWIS, W. M. J. 1973. Thermal regime of lake Lanao (Philipphines) and its theoretical implications for tropical lakes. *Limnology and Oceanography*, 18: 200–217.

LEWIS, W. M. J. 1978. Dynamics and succession of the phytoplankton in a tropical lake: Lake Lanao, Philippines. *Journal of Ecology*, 66: 849–880.

LEWIS, W. M. J. 2000. Basis for the protection and management of tropical lakes. *Lakes and Reservoirs: Research and Management*, 5: 35–48.

LOPES, M. R., C. FERRAGUT & C. E. M. BICUDO. 2009. Phytoplankton diversity and strategies in regard to physical disturbances in a shallow, oligotrophic, tropical reservoir in Southeast Brazil. *Limnetica*, 28: 159–174.

MAC DONAGH, M. E., M. A. CASCO & M. C. CLAPS. 2009. Plankton relationships under small water level fluctuations in a subtropical reservoir. *Aquatic Ecology*, 43: 371–381.

MARGALEF, R. 1983. *Limnología*. Omega. Barcelona, Spain. 1010 pp.

MARTÍNEZ-ALMEIDA, V. & R. TAVERA. 2005. A hydrobiological study to interpret the presence of desmids in Lake Zirahuén, México. *Limnologica*, 35: 61–69.

MATSUMURA-TUNDISI, T., J. G. TUNDISI, A. P. LUZIA & R. M. DEGANI. 2010. Occurrence of Ceratium furcoides (Levander) Langhans 1925 bloom at the Billings Reservoir, São Paulo

State, Brazil. *Ocorrência de floração de Ceratium furcoides (Levander) Langhans 1925, na represa Billings, Estado de São Paulo, Brasil*, 70: 825–829.

NASELLI-FLORES, L. 2000. Phytoplankton assemblages in twenty-one Sicilian reservoirs: relationships between species composition and environmental factors. *Hydrobiologia*, 424: 1–11.

NASELLI-FLORES, L. & R. BARONE. 2005. Water-level fluctuations in Mediterranean reservoirs: Setting a dewatering threshold as a management tool to improve water quality. *Hydrobiologia*, 548: 85–99.

NASELLI-FLORES, L., J. PADISÁK & M. ALBAY. 2007. Shape and size in phytoplankton ecology: Do they matter? *Hydrobiologia*, 578: 157–161.

PACHECO, J. P., C. IGLESIAS, M. MEERHOFF, C. FOSALBA, G. GOYENOLA, F. TEIXEIRA-DE MELLO, S. GARCÍA, M. GELÓS & F. GARCÍA-RODRÍGUEZ. 2010. Phytoplankton community structure in five subtropical shallow lakes with different trophic status (Uruguay): A morphology-based approach. *Hydrobiologia*, 646: 187–197.

PADISAK, J., E. HAJNAL, L. NASELLI-FLORES, M. T. DOKULIL, P. NOGES & T. ZOHARY. 2010. Convergence and divergence in organization of phytoplankton communities under various regimes of physical and biological control. *Hydrobiologia*, 639: 205–220.

PANNARD, A., M. BORMANS & Y. LAGADEUC. 2008. Phytoplankton species turnover controlled by physical forcing at different time scales. *Canadian Journal of Fisheries and Aquatic Sciences*, 65: 47–60.

POLLINGHER, U. & C. SERRUYA. 1976. Phased division of Peridinium cinctum fa. Westii and the development of blooms in Lake Kinneret. *Journal of Phycology*, 11: 155–162.

REYES, I., M. A. CASCO, J. TOJA & L. SERRANO. 2008. Hydrological complexity supports high phytoplankton richness in the Doñana marshland (SW Spain). *Hydrobiologia*, 614: 47–54.

REYNOLDS, C. S. 1984. *The ecology of freshwater phytoplankton*. Cambridge University Press. Cambridge, UK. 384 pp.

REYNOLDS, C. S. 1997. *Vegetation processes in the pelagic: A model for ecosystem theory.* Ecology Institute. Luhe, Germany. 371 pp.

REYNOLDS, C. S. 2006. *The Ecology of Phytoplankton (Ecology, Biodiversity and Conservation).* Cambridge University Press. Cambridge, UK. 552 pp.

RIVERA, C., D. SOLANO, A. ZAPATA & J. DONATO. 2005. Phytoplankton diversity in a tropical high mountain lake. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie*, 29: 418–421.

SEELIGMANN, C. & B. C. TRACANNA. 2009. Phytoplankton dynamics in a high elevation reservoir of Northwestern Argentina (Tucuman). *Limnetica*, 28: 105–124.

SOARES, M. C., M. M. MARINHO, V. L. M. HUSZAR, C. BRANCO & S. AZEVEDO. 2008. The effects of water retention time and watershed features on the limnology of two tropical reservoirs in Brazil. *Lakes & Reservoirs: Research & Management*, 13: 257–269.

SOARES, M. C. S., L. O. VIDAL, F. ROLAND & V. L. M. HUSZAR. 2009. Cyanobacterial equilibrium phases in a small tropical impoundment. *Journal of Plankton Research*, 31: 1331–1338.

SOMMER, U., J. PADISÁK, C. S. REYNOLDS & P. JUHÁSZ-NAGY. 1993. Hutchinson's heritage: the diversity-disturbance relationship in phytoplankton. *Hydrobiologia*, 249: 1–7.

SOUZA, M. B. G., C. F. A. BARROS, F. BARBOSA, E. HAJNAL & J. PADISAK. 2008. Role of atelomixis in replacement of phytoplankton assemblages in Dom Helvecio Lake, South-East Brazil. *Hydrobiologia*, 607: 211–224.

SUN, J. & D. LIU. 2003. Geometric models for calculating cell biovolume and surface area for phytoplankton. *Journal of Plankton Research*, 25: 1331–1346.

TOLOTTI, M., A. BOSCAINI & N. SALMASO. 2010. Comparative analysis of phytoplankton patterns in two modified lakes with contrasting hydrological features. *Aquatic Sciences - Research Across Boundaries*, 72: 213–226.

TOWNSEND, S. A. 2001. Perennial domination of phytoplankton by Botryococcus and Peridinium in a discontinuously polymictic reservoir (tropical Australia). *Archiv Fur Hydrobiologie*, 151: 529–548.

TOWNSEND, S. A. & J. T. LUONG-VAN. 1998. Phytoplankton biomass and composition in Manton River Reservoir, a mesotrophic impoundment in the Australian wet/dry tropics. *International Review of Hydrobiology*, 83: 113–120.

TUNDISI, J. G., T. MATSUMURA-TUNDISI & D. S. ABE. 2008. The ecological dynamics of Barra

Bonita (Tietê River, SP, Brazil) reservoir: Implications for its biodiversity. *Brazilian Journal of Biology*, 68: 1079–1098.

UTERMÖHL, H. 1958. Zur vervollkommung der quantitativen phytoplankton-Methodik. *Mitteilungen der Internationa*le Vereinigung für Theoretische und Angewandte Limnologie, 9: 1–38.

WACKLIN, P., L. HOFFMANN & J. KOMÁREK. 2009. Nomenclatural validation of the genetically revised cyanobacterial genus Dolichospermum (Ralfs ex Bornet et Flahault) comb, nova. *Fottea*, 9: 59–64.

WETZEL, R. G. & G. E. LIKENS. 2000. *Limnological Analyses*. Springer-Verlag. New York, USA. 429 pp.

WHITTINGTON, J., B. SHERMAN, D. GREEN & R. L. OLIVER. 2000. Growth of Ceratium hirundinella in a subtropical Australian reservoir: The role of vertical migration. *Journal of Plankton Research*, 22: 1025–1045.

WYNNE, D., N.J. PATNI, S. AARONSON & T. BERMAN. 1982. The relationship between nutrient status and chemical composition of Peridinium cinctum during the bloom in Lake Kinneret. *Journal of Plankton Research*, 4: 125–136.

ZAPATA-ANZOLA, A. M., C. A. RIVERA-RONDÓN & J. C. DONATO-RONDÓN. 2006. Dynamics of photosynthetic pigments in an Andean lake in Colombia. *Lakes and Reservoirs: Research and Management*, 11: 29–38.

ZOHARY, T., J. PADISÁK & L. NASELLI-FLORES. 2010. Phytoplankton in the physical environment: beyond nutrients, at the end, there is some light. *Hydrobiologia*, 639: 261–269.

Limnetica, 31 (2): 323-326 (2012)

The first occurrence of *Cobitis paludica* (de Buen, 1930) in the Segura River Basin (SE Iberian Peninsula)

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Received: 18/11/11 Accepted: 30/1/12

ABSTRACT

The first occurrence of *Cobitis paludica* (de Buen, 1930) in the Segura River Basin (SE Iberian Peninsula)

The aim of the present report is to describe the establishment of viable populations of *Cobitis paludica* (de Buen, 1930) in the Segura River Basin. We found two isolated populations: one located in the upper part of the Segura River and the mouth of its tributary, the Zumeta River, and another in the Mundo River, between the Talave and Camarillas reservoirs. We hypothesised that the introduction of this species may be attributable to the deliberate or accidental introduction by anglers or fish translocation from the Tajo-Segura interbasin water transfer system. *C. paludica* is a threatened endemic fish species from the Iberian Peninsula, and it exhibits sharply declining populations. Therefore, further investigation is needed to assess the genetic origin of the populations reported in this report and to monitor the population trends to determine the population status and the appropriate management plan in the Segura River Basin.

Key words: *Cobitis paludica*, Cobitidae, freshwater fish, Segura River, Mundo River.

RESUMEN

Primera cita de* Cobitis paludica *(de Buen, 1930) en la cuenca del río Segura (SE Península Ibérica)

El presente trabajo constituye la primera referencia al establecimiento de poblaciones viables de Cobitis paludica *(de Buen, 1930) en la cuenca del río Segura. Se han detectado dos poblaciones separadas geográficamente: una localizada en la zona alta del río Segura y la desembocadura del río Zumeta, y otra en el río Mundo, entre los embalses de Talave y Camarillas. Su presencia puede ser debida a la introducción deliberada o accidental por parte de los pescadores, o a la translocación de ejemplares a través del trasvase Tajo-Segura.* C. paludica *es una especie amenazada endémica de la Península Ibérica cuyas poblaciones se encuentran actualmente en declive. En este sentido, es necesario realizar estudios genéticos que confirmen el origen de estas poblaciones y desarrollar protocolos de seguimiento para establecer su estado poblacional y el plan de gestión de esta especie en la cuenca del río Segura.*

Palabras clave: Cobitis paludica, *Cobitidae, peces de agua dulce, río Segura, río Mundo.*

INTRODUCTION

The Southern Iberian spined-loach [*Cobitis paludica* (de Buen, 1930)] is an endemic loach that is widely distributed throughout numerous river basins in the central and southern regions of the Iberian Peninsula (Kottelat & Freyhof, 2007). In Spain, the *C. paludica* distribution comprises the basins of the Ebro, Tajo, Guadiana, Guadalquivir, Guadalete, Guadalmedina, Barbate, Jara, Piedras, Vega, Peñíscola, Odiel, Júcar, Turia, Mijares, Bullent and Racons Rivers, Albufera de Valencia, and tributaries of the western margin of the Duero Basin (Doadrio, 2002). Recently, new populations of *C. paludica* were reported from the Limia and Serpis River Basins (Perea *et al*., 2011).

The aim of the present study is to report the viable establishment of *C. paludica* in the Segura River Basin.

MATERIALS AND METHODS

A total of 65 specimens (Table 1) were collected in 7 out of a total of 35 sampling localities established in the rivers of the Segura Basin: Segura, Mundo, Taibilla, Zumeta and Tus. At each sampling locality (100-150 m long), electrofishing was performed from October 2008 to October 2011 with a standard equipment using a 2500 W generator (200-350 V, 2-3 A). The specimens were anaesthetised and preserved in 10 % formalin solution. The total length (TL ± 1 mm) was obtained for each individual at the laboratory. Some specimens are preserved in the ichthyological collections of the Zoology and Anthropology Department at the University of Murcia (CpSE04-1/CpSE04-25).

RESULTS AND DISCUSSION

We found two isolated populations that were geographically separated: one located in a 5 km-long stretch in the upper part of Segura River and the mouth of its tributary, Zumeta River, and another in a long stretch of approximately 20 km in the Mundo River, between the Talave and Camarillas reservoirs (Table 1).

There are no historic records of *C. paludica* in the Segura River Basin (Mas, 1986; Torralva *et al.*, 2005; Andreu-Soler *et al.*, 2006). However, the observed abundance, size-groups and maximum lengths of this species in some of the sampling sites (Table 1) and the confirmed reproduction, as observed by the capture of juveniles and 0+ individuals (less than 55 mm TL according to Oliva-Paterna *et al.*, 2002), point to the viable establishment of the species in this river basin. The incipient populations of *C. paludica* demonstrated a low density compared to the coexisting translocated Iberian species, the Pyrenean gudgeon *Gobio lozanoi* (Doadrio & Madeira, 2004) and the Iberian straight-mouth nase *Pseudochondrostoma polylepis* (Steindachner, 1864) (Martínez-Morales *et al.*, 2010; Verdiell-Cubedo *et al*., 2011).

We hypothesised that the colonisation of the Segura River basin by *C. paludica* may be attributed to either one or a combination of the following causes: (1) its deliberate or accidental introduction by anglers because sport fishing is extremely popular in the sectors of the rivers where the species has been detected and because of the popular use of the species as bait (Doadrio, 2002) and (2) a consequence of fish translocation along the Tajo-Segura interbasin water transfer system, such as has been postulated for other introduced fish species in the Segura River Basin (García de Jalón *et al.*, 1992; Torralva & Oliva-Paterna, 1997; Andreu-Soler *et al*., 2004; Oliva-Paterna *et al.*, 2005). Nevertheless, because *C. paludica*

Table 1. Sampling localities of the Segura River Basin where *Cobitis paludica* has been detected. The date of capture, UTM coordinates, number of captured individuals (n) and size range (total length ± 1 mm) are indicated. *Localidades de muestreo donde ha sido detectada la presencia de Cobitis paludica en la cuenca del río Segura. Se indican la fecha de captura, coordenadas UTM, número de individuos capturados (n) y rango de tallas (longitud total ± 1 mm).*

River	Locality	Date	UTM	*n*	Size range (TL ± 1 mm)
Mundo	Tavizna	November 2010	30S 0609845 4254770	4	46-92
Mundo	Mingogil	November 2010	30S 0607953 4257440	16	30-90
Mundo	Isso	October 2011	30S 0605999 4258359	8	43-85
Mundo	Talave	November 2008	30S 0596224 4263787	3	62-80
Segura	Los Hornos	October 2009	30S 0548673 4233250	8	42-81
Segura	Las Juntas	October 2008	30S 0547822 4230254	14	47-90
Zumeta	Las Juntas	October 2008	30S 0547820 4230129	12	31-84

is a threatened endemic species from the Iberian Peninsula and it presents sharply declining populations (Doadrio, 2002), further investigation is needed to assess the genetic origin of the populations reported here and to monitor the population trends to determine their status and the management plan in the Segura River Basin.

In the last decade, five non-native freshwater fishes have become established in the Segura River Basin (Torralva *et al*., 2005; Andreu-Soler *et al*., 2006), which, together with previously established non-native fish species, represent approximately 70 % of the current freshwater fish fauna of this basin. The potential impact of the introduced species on the native fish fauna is difficult to ascertain because of the lack of specific studies concerning the interactions of the species or focusing on the biological traits of introduced fishes in the recipient novel aquatic habitats (Leunda, 2010). Taking into account the precarious conservation status of the Segura Basin freshwater fish fauna (Torralva *et al.*, 2005), the translocation and establishment of a new species such as *C. paludica*, combined with the recent proliferation of several non-native invasive fish species, including bleak *Alburnus alburnus* (Linnaeus, 1758) and pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758), suggest that monitoring studies are urgently needed to reinforce the scientific knowledge about the artificial pathways of fish introductions and the mechanisms by which the introduced fish may impact other species. Moreover, because anglers are known to be responsible for some recent invasions in the Iberian Peninsula (Leunda, 2010), increased public awareness and effective control of illegal introductions are needed.

ACKNOWLEDGMENTS

We thank all of those have helped us in the fieldwork: A. Andreu, R. Moreno, I. Martínez, D. Castejón and J. Caravaca. This study was financially supported by the projects "Efecto de la modificación antrópica del régimen hídrico sobre los peces epicontinentales nativos y exóticos de la cuenca del río Segura" (08728/PI/08, Fundación Séneca-Agencia de Ciencia y Tecnología de la Región de Murcia) and "Realización de las tareas de asesoramiento y supervisión de los trabajos de explotación de la red de control biológico en la cuenca del Segura y el establecimiento de las condiciones de referencia" (Confederación Hidrográfica del Segura).

REFERENCES

ANDREU-SOLER, A., F. J. OLIVA-PATERNA, D. VERDIELL-CUBEDO & M. TORRALVA. 2004. Primeras citas de *Alburnus alburnus* (Linnaeus, 1758) y *Tinca tinca* (Linnaeus, 1758) (Actinopterygii, Cyprinidae) en la cuenca del río Segura (Murcia, sudeste de la Península Ibérica). *Anales de Biología*, 26: 222–224.

ANDREU-SOLER, A., F. J. OLIVA-PATERNA, D. VERDIELL-CUBEDO, A. EGEA-SERRANO, A. RUIZ-NAVARRO & M. TORRALVA. 2006. Peces Continentales de la Región de Murcia (SE Península Ibérica): Inventario y Distribución. *Zoologica Baetica*, 17: 11–31.

DOADRIO, I. 2002. *Atlas y Libro Rojo de los Peces Continentales de España*. Dirección General de Conservación de la Naturaleza/Museo Nacional de Ciencias Naturales-CSIC. Madrid. 364 pp.

GARCÍA DE JALÓN, D., M. GONZÁLEZ DEL TÁNAGO & C. CASADO. 1992. Ecology of regulated streams in Spain: An overview. *Limnetica*, 8: 161–166.

KOTTELAT, M. & J. FREYHOF. 2007. *Handbook of European freshwater fishes*. Cornol. 646 pp.

LEUNDA, P. M. 2010. Impacts of non-native fishes on Iberian freshwater ichthyofauna: current knowledge and gaps. *Aquatic Invasions*, 5: 239–262.

MARTÍNEZ-MORALES, I., F. J. OLIVA-PATERNA, D. VERDIELL-CUBEDO & M. TORRALVA. 2010. Inventario y estado de conservación de la fauna piscícola en la cuenca alta del río Segura (SE Península Ibérica). *Anales de Biología*, 32: 23–35.

MAS, J. 1986. La ictiofauna continental de la cuenca del río Segura. Evolución histórica y estado actual. *Anales de Biología*, 8: 3–17

OLIVA-PATERNA, F. J., A. ANDREU-SOLER, D. VERDIELL-CUBEDO & M. TORRALVA. 2005. First occurrence of *Lepomis gibbosus* (L.,1758) in

the Segura river basin (SE, Spain). *Limnetica,* 24: 199–202.

OLIVA-PATERNA, F. J., M. TORRALVA & C. FERNÁNDEZ-DELGADO. 2002. Age, growth and reproduction of *Cobitis paludica* in a seasonal stream. *Journal of Fish Biology,* 60: 389–404.

PEREA, S., P. GARZÓN, J. L. GONZÁLEZ, V. C. ALMADA, A. PEREIRA & I. DOADRIO. 2011. New distribution data on Spanish autochtonous species of freshwater fish. *Graellsia,* 67: 91–102.

TORRALVA, M. & F. J. OLIVA-PATERNA. 1997. First record of *Chondrostoma polylepis* Steindachner, 1865 (Ostariophisi, Cyprinidae) in the basin of the river Segura, S.E. of Spain. *Limnetica*, 13: 1–3.

TORRALVA, M., F. J. OLIVA-PATERNA, A. ANDREU-SOLER, D. VERDIELL-CUBEDO, P. MIÑANO & A. EGEA-SERRANO. 2005. *Atlas de Distribución de Peces Epicontinentales de la Región de Murcia*. Dirección General del Medio Natural, Consejería de Industria y Medio Ambiente, CARM. 167 pp.

VERDIELL-CUBEDO, D., F. J. OLIVA-PATERNA, I. MARTÍNEZ-MORALES & M. TORRALVA. 2011. Efectos de la modificación antrópica de los regímenes hidrológicos naturales sobre poblaciones de ciprínidos bentónicos de la Península Ibérica. In: *Actas VII Congreso Ibérico sobre Gestión y Planificación del Agua*. Fundación Nueva Cultura del Agua. Talavera de la Reina, Toledo.

Limnetica, 31 (2): 327-340 (2012)

Physical and chemical characterisation of superficial sediment of the Ribarroja Reservoir (River Ebro, NE Spain)

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Received: 29/11/11 Accepted: 29/5/12

ABSTRACT

Physical and chemical characterisation of superficial sediment of the Ribarroja Reservoir (River Ebro, NE Spain)

To determine the spatial heterogeneity of the physical and chemical characteristics of superficial sediments from the Ribarroja Reservoir, we have analysed particle size distribution and concentrations of major (Al, Fe, Si, K, Ca, Mg, Ti, Mn and P) and minor (Mo, Nb, Zr, Y, Sr, Rb, Th, Pb, Sn, Ce, Ga, Zn, W, Cu, Co, Ni and V) elements at sixteen sites distributed along the reservoir. Globally, the sediment was quite homogeneous: the dominant grain sizes were silt and clay, and the major element composition agreed with that expected for a mixture of carbonates and weathered silicates, with moderate levels of nitrogen and phosphorus. Concentrations of minor elements did not surpass the Probable Effect Levels, although the concentrations of nickel and chromium exceeded the Threshold Effect Level. A Principal Component Analysis performed on normalised minor elements indicated that the main processes determining the variation of sediment composition were the degree of alteration/weathering of materials, and the association of some metals with organic/clay aggregates.

Key words: Superficial sediment, reservoir sediment, granulometry, Probable Effect level, Threshold Effect Level.

RESUMEN

El sedimento superficial del embalse de Ribarroja (río Ebro, NE de España): su caracterización física y química

Con el objetivo de determinar la heterogeneidad especial de las características físicas y químicas de los sedimentos superficiales del embalse de Ribarroja, se ha analizado la distribución de tamaños de las partículas y las concentraciones de los elementos mayoritarios (Al, Fe, Si, K, Ca, Mg, Ti, Mn, P) y minoritarios (Mo, Nb, Zr, Y, Sr, Rb, Th, Pb, Sn, Ce, Ga, Zn, W, Cu, Co, Ni y V) en dieciséis puntos distribuidos a lo largo del embalse. Globalmente, el sedimento era bastante homogéneo: el tamaño del grano estaba dominado por limo y arcilla, y los componentes de mayor tamaño se relacionan con una mezcla de carbonatos y silicatos meteorizados, con niveles moderados de nitrógeno y fósforo. Las concentraciones de los elementos minoritarios no sobrepasaron los niveles de Nivel de Toxicidad Probable, aunque el níquel y el cromo sobrepasaron el Nivel Umbral de Toxicidad. Un análisis de Componentes Principales realizado con los valores normalizados de los elementos minoritarios ha mostrado cuales son los principales procesos que determinan la variabilidad en la composición de los sedimentos, el grado de alteración/meteorización de los materiales y la asociación de algunos metales a los agregados orgánicos/arcilla.

Palabras clave: *Sedimento superficial, sedimento de embalse, granulometría, Nivel de Toxicidad Probable, Nivel Umbral de Toxicidad.*

"Represas artificiais são ecossistemas aquáticos de extrema importância estratégica, uma vez que, além da base teórica limnológica e ecológica que proporcionam, são utilizadas para diversos e variados usos que interferem com a qualidade da agua, os mecanismos de funcionamento e a sucessão das comunidades aquáticas nos rios e bacias hidrográficas."

(J. G. TUNDISI & T. MATSUMURA TUNDISI, 2008)

INTRODUCTION

Reservoirs play a crucial role in the transportation and sedimentation of particles along riverbeds, altering the hydrological system and retaining materials in the river. The retention of suspended material may, in some cases, reach levels higher than 95 %; this material may lead to negative consequences for the system, such as a decrease in hydric storage capacity and changes in the nature and amount of the sediment provided to the riverbed beyond the reservoir's dam (Loizeau *et al*., 1997). However, depending on the bio-geochemical characteristics of the reservoir, this accumulation of sediment may also lead to positive consequences for the utilisation of hydric resources. For example, the retention of sedimentary phosphorous in the reservoir contributes to the reduction of eutrophication in the stretch of riverbed on the other side of the dam (Armengol *et al*., 1986; Lopez *et al*., 2009).

Although the accumulated material of the sediment is composed of settled matter from the water, the physical and chemical characteristics of sediment and water column materials are different. The selection processes during transport, which are due to the selective displacement of particles according to their size and the energy required to transport them, confer a considerable spatial heterogeneity on the physical structure of the sediment. The presence of dams mainly affects the transport of particles larger than 4 microns, while the transport of clay (particles smaller than 4 microns) is relatively unaffected (Anselmetti *et al*., 2007). Furthermore, numerous bio-geochemical processes occur in the sediment and modify the nature and structure of the sediment material (Lopez, 2009). Greater variety and intensity of these processes lead to greater chemical heterogeneity of the sediment (Kienel & Kumke, 2002, Kumke *et al*., 2005).

In many cases, contaminants and nutrients can accumulate in the sediment at higher concentrations than those observed in the water column. Due to the persistence of these materials in the sediment, monitoring their presence is an especially useful tool for evaluating the ecological quality of aquatic systems (Swartz *et al*., 1982). Additionally, the balance between dissolved and particulate forms of these materials depends on the physical-chemical conditions of the system, and the sediment may therefore become a source of undesirable materials for the water if the physical-chemical conditions are altered by hydrodynamic, biological or anthropogenic factors (Abrams & Jarrell, 1995, Nurnberg, 1999). This consequence adds to the importance of the study of sediment characteristics, and knowledge of these characteristics is necessary information for the efficient management of aquatic systems.

The Ribarroja Reservoir, located on the Ebro River, receives suspended materials from three main inlets: the exits of the Mequinenza Reservoir (also on the Ebro), the Segre River, and the Matarraña River. Given that the Mequinenza dam retains over 95 % of the suspended material transported by the Ebro River (Roura, 2004), the major contributors of sediment to the Ribarroja Reservoir are most likely the Reservoir itself (sediment of autochthonous origin) and the Matarraña and Segre Rivers. These different contributors could be important determinants of sediment spatial heterogeneity. The main objective of the present study is to describe the spatial variability of the physical structure and the main chemical characteristics of the superficial sediment of the Ribarroja Reservoir. The information obtained in this study will serve as a baseline for present and future evaluations of the quality of the sediment of this reservoir and will contribute to the construction of an appropriate management strategy for the system.

MATERIAL AND METHODS

Sediment sampling was done in April 2008. Sixteen sampling points were selected (Table 1) based on the preliminary results of a precision bathymetry study of the reservoir. Given that the available results indicated the existence of a marked sediment tongue coming from the Segre River, this zone was sampled more rigorously. The positions of the sampling site were registered using GPS. Superficial sediment (0-4 cm) was collected using a Lenz-type dredge in a 400 cm^2 area. Additionally, for seven points at which sufficiently deep sediment was extracted, the samples were subdivided *in situ* every 4 cm of depth to obtain an estimate of their vertical variability. The samples were distributed into three aliquots and kept in jars and/or PVC bags under refrigerated conditions until their analysis in the laboratory.

In the laboratory, two aliquots were allotted to a granulometric analysis, which was conducted with a Beckman-Coulter LS 230 particle analyser. One aliquot was analysed directly after dispersion with pyrophosphate and ultrasound, while the other was first treated for organic matter elimination by adding H_2O_2 before being processed in the same way as the untreated subsample. The third aliquot was dried at 70 °C until it reached a constant weight for dry weight determination. This dry material was then ground using an agate mortar until it was completely homogenised. The concentrations of carbon (C) and nitrogen (N) in the dry material were determined using an elemental CN auto-analyser. For the determination of the most abundant elements, X-ray fluorescence (XRF; Panalytical, PW2400) was used after fusion at 1100 °C with Lithium tetraborate. The concentration of trace metals was also determined using XRF after adhesion using Elvactite 2044 and posterior pressing.

RESULTS AND DISCUSSION

Physical structure of the superficial sediment

Throughout the majority of the Reservoir, the sediments are of a lime-clay texture, with a lime percentage ($4\ \mu m < \phi < 63\ \mu m$) of between 56 % and 74 % and a clay percentage ($\phi < 4\ \mu m$) of between 18 % and 43 %. The G, J and D stations are exceptions, and sediments from these sites present a relatively elevated percentage of sands (≈ 10 %) along with a lower lime proportion (Fig. 1).

Regarding the texture of the sediment, it is important to note the similarity between the sediments located in the stretch next to the dam (stations L through P) and the station located at the tail end of the reservoir (station A). At the river

Table 1. Description and location of the sampling points. *Descripción y localización de los puntos de muestreo.*

Station	Description	Latitude	Longitude	depth meters
A	Reservoir Entrance	273791	4582544	10.9
B	Segre River	274711	4582674	3.5
C	Sediment Head	275271	4582104	8.9
D	Sediment Head	275261	4582174	7.6
E	Sediment Head	276881	4582034	9.7
F	Sediment Head	276911	4582404	5.4
G	Sediment Head	277571	4582504	8.2
H	Middle Stretch	278681	4581554	12.6
I	Middle Stretch	279181	4580514	15.3
J	Middle Stretch	279881	4577634	17.4
K	Middle Stretch	277311	4573984	18.2
L	Middle Stretch	278331	4570244	21.3
M	Matarraña Entrance	279351	4568714	17.5
N	Dam Stretch	281101	4568614	24.2
O	Dam Stretch	283211	4569654	26.3
P	Dam Stretch	283921	4569894	26.3

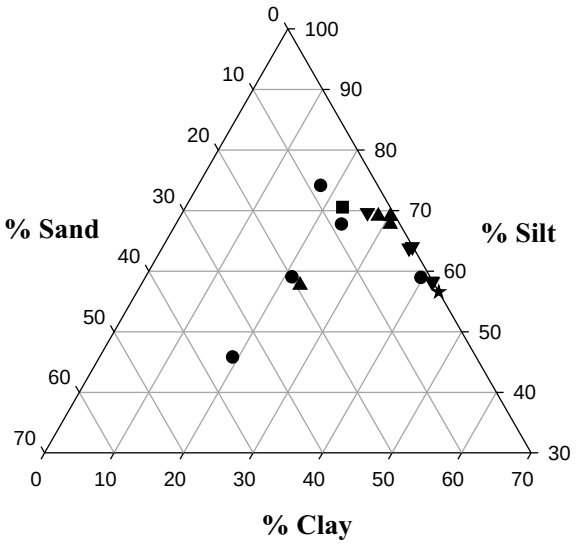

Figure 1. Shepard diagram indicating the percentage composition of clay, silt and sands in the superficial sediments of Ribarroja. The symbols indicate the different stretches. Star: station A; square: station B; circles: stations C through G; triangles: stations H through K; inverted triangles: stations L through P. *Diagrama de Shepard indicando la composición porcentual de arcilla, limo y arena en los sedimentos superficiales de Ribarroja. Los símbolos indican los diferentes tramos. Estrella: estación A; cuadrado: estación B; círculos: estaciones de la C a la G; triángulos: estaciones de la H a la K; triángulos invertidos: estaciones de la L a la P.*

bends (stations H through K), the sediment shows a similar structure, but with a slightly higher percentage of lime. In the upper stretch, from the entrance of the Segre River to the beginning of the meandering zone (stations C through K), the greatest variability in sedimentary texture is found. Some sediments in this region are of a lime-clay type (station C), while others (station G) are of a sandy-clay type, which can be linked to the furthermost frontal zone of the sediment entrance proceeding from the Segre River.

The statistical parameters of the particle distribution observed for each sample depend on such factors as the time of transport, the type of deposition environment, and the energy of the sedimentation environment (Stevens *et al*., 1996, Garcia *et al*., 2005). The results (Table 2) show elevated values for the standard deviation of particle size (especially for stations D, G and J), evidencing a highly heterogenic sedimentary environment. In every reservoir, the distribution of particle size shows positive asymmetry, indicating that the sediment is formed by a mixture of mostly fine materials. Furthermore, in Ribarroja the asymmetry is closely related to the kurtosis, which (like the standard deviation) hints at

Table 2. Statistical parameters of the distribution of particle sizes in the superficial sediment. *Parámetros estadísticos de la distribución de partículas en el sediment superficial.*

Station	Mean micron	SD	Asymmetry	Kurtosis
A	7.2	7.5	2.1	5.8
B	20.0	26.9	2.8	9.4
C	9.5	14.5	4.6	28.1
D	46.3	92.1	3.6	14.0
E	22.9	42.1	4.5	25.3
F	23.1	28.0	2.5	7.3
G	106.9	187.9	2.8	8.9
H	13.3	17.9	3.7	18.5
I	11.2	14.1	3.7	20.4
J	43.9	83.0	3.6	14.7
K	10.4	11.5	3.5	21.0
L	8.1	8.5	2.5	8.9
M	7.8	9.1	2.7	9.7
N	9.9	11.3	3.8	24.4
O	15.3	20.3	3.1	12.1
P	7.5	8.5	2.7	9.1

the grade of selection of the sedimented material. Station A presents the lowest asymmetry and kurtosis values of all sampling sites (Table 2), which indicates low material selection that leads to a mixture of particles not dominated by a particular fraction. On the other hand, those stations immediately posterior to the entrance of the Segre River (stations C and E) and the entrance of the Matarraña River (station N) are the ones that present the highest values of these parameters, indicating that these zones have sedimentation which is highly selective for very fine materials.

The distribution of particle size in the sediment is related to the content of its organic material, as organic material can incorporate itself into microaggregates of clay and lime or even adsorb itself onto their surfaces (Zonta, *et al*., 1994). The comparison between the size spectrum of an untreated sediment sample and another sample from the same location in which the organic material has been eliminated provides a measurement of the particle size of the organic matter (Fig. 2). The results indicate that most of the organic matter is present in the lime fraction because when organic matter is eliminated, the percentage of lime decreases as the smaller-sized clay fraction increases (Fig. 2). This pattern appears throughout most of the reservoir, but it is especially evident in those stations situated on the final stretch (stations K through P). In some stations located on the superior and medium stretches (D, E, G and J), the decrease in the proportion of lime due to the elimination of organic material is not associated with an increase in the finer fraction but instead with an increase of the thicker fraction. Although these results must be interpreted with caution, as these stations are characterised by their elevated heterogeneity, the change observed in percentage of composition could correspond to the presence of abundant organic particles of a size similar to the lime and clay (i.e., under 63 μ m) mixed with sands of inorganic nature. These results suggest the presence of an accumulation of small-sized organic matter in the higher heterogeneity sedimentary environments in the upper stretch of the reservoir.

Chemical characterisation of the superficial sediment most abundant elements

The elemental composition of the sediment of the Ribarroja Reservoir corresponds to the composition expected for a mixture of weathered silicates and carbonates. Silicon, aluminium and potassium, the main components of weathered silicates, are found in high concentrations, while the concentration of calcium, an element mainly associated with carbonates, is present in the same order as silica (Table 3). Regarding those elements associated with organic matter, the con-

Table 3. Mean concentration, standard deviation (SD) and variation coefficient (CV = Mean*100/SD) of the most abundant elements in the superficial sediment of Ribarroja. *Concentración media, Desviación Estándar (SD) y coeficiente de variación (CV = Media*100/SD) de los elementos más abundantes en el sedimento superficial de Ribarroja.*

		Mean	SD	CV
TC	%	5.5	0.6	10.7
TN	%	0.2	0.1	22.0
P	mg/g	1.2	0.2	15.6
Si	mg/g	171.4	15.4	9.0
Ca	mg/g	138.0	13.4	9.7
Al	mg/g	69.1	11.8	17.0
Fe	mg/g	32.8	4.7	14.4
Ti	mg/g	3.0	0.3	11.0
K	mg/g	21.0	3.0	14.5
Mg	mg/g	12.9	1.5	11.8
Mn	mg/g	0.6	0.1	11.3

centrations of N and phosphorus (P) present values akin to those of moderately eutrophic systems (Lopez & Morgui, 1993), with an N/P stoichiometric relationship that oscillates between 3 and 5 (expressed in atoms); this result indicates that the sediment is poor in N content with respect to organic matter. It is important to note that the P/Al relation in the superficial sediment presents a mean value of 16. Because these sediments have important carbonate contents, this value suggests that phosphorous retention by the sediment is very near saturation (Jensen *et al*., 1992, Lopez *et al*., 2006).

Analyses of the subsamples taken from different depths (between 0 and 10 cm) show that the superficial sediment is nearly homogeneous for the most abundant elements, with the variation coefficient being lower than 3 % for all the analysed elements. With respect to the longitudinal variation observed along the reservoir, aluminium, potassium, and iron show very similar patterns of variability. These elements present uniform and elevated concentrations on the lower stretch (stations K through P), while in the tail and at the Segre River (stations A through C), similar yet more varying concentrations are ob-

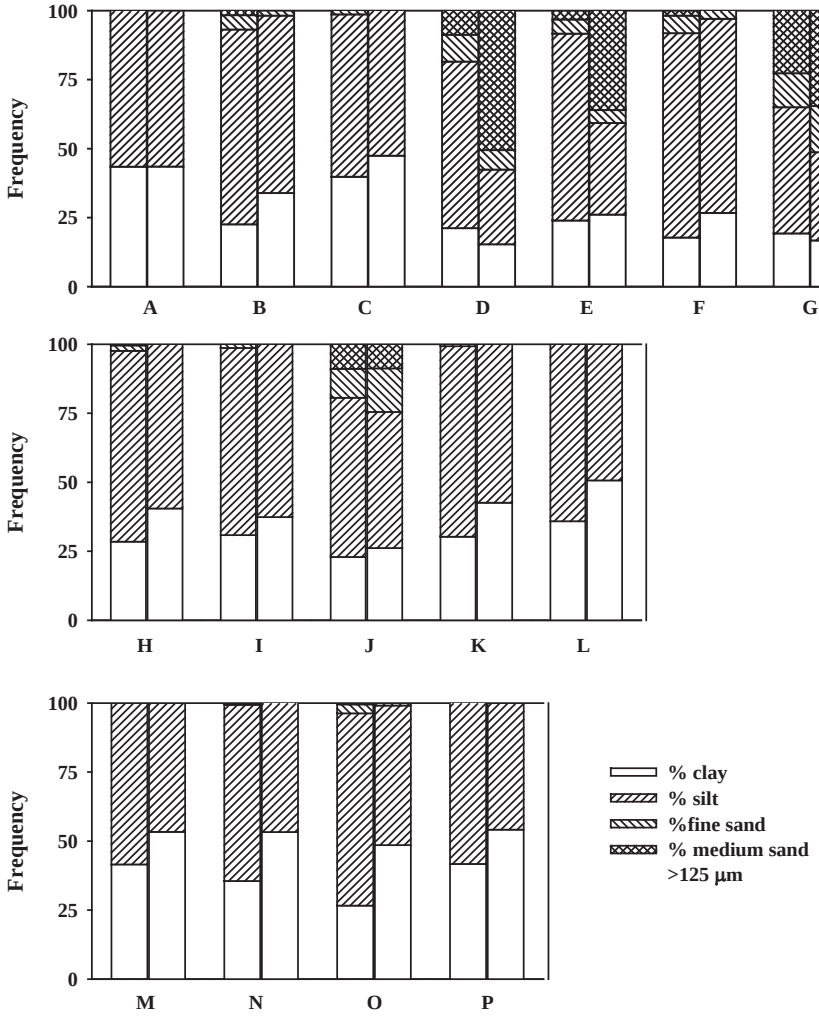

Figure 2. Percentages of clay, silt and sands in untreated replicas (left) and in replicas where the organic matter has been eliminated (right). *Tanto por ciento de arcillas, limos y arenas en réplicas no tratadas (izquierda) y en réplicas en las que la materia orgánica ha sido eliminada (derecha).*

served. The intermediate stretch shows the greatest variability, along with the lowest concentrations of the reservoir (Fig. 3A). Calcium and silica follow a somewhat different variation pattern; the largest concentrations for these materials are in the zone between stations D and K, with silica maximums very clear at stations D and G (Fig. 3B). N and P tend to accumulate in the lower stretch, where N reaches values close to 3 $mg \cdot g^{-1}$, and P reaches values close to 1.5 $mg \cdot g^{-1}$ (Fig. 3C). The pattern of C variability is similar to that of the concentration of Ca, with the largest concentrations (6.8 %) being found at stations F and G. This observation suggests that

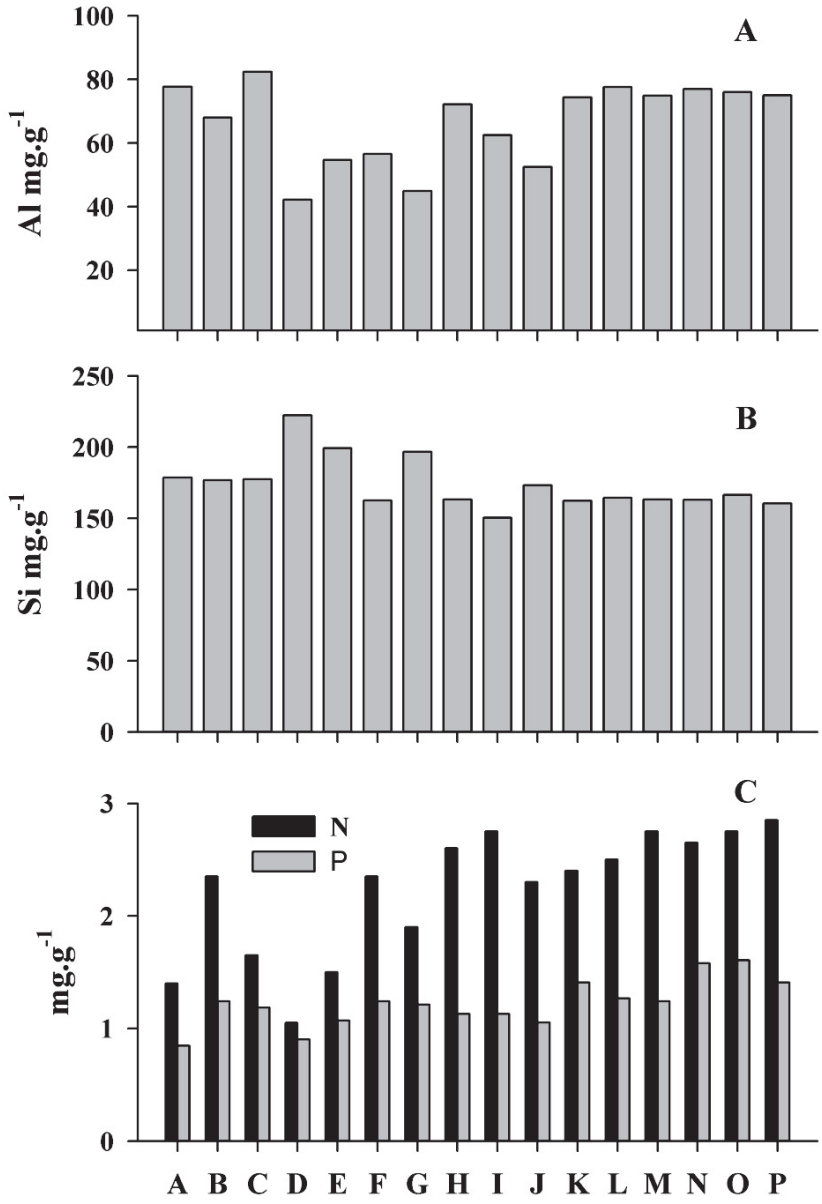

Figure 3. Spatial variation along the reservoir of the concentrations of aluminium (A), silicon (B) and nitrogen and phosphorous (C) in the superficial sediment along the reservoir. *Variación espacial a lo largo del embalse de la concentración de aluminio (A), silicio (B) y nitrógeno y fósforo (C) en los sedimentos superficiales.*

the variability of C in the sediment of Ribarroja is more closely associated with the inorganic fraction than with the organic fraction. However, the elemental coefficient between C and Ca is always greater than 1, with the amount over 1 indicating the fraction of C associated with organic matter. This value is, on average, higher in the final stretch (stations K through P), although it also presents two significant maximums at station B (Segre River on the confluence with the reservoir) and at station G (Fig. 4A).

The analysis of the elemental quotients provides additional information about the biogeochemical dynamics of the sediment (Lopez *et*

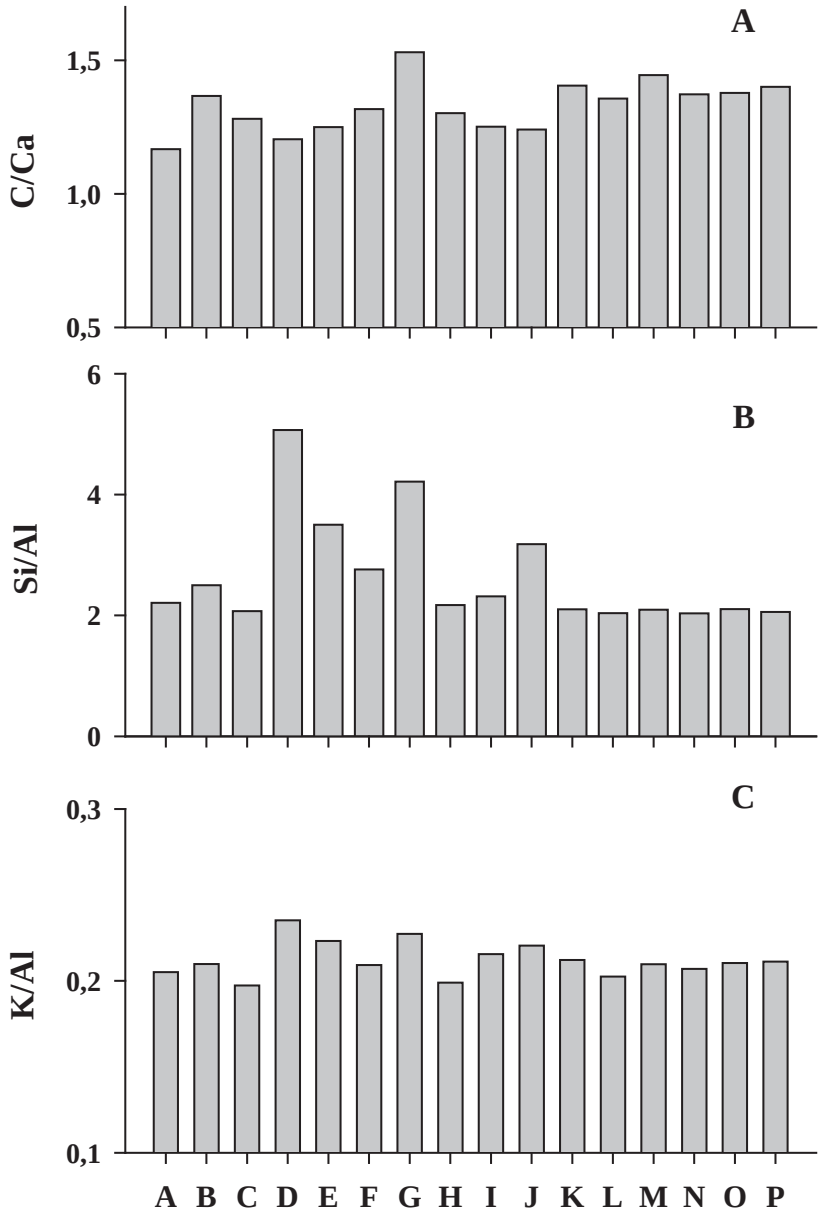

Figure 4. Spatial variation along the reservoir of the elemental quotiens C/Ca (A), Si/Al (B) and K/Al (C) in the superficial sediment along the reservoir. Ratios expressed in atoms. *Variación espacial a lo largo del embalse de los coeficientes elementales C/Ca (A), Si/Al (B) y K/Al (C). Cocientes expresados en átomos.*

al., 2006). The Si/Al quotient is an indirect estimator of the proportion of quartz, associated with the sedimentation of thicker materials that require larger transport energy, and clays, associated with the sedimentation of finer materials that require little energy to be transported. The variability of the Si/Al quotient along the reservoir (Fig. 4B), indicates that a greater proportion of quartz appears in the intermediate stations, especially in stations G, D and J; these zones are located where materials of greater size settle. This result is in agreement with the granulometric distribution discussed previously. The K/Al quotient is closely related to the nature and degree of weathering of the clays. In rocks, the average value of this quotient is approximately 0.24, while in the highly weathered material usually transported by rivers, the value is relatively lower, as K is lost through mobilisation (K/Al = 0.15) (Viers *et al*., 2009). The sediment of Ribarroja presents an intermediate value, 0.21, closer to that of rocks, indicating the presence of clays with an intermediate degree of weathering. The highest values for this quotient are measured in the stretch of river bends (stations D through K), where the least altered materials would be found, while in the final stretch and at the head of the reservoir lower quotients are measured, indicating the presence of more altered clays (Fig. 4C).

Trace elements

The mean concentrations of the trace elements analysed in the superficial sediment of Ribarroja are given in Table 4. Among the analysed elements, the ones most frequently associated with agricultural and/or industrial anthropogenic contamination are zinc (Zn), copper (Cu), nickel (Ni), lead (Pb), and chromium (Cr). These elements can have adverse effects on the biota when their concentrations exceed certain limits. The observed concentrations for these elements are

Table 4. Mean concentration of trace elements in the superficial sediment of Ribarroja. N = 26. Data in $\mu\ g \cdot g^{-1}$. As a comparison, the values of these metals in different types of materials are given: 2 Mean concentration in the sediment in suspension in rivers of the world (Viers *et al*., 2009); 3 Mean concentration in calcareous rocks (a: Guo *et al*., 1998; b: Potts *et al*., 1992). *Concentración media de los elementos traza en los sedimentos superficiales de Ribarroja.* N= *26. Datos en* $\mu\ g \cdot g^{-1}$. *Como comparación se dan valores de estos metales en diferentes tipos de materiales: 2 Concentración media en los sedimentos en suspensión en ríos del mundo (Viers* et al., *2009): 3 Concentración media en rocas calcáreas (a: de Guo* et al., *1998; b: de Potts* et al., *1992).*

	Mean	2	3	
Zn	105.5	208.0	30.0	b
Cu	30.2	75.9	4.0	b
Ni	30.9	74.5	5.0	b
Pb	24.0	61.1	13.0	b
Cr	56.8	130.0	10.0	b
Mo	2.2	3.0	0.5	a
Nb	13.0	13.5	4.1	a
Zr	97.5	160.0	29.0	a
Y	17.3	21.9	3.9	a
Sr	457.8	187.0	218.0	a
Rb	114.4	78.5	21.0	a
Th	11.9	12.1	1.6	a
Ga	14.9	18.1	2.8	a
W	3.7	2.0	0.3	a
V	97.6	129.0	14.0	a
Ce	40.1	73.6	—	
Co	14.8	22.5	2.1	a
Ba	318.6	522.0	374.0	a

lower than those described for the material transported by the rivers, while the enrichment factor with respect to limestone (the ratio between concentrations in the sediment and in the rock) is higher for Cu, Ni, and Cr (7.5, 6 and 5.8, respectively) than for Zn and Pb (3.5 and 1.8, respectively). When comparing the results with the critical values of toxicity threshold (TEL) and probable level of toxicity (PEL) employed by other authors (Evans and Gottgens, 2007), it is important to note that Zn and Pb are always found at lower concentrations than the levels considered as the toxicity thresholds (123 $mg \cdot g^{-1}$ and 35 $mg \cdot g^{-1}$, respectively). The levels of Cu are close to the toxicity threshold (35.7 $mg \cdot g^{-1}$) at stations L and M (entrance to the Matarraña and the station immediately upstream) and are lower across the rest of the reservoir, while the concentrations of Cr and Ni are above the toxicity threshold (37 $mg \cdot g^{-1}$ and 18 $mg \cdot g^{-1}$, respectively) throughout the reservoir, although at no point is the level of probable toxicity reached (90 $mg \cdot g^{-1}$ and 36 $mg \cdot g^{-1}$, respectively).

To integrate all the available information on the concentration of trace elements in the sediment of Ribarroja, an analysis of principal components (PCA) was conducted, with the intention of reducing the high number of variables to a few combined variables. These variables were meant to integrate the previously unmanageable number of variables and associate them with the main processes that determine the chemical composition of the sediment. Following Kumke *et al*. (2005), the PCA was conducted on the normalised concentrations with respect to aluminium.

The analysis has allowed the extraction of four principal components that explain 84 % of the variance. The first component explains 40 % of the variance and is mainly determined by the concentrations of niobium (Nb), zirconium (Zr), yttrium (Y), lead (Pb), and zinc (Zn), which present load factors higher than 0.85, and to a lesser degree by vanadium (V) and cobalt (Co) (load factor > 0.75) (Table 5). This component is also found to be narrowly correlated with the Si/Al elemental quotient ($r^2 = 0.870$, $p < 0.005$).

Table 5. Percentage of variance explained by the four principal components and loads for the variables introduced in the PCA analysis. Only values higher than 0.500 are given. *Porcentaje de la varianza explicada por las cuatro primeras componentes y factores de carga de las variables usadas en el análisis de componentes principales. Solamente se muestran los valores superiores a 0.500.*

Component	1	2	3	4
% Variance explained	40.1	67.9	76.3	83.7
Mo		0.787		
Nb	0.941			
Zr	0.897			
Y	0.871			
Sr	0.710		−0.530	
Rb		0.823		
Th			0.632	
Ga		0.913		
Zn	0.877			
W			−0.541	
Cu		0.741		
Ni		0.955		
V	0.785			
Ce				0.834
Co	0.761			
Pb	0.920			
Ba	0.588	0.546		
Cr	0.,663	−0.611		

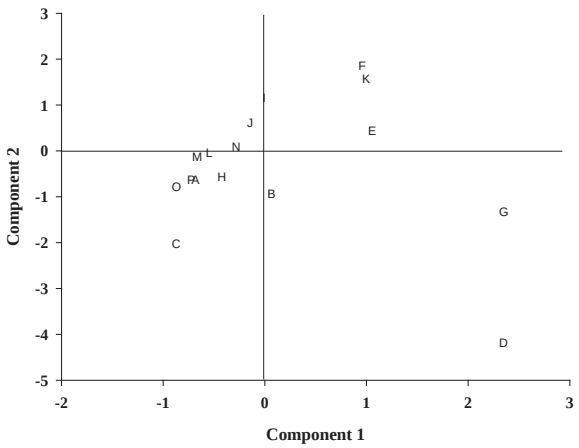

Figure 5. Values of the two first principal components in the superficial sediment of the different sampled stations along the reservoir. *Valores de los dos componentes principales en los sedimentos superficiales de las diferentes estaciones muestreadas a lo largo del embalse.*

All the elements associated with component 1 are characterised by the presence of elevated aluminium concentrations in dolomitic lime and in the earth crust, while the clays originating in the watershed are relatively poor in these elements. The impoverishment of Pb, Zn, V, Co, and Cr in the clays is due to its moderately high mobility. The impoverishment of zirconium, however, is due to the fact that this element is only lost in rock from physical but not from chemical weathering (Riebe *et al*., 2003). From these considerations, and in accordance with the observed correlations with the most common elements in the Ribarroja sediment, we can interpret component 1 as an estimate of the degree of chemical alteration of the sedimented materials. The highest values of this component correspond to the stations that present higher percentages of relatively unaltered materials, those with a significant amount of quartz and lime and a lower proportion of clays. The spatial variability of the component for the superficial sediment agrees with this interpretation, as higher values are found in the river bend zone (D, G, E, F, K) than on the dam and on the tail of the reservoir (A, C, P, M) (Fig. 5).

The 2nd component, which explains 27.8 % of the variance, is determined by the concentration of nickel (Ni), molybdenum (Mo), gallium (Ga), rubidium (Rb), and copper (Cu), and it is negatively correlated to the concentration of chromium (Table 5). Furthermore, it presents a significant correlation with the N concentration ($r^2 = 0.26$, $p < 0.05$). In the Ribarroja sediment, Ni and Cu present a relatively high enrichment coefficient (Table 4), and the association of these elements to the concentration of N suggests that the 2nd component is related to a process of organic contamination. The transition metals, which include Ni and Cu, can form colloids and aggregates with clay and organic material, which would explain the observed relationship. Molybdenum is a scarce element that frequently appears in association with nickel, which is why its association with component 2 is not unusual. The interpretation of the results as they pertain to gallium and rubidium is less evident. The concentration of gallium in the Ribarroja sediment is on the same order as the concentration observed in the earth crust or in clays originating in the watershed (Table 4), while the concentration of Rb is higher in these sources than it is in lime and earthly sediment. Although rubidium is a mobile element, it may be relatively enriched due to its higher adsorption affinity to clays, where it displaces lower atomic mass elements such as potassium (Kerr *et al*., 2008). In light of this information, the 2nd component may describe the process of formation of clay-organic matter-metal complexes. It should be noted that the negative correlation between this component and chromium suggests that, in the Ribarroja Reservoir, this element is linked to inorganic complexes. The spatial variability in the superficial sediment shows that the stations with higher values of this component are located in the central zone, especially stations F, K and I, while the lower values appear in those stations close to the tail (C and D).

Components 3 and 4, which explain 8.4 % and 7.4 % of the variance, respectively, are more difficult to interpret and seem to be related to the mineralogy of the basin. The elements that define both components, wolfram, thorium and cerium, are very minor and are found at very low levels in the Ribarroja sediment. The negative weight of the concentration of strontium with component 3

suggests that it is related to presence of carbonates, (which contain low concentrations of thorium).

Spatial heterogeneity

In general terms, the sediment of Ribarroja is relatively homogeneous. Although important differences exist regarding the amount of sediment accumulation in different areas of the reservoir, there are no great differences in either the chemical or physical characteristics of the superficial sediment, reflecting a similar source of matter across the reservoir. The detailed analysis of the most and least abundant elements in the sediment, combined with the detailed study of the physical structure, allows for the distinction of different sedimentary areas, which reflect a process of selective sedimentation along the reservoir and cause a certain spatial heterogeneity of the sediment. These areas are described below, with emphasis on their most relevant characteristics.

Upper stretch

A great accumulation of sediment proceeding mostly from the Segre River is located in the upper stretch. From a qualitative point of view, two clearly differentiated areas can be distinguished. The first corresponds to the area before the entrance of the Segre River, next to the Mequinenza dam. In this area, the sediment is characterised by a mix of very fine materials, with an abundant contribution of highly altered materials and a scarcity of organic material and associated metals. However, because the finer fraction is not "diluted" by the presence of larger materials, the concentration per unit of dry weight of some metals, such as nickel, is relatively high.

The second area corresponds to the zone where the contributions from the Segre River have the most influence. This sediment is distinguished by its mixture of lime, highly weathered clay and barely altered sands. In addition, part of the lime corresponds to organic matter, which is found in moderate quantities. Along with the presence of this type of organic matter, the sediment presents moderate concentrations of copper, nickel, and zinc. In the reservoir zone between the entrance of the Segre River and the front of the sediment tongue (station G), the sediment presents characteristics that are compatible with the differential sedimentation of materials such as those found on the Segre River. The zone closest to the entrance to the river (station B) is characterised by the predominance of more weathered materials; as the sediment front advances, less altered materials become more abundant. Less coherent materials, such as sands and very fine particles, are transported more easily, and these materials appear in larger proportions in the frontal zone of the sediment tongue (station G) and in the littoral zone (station D). In these zones, the sediment appears to be formed by a heterogeneous mix of materials, with a low proportion of lime and a variable proportion of organic matter, which is greatest at the most advanced station (G).

Intermediate stretch

This stretch, which includes the river meandering zone of the Ebro River, presents quite homogeneous characteristics. The sediments are of a lime-clay texture in which the dominant materials are those of lesser size. The organic matter of this section is associated with the lime portion, and its concentration increases downstream, with the highest concentrations of nutrients found at station K. The levels of metal concentration are moderate-low, with intermediate values between those observed in the Segre River and in the advancing front (station G). However, station J shows very different characteristics from the others in the stretch and is more similar to littoral station D. Just as at that location, the sediment is characterised by a heterogeneous mixture of clay, sands and a low percentage of lime. The organic matter is not associated to lime here, but the concentrations of C, N and P are much greater than those observed in the littoral station of the upper stretch. Similarly, although the concentrations of metals in this station are inferior to the rest of the middle stretch (as expected from the lesser proportion of lime), they are clearly superior to those of station D.

Lower stretch

The lower stretch of the reservoir, from slightly before the entrance to the Matarraña River to the Ribarroja Reservoir, presents some exceedingly homogeneous characteristics. As in the intermediate stretch, the sediment is characterised by a lime-clay texture, but although the proportion of lime is similar to that of the aforementioned stretch, the proportion of very fine materials increases slightly. The most abundant elements are those expected from highly weathered materials. The entrance of the Matarraña River has little effect on the composition of the sediment located downstream and is only notable due to a slight increase in the asymmetry of the distribution of the particle sizes behind the river entrance. Just as in the intermediate stretch, a portion of the organic matter is found in the lime fraction. A gradual increase in the concentration of nutrients, N, and P in the sediment in the direction of water flow is detectable, with the highest concentrations being reached just before the Ribarroja dam (stations O and P). The elevated proportions of lime and organic matter are in agreement with the larger concentrations of metals such as nickel, copper, and zinc, which are present in concentrations per unit of dry weight that are either similar to or higher than those observed in the Segre River. Nevertheless, if the lower presence of thick material in the final stretch of the reservoir relative to the Segre River is considered, the concentration of metals in the sediment of the final stretch is slightly lower than that detected in the river.

ACKNOWLEDGEMENTS

In this paper, the authors want to acknowledge the professors J. G. Tundisi and T. Matsumura Tundisi for their contributions to the knowledge of the ecology of the Brazilian continental waters. The studies of the limnology of reservoirs conducted by these scientists have been especially important to the development of a methodology to manage reservoirs and to minimise their impact. The Spanish Government (projects CGL2004-05503-C02-01 and 02, and CGL2008-06377-C02-01 and 02) provided financial support for this study.

REFERENCES

ABRAMS, M. M. & W. M. JARRELL. 1995. Soil-Phosphorus as a Potential Nonpoint-Source for Elevated Stream Phosphorus Levels. *J. Environ. Qual*., 24(1): 132–138.

ANSELMETTI, F. S., R. BUHLER, D. FINGER, S. GIRARDCLOS, A. LANCINI, C. RELLSTAB & M. STURM. 2007. Effects of Alpine hydropower dams on particle transport and lacustrine sedimentation. *Aquat. Sci*., 69(2): 179–198.

ARMENGOL, J., M. CRESPO, J. A. MORGUÍ & A. VIDAL. 1986. Phosphorus budgets and forms of phosphorus in the Sau reservoir sediment: An interpretation of the limnological record. *Hydrobiologia*, 143: 331–336.

EVANS, J. E. & J. F. GOTTGENS. 2007. Contaminant stratigraphy of the Ballville Reservoir, Sandusky River, NW Ohio: implications for dam removal. *J.Great Lakes Res*. 33: 182–193.

GARCIA, T., A. VELO, S. FERNANDEZ-BASTERO, L. GAGO-DUPORT, A. SANTOS, I. ALEJO & F. VILAS. 2005. Coupled transport-reaction pathways and distribution patterns between siliciclastic-carbonate sediments at the Ria de Vigo. *J. Mar. Syst*., 54: 227–244.

GUO, S., T. C. LUO, B. R. ZHANG, H. F. ZHANG, Y. W. Z. HAN, D. ZHAO, & Y. K. HU 1998. Chemical composition of the continental crust as revealed by studies in East China. *Geochim.Cosmochim. Acta* 62: 1959–1975

JENSEN, H. S., P. KRISTENSEN, E. JEPPESEN & A. SKYTTHE. 1992. Iron-Phosphorus Ratio in Surface Sediment as an Indicator of Phosphate Release from Aerobic Sediments in Shallow Lakes. *Hydrobiologia*, 235: 731–743.

KERR, S. C., M. M. SHAFER, J. OVERDIER. & D. E. ARMSTRONG. 2008. Hydrologic and biogeochemical controls on trace element export from northern Wisconsin wetlands. *Biogeochemistry*, 89: 273–294.

KIENEL, U. & T. KUMKE. 2002. Combining ordination techniques and geostatistics to determine the patterns of diatom distribution at Lake Lama, Central Siberia. *J. Paelolim*., 28: 181–194.

KUMKE, T., A. SCHOONDERWALDT & U. KIENEL. 2005. Spatial variability of sedimentological properties in a large Siberian lake. *Aquat. Sci*., 67: 86–96.

LOIZEAU, J. L., J. DOMINIK, T. LUZZI & J. P. VERNET. 1997. Sediment core correlation and mapping of sediment accumulation rates in Lake Geneva (Switzerland, France) using Volume Magnetic Susceptibility. *J. Great Lakes Res.,* 23: 391–402.

LOPEZ, P. 2009. Los sedimentos y su incidencia en la eutrofización de los embalses. Caso del río Lozoya. *Ingeniería del Agua,* 16: 273–283.

LOPEZ, P. & J. A. MORGUI. 1993. Factors Influencing Fractional Phosphorus Composition in Sediments of Spanish Reservoirs. *Hydrobiologia,* 253: 73–82.

LOPEZ, P., R. MARCE, J. ORDONEZ, I. URRUTIA & J. ARMENGOL. 2009. Sedimentary phosphorus in a cascade of five reservoirs (Lozoya River, Central Spain). *Lake Reserv. Manage.,* 25: 39–48.

LOPEZ, P., E. NAVARRO, R. MARCE, J. ORDONEZ, L. CAPUTO & J. ARMENGOL. 2006. Elemental ratios in sediments as indicators of ecological processes in Spanish reservoirs. *Limnetica,* 21: 499–512.

NURNBERG, G. K. 1999. Determining trophic state in experimental lakes. *Limnol.Oceanogr*., 44: 1176–1179.

POTTS, P. J., A. G. TINDLE & P. C. WEBB 1992. Geochemical reference material compositions: rocks, minerals, sediments, soils, carbonates. CRC.

RIEBE, C. S., J. W. KIRCHNER & R. C. FINKEL. 2003. Long-term rates of chemical weathering and physical erosion from cosmogenic nuclides and geochemical mass balance. *Geochim. Cosmochim. Acta,* 67(22): 4411–4427.

ROURA, M. 2004. *Incidència de l'Embassament de Mequinensa en el transport de sòlids en suspensió i la qualitat de l'aigua del riu Ebre*. Tesis Doctoral, Universidad de Barcelona. 236 pp.

STEVENS, R. L., H. BENGTSSON & A. LEPLAND. 1996. Textural provinces and transport interpretations with fine-grained sediments in the Skagerrak. *J. Sea Res.,* 35: 99–110.

SWARTZ, R. C., W. A. DEBEN, K. A. SERCU & J. O. LAMBERSON. 1982. Sediment Toxicity and the Distribution of Amphipods in Commencement Bay, Washington, United-States. *Mar. Pollut. Bull.,* 13: 359–364.

TUNDISI, J. G. & T. MATSUMURA TUNDISI. 2008. *Limnologia*. Oficina de Textos, Sao Paulo, SP. Brasil. 631 pp.

VIERS, J., B. DUPRE & J. GAILLARDET. 2009. Chemical composition of suspended sediments in World Rivers: New insights from a new database. *Sci.Total Environ.* 407(2): 853–868.

ZONTA, R., L. ZAGGIA & E. ARGESE. 1994. Heavy-Metal and Grain-Size Distributions in Estuarine Shallow-Water Sediments of the Cona Marsh (Venice Lagoon, Italy). *Sci. Total Environ.* 151: 19–28.

Limnetica, 31 (2): 341-348 (2012)

Kyliniella latvica Skuja (Stylonemataceae, Stylonematophyceae), un rodófito indicador de buena calidad del agua

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Received: 29/12/11 Accepted: 2/3/12

ABSTRACT

The Rhodophyta *Kyliniella latvica* Skuja (Stylonemataceae, Stylonematophyceae), a good water quality indicator

Kyliniella latvica Skuja is a wide spread Rhodophyta scarcely reported because of its seasonality. Its presence is always linked to low-nutrient environments, and may be considered a good indicator of oligotrophy. The species has been collected in lakes and streams in America and Europe. This is the first record of the filamentous mature thallus for Spain.

Key words: Stylonematales, Rhodophyta, *Kyliniella*, seasonality, distribution, SE Spain.

RESUMEN

Kyliniella latvica *Skuja (Stylonemataceae, Stylonematophyceae), un rodófito indicador de buena calidad del agua*

Kyliniella latvica *Skuja es un rodófito de amplia distribución pero escasamente citado debido a su carácter estacional. Su presencia siempre está ligada a ambientes bajos en nutrientes, y podría considerarse un buen indicador de oligotrofía. La especie ha sido recolectada en lagos y arroyos de America y Europa. Esta es la primera vez que se cita para España de la parte madura filamentosa.*

Palabras clave: *Stylonematales, Rhodophyta,* Kyliniella*, estacionalidad, distribución, SE España.*

INTRODUCCIÓN

Las algas rojas continentales (Rhodophyta) han sido escasamente estudiadas en la Península Ibérica hasta tiempos recientes. Aparte de los trabajos de Margalef (recogidos por Álvarez-Cobelas, 1984; Ballesteros *et al*., 1985) se han publicado escasas aportaciones sobre el tema, que incluyen el estudio de áreas más o menos extensas como la cuenca del río Segura (Aboal, 1989a), o zonas del NE y SE de España (Sabater *et al*.,1989), junto con nuevas citas para la flora: *Batrachospermum boryanum* Sirodot (Prefasi & Aboal, 1994), *Batrachospermum atrum* (Hudson) Harvey (Aboal *et al*., 1995), *Hildenbrandia angolensis* Welwitsch ex West & G. S. West (Ros *et al*., 1997), *Thorea violacea* Bory de Saint-Vincent (Egidos & Aboal, 2003) o *Batrachospermum arcuatum* Kylin (Marco & Aboal, 2008).

El género *Kyliniella* Skuja es monoespecífico y pertenece al orden Stylonematales que incluye además los géneros *Stylonema* Reinsch, *Ban-*

giopsis F. Schmitz in Engler & Prantl, *Chroodactylon* Hansgirg, *Chroothece* Hansgirg in Wittrock & Nordstedt, *Purpureofilum* J. A. West, Zuccarello & J. L. Scott in J. A. West, Zuccarello, J. L. Scott, J. Pickett-Heaps & G. H. Kim, *Rhodosorus* Geitler, *Rhodospora* Geitler, y *Rufusia* D. E. Wujek & P. Timpano (Sheath & Wehr, 2003). En este orden se incluyen los rodófitos unicelulares, filamentosos o pseudofilamentosos, con varios cloroplastos, con o sin pirenoide y reproducción por división celular o monósporas (Yoon *et al*., 2006). Anteriormente el género *Kyliniella* se incluía dentro del orden Porphyriadiales junto con los géneros *Cyanidium*, *Flintiella*, *Porphyridium*, *Chroodactylon*, *Chroothece* y *Rufusia* (Sheath & Wehr, 2003), pero los análisis moleculares actuales han esclarecido la filogenia de los mayores linajes de las algas rojas continentales y modificado su clasificación.

Kyliniella se caracteriza principalmente por presentar una parte basal discoidal, de donde parten filamentos uniseriados no ramificados que pueden alcanzar varios centímetros, con células que pueden elongarse lateralmente en forma de rizoides, que contienen cloroplastos parietales acintados de color rosáceo (Bourrelly, 1970).

Ha sido citada escasamente en cursos de agua de localidades de Europa y América (Tabla 1), aunque se le atribuye una distribución cosmopolita (Bourrelly, 1970). En este trabajo se aporta una nueva cita de esta especie para la flora algal continental española.

Tabla 1. Comparación de poblaciones de *Kyliniella latvica* del río Alhárabe con la bibliografía. *Comparison of the populations of* Kyliniella latvica *in Alhárabe river with the literature.*

	Poblaciones	Ø Célula (µm)	Long. Célula (µm)	Ø Rizoide (µm)	Long Rizoide (µm)	Ø Filamento (µm)	Ambiente	Características ecológicas	Referencias
América	New Hampshire (Estados Unidos)	7.4-14.8	4.9-11.1	7.4-9.9	17.3-24.7	12.4-32.1	Arroyo	Poco común en la zona litoral de los ríos, en la región de bosque caducifolio de Norte América	Flint 1953, Vis & Sheath 1993
	Rhode Island (Estados Unidos)	8.0-11.0	5.0-9.0	7.0-10.0	18.0-25.0	24.0	Arroyo		Sheath & Burkholder 1985
	Río San Francisco, Canastra (Brasil)	—	—	—	—	—	Arroyo	Recolectada sólo en invierno en zonas con sustratos poco rocosos y con poca abundancia de especies	Necchi *et al.* 2003
Europa	Lago Usma (Letonia)	9.0-10.0	14.0-22.0	7.4-9.9	10.0-150.0	10.0-19.1	Laguna	Epífita sobre *Chara*, *Phragmites* y *Scirpus*	Skuja 1926
	Río Alhárabe, Murcia (España)	8.3-29.9	17.4-40.66	8.9-12.5	156.3-170	35.78-50.92	Arroyo	Filamentos primero fijados a las rocas en zonas de corriente y después flotan en aguas remansadas oligotróficas	Este trabajo
	Austria	—	—	—	—	—	Laguna	Aguas alcalinas	Geitler 1954, Bourrelly 1970
	Francia	—	—	—	—	—	Laguna	—	Bourrelly 1970
	Suecia	—	—	—	—	—	Laguna	—	Israelson 1938

MATERIALES Y MÉTODOS

Kyliniella latvica fue recolectada en el río Alhárabe situado en la localidad de Moratalla (NO Murcia) en las coordenadas UTM WH 9130 (Fig. 1). Este río nace a 1440 m de altura y se incorpora al río Segura 50 km más abajo. Se caracteriza por tener un curso breve, un caudal irregular, superficie de 348 875 km^2 y una pendiente media del 24 % (López-Bermúdez, 1973). Los materiales litológicos predominantes de la cuenca son calizas, dolomías y margas. La vegetación de ribera está dominada por saucedas y helófitos como *Arundo donax* L. y *Phragmites australis* (Cav.) Trin. ex Steud. En zonas de aguas remansadas o en las represas proliferan los céspedes monospecíficos de *Zannichellia palustris* L. o *Potamogeton coloratus* L. (Aboal, 1989b). El clima es mediterráneo subhúmedo con menos de 550 mm de precipitación anual, con picos en otoño y en primavera. La temperatura media anual es de 11.7 °C.

Dentro del contexto de un proyecto extensivo realizado a lo largo de un año para caracterizar los principales factores ambientales que afectan al desarrollo de las comunidades de algas en el río Alhárabe, se recolectaron muestras que se conservaron en frío hasta la llegada al laboratorio. En el campo se midieron algunas variables limnológicas (temperatura, pH, conductividad, velocidad de la corriente y profundidad). Paralelamente se tomaron muestras de agua, se filtraron con filtros de 0.45 μm de tamaño de poro y se analizó su composición química (fósforo total, ortofosfato, NO_3^-, NO_2^- y Si) con los kits de análisis de aguas Merck (Spectroquant).

En el laboratorio se realizó el estudio morfológico y morfométrico del material vegetal con un microscopio óptico dotado de contraste interdiferencial y cámara digital (OLYMPUS BX50). Parte del material se conservó en seco y se depositó en el Herbario MUB-ALGAS. El estudio morfométrico (realizado en 40 células) se basó en los siguientes parámetros: diámetro y longitud

Figura 1. Localización del río Alhárabe (Moratalla, Murcia). *Location of the Alhárabe river (Moratalla, Murcia).*

celular, diámetro y longitud del rizoide y diámetro del filamento. Además, se valoró la actividad fosfatásica microscópicamente (la producción de las enzimas fosfatasas es una estrategia eficiente para la mineralización del fósforo orgánico disponible en el medio por las algas) con BCIPT/TNBT (5-bromo-4-cloro-3-indoxil fosfato y cloruro de nitro-azul de tetrazolio) (Elwood & Whitton, 2007). Como resultado de la tinción para la actividad fosfomonoesterasa, el BCIPT/TNBT se hidrolizó y se obtuvo un precipitado azulado-purpúreo y por tanto la localización de la enzima. *Kyliniella* fue incubada en 4 ml de solución BCIPT/TNBT a temperatura ambiente (20 °C) durante 15-20 minutos antes de añadir 0.5 M NaOH y lavar con agua desionizada. Las muestras se observaron al microscopio.

RESULTADOS

Kyliniella latvica se desarrolla durante un corto periodo de tiempo a finales del invierno o inicios de la primavera. El pH del agua es básico y la conductividad moderada. La temperatura puede alcanzar valores de hasta 9.4 °C en verano, pero en invierno, aunque no llega a congelarse, puede descender hasta 4.7 °C (Aboal *et al*., 2005). El caudal es el parámetro que más oscila durante el periodo invierno-primavera. Las concentraciones de nutrientes son escasas, los silicatos y los nitratos son los que aparecen en concentraciones mayores mientras que el ortofosfato y nitritos permanecen en niveles menores (Tabla 2). La especie posee una elevada actividad fosfatasa (BCIPT/TNBT) a lo largo de todo el año que le permite convertir el fósforo orgánico en inorgánico para poder incorporarlo.

Las matitas son de un color pardoamarillento y pueden alcanzar varios centímetros de longitud. A pesar de que aparentemente suelen vivir fijadas a plantas, en el río Alhárabe son más frecuentes sobre rocas y pueden flotar libremente en su madurez y acumularse en los remansos. La parte basal, adherida al substrato, es discoidal y de ella parte un filamento no ramificado de 35.78-50.92 μm de diámetro o con ramas cortas (Tabla 1). Las células son más o menos discoidales de 8.3-29.9 μm de diámetro, 17.4-40.66 μm de altura, con varios cloroplastos acintados parietales, de color rosado. Poseen una gruesa vaina mucilaginosa en la que abundan bacterias epífitas. Es frecuente observar la formación de rizoides a partir de las células del filamento (Fig. 2). Las dimensiones del material recolectado en el río Alhárabe son más grandes que las publicadas para las muestras de los ríos americanos (Flint, 1953; Vis & Sheath, 1993; Sheath & Burkholder, 1985; Necchi *et al.*, 2003) y se asemejan a las de la localidad tipo de Letonia (Skuja, 1926).

Tabla 2. Características físico-químicas del agua del río Alhárabe durante el periodo invierno-primavera. *Physical and chemical characteristics of Alhárabe river water during the winter-spring period.*

Características físico-químicas	Media	Mínimo	Máximo
T^a (°C)	7.03	4.70	9.40
pH	8.35	8.20	8.50
Conductividad (μS/cm)	649	515	785
Caudal (L/s)	39.48	3.90	64.50
Profundidad (cm)	6.95	3.90	8.40
Radiación (PAR) (μE/m^2/s)	38.9	14.26	63.69
Alcalinidad (meq/L)	4.02	3.39	4.40
NO_3^- (mg/L)	2.85	2.85	2.86
NO_2^- (μg/L)	8.5	6.03	10.99
Si (mg/L)	2.8	2.42	3.19
Ortofosfato (μg/L)	56.13	41.03	71.23
Fósforo total (μg P/L)	73.84	55.46	92.22

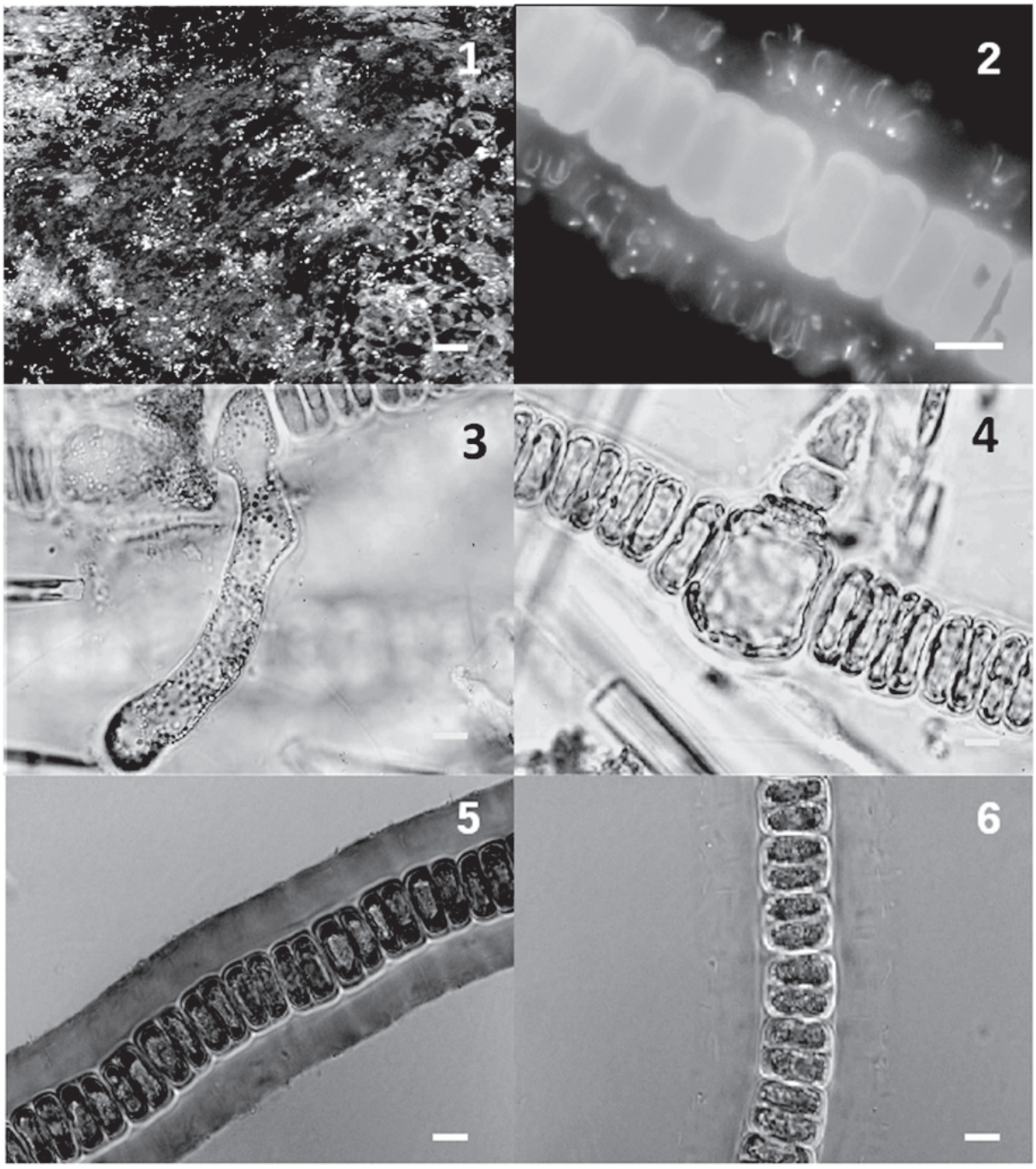

Figura 2. 1. Aspecto general de las poblaciones epilíticas de *Kyliniella latvica* en el río Alhárabe (escala 5 cm). 2. Bacterias epífitas en la vaina mucilaginosa con microscopía de fluorescencia (escala 10 μm). 3. Rizoide lateral (escala 10 μm). 4. Detalle de la formación de una pequeña rama (escala 10 μm). 5. Coloración negruzca que indica la transformación de fósforo orgánico en inorgánico por las enzimas fosfatasa alcalinas (BCIPT/TNBT) (escala 10 μm). 6. Control de la tinción BCIPT/TNBT, no se aprecia coloración (escala 10 μm). *1. General view of the epilithic populations of* Kyliniella latvica *in Alhárabe river (scale 5 cm). 2. Epiphytic bacteria in the mucilaginous sheath with fluorescence microscopy (scale 10 μm). 3. Lateral rhizoid (scale 10 μm). Small branch formation (scale 10 μm). 5. Black staining due to the transformation of organic to inorganic phosphorus by alkaline phosphatases (BCIPT/TNBT) (scale 10 μm). 6. BCIPT/TNBT staining control, no colour (scale 10 μm).*

DISCUSIÓN

Kyliniella latvica ha sido citada en cursos de agua de Rhode Island y New Hampshire en Estados Unidos (Flint, 1953; Sheath & Burkholder, 1985; Vis & Sheath, 1993), en ríos de Brasil (río San Francisco) (Necchi *et al.*, 2003), en el lago Usma de Letonia (Skuja, 1926), y en lagos de Suecia (Israelson, 1938), Austria y Francia (Geitler, 1954; Bourrelly, 1970). En España Cambra cita la presencia de los estados juveniles sobre *Cladium mariscus* L. en el lago de Basturs (Cambra, 1989; Cambra, 1991). Aunque Bourrelly (1970) le atribuye una distribución cosmopolita sería conveniente realizar un estudio de la especie en profundidad para tratar de dilucidar si se trata de una especie con gran variabilidad morfológica y ecológica o podría tratarse de varios taxones próximos. La distribución de la especie es probablemente mucho más amplia en nuestro país pero su marcada estacionalidad y su corto periodo de desarrollo probablemente dificulten su identificación.

Las especies acompañantes más frecuentes de *Kyliniella* son *Chaetophora incrassata* (Hudosn) Hazen, que tiene un desarrollo estacional, y *Rivularia biassolettiana* Meneghini ex Bornet & Flahault que puede observarse todo el año. La sencillez de su identificación y su presencia ligada a la escasez de nutrientes de las cabeceras de ríos calcáreos, parecen aconsejar incluirla en la lista de especies indicadoras de condiciones oligotróficas.

AGRADECIMIENTOS

Este trabajo ha sido financiado por la Comunidad Autónoma de Murcia (PEPLAN 2007-2011) y por la Fundación Séneca de la Región de Murcia (0572/PI/07).

REFERENCIAS

ABOAL, M. 1989a. Aportación al conocimiento de las algas epicontinentales del SE de España. II. Rodofíceas (Rhodophyceae). *Lazaroa,* 11: 115–122.

ABOAL, M. 1989b. Flora algal del río Benamor (cuenca del Segura, SE de España). *Limnetica,* 5: 1–11.

ABOAL, M., E. LÓPEZ-JIMÉNEZ & A.D. ASENCIO. 1995. *Batrachospermum atrum* (Huds.) Harv. (Batrachospermales, Rodophyceae), novedad para la flora algal epicontinental española. *Anales del Jardín Botánico de Madrid*, 53(1): 121–123.

ABOAL, M., M. A. PUIG & A. D. ASENCIO. 2005. Production of microcystins in calcareous Mediterranean streams: The Alhárabe, Segura river Basin in S.E. Spain. *Journal of Applied Phycology*, 17(3): 231–243.

ÁLVAREZ-COBELAS, M. 1984. Catálogo de las algas continentales españolas II: Craspedophyceae, Cryptophyceae, Chrysophyceae, Dinophyceae, Euglenophyceae, Haptophyceae, Phaeophyceae, Rhodophyceae, Xanthophyceae. *Acta Botanica Malacitana*, 9: 27–40.

BALLESTEROS, E., C. F. BOUDOURESQUE, M. P. BOUDOURESQUE, M. BRUGUÉS, J. CATALÁN, F. A. COMÍN, J. CAMBRA, R. M. CROS, M. COMELLES, M. DELGADO, M. HERNÁNDEZ, X. LLIMONA, J. MOLERO, M. A. RIBERA, J. ROMERO, X. TOMÁS & F. TORRELLA.1985. *Història natural dels Països Catalans: Plantes inferiors, vol. 4.* Enciclopèdia Catalana S. A. Barcelona. 558 pp.

BOURRELLY, P. 1970. *Les Algues d'eau douce. Les algues bleues et rouges. III*. Ed. Boubée. París. 512 pp.

CAMBRA, J. 1989. *Estudi sobre les algues epifitiques en sistemes lacustres.* Ph.D. Thesis. University of Barcelona. 546 pp.

CAMBRA, J. 1991. Contribució a l'estudi de les algues epifítiques dels estanys de Banyoles, Basturs i Estanya. *Orsis,* 6: 27–44.

EGIDOS, A. I. & M. ABOAL. 2003. *Thorea violacea* (Thoreaceae, Rhodophyceae) en fuentes del Marjal Pego-Oliva, Comunidad Valenciana. Nueva cita para la flora española. *Anales del Jardín Botánico de. Madrid*, 60: 27–32.

ELWOOD, N. & B. WHITTON. 2007. Importance of organic phosphate hydrolyzed in stalks of the lotic diatom *Didymosphenia gemianta* and the possible impact of atmospheric and climatic changes. *Hydrobiologia,* 592: 121–133.

FLINT, L.H. 1953. *Kyliniella* in America. *Phytomorphology,* 3: 76–80.

GEITLER, L. 1954. Die Süsswasserbangiaceae *Kyliniella latvica* und ihr obligater bakterieller Bewohner. *Österreichisches Botanisches Zeitschrift.,* 101: 304–314.

ISRAELSON, G. 1938. *Kyliniella latvica*, in Schweden gefunden nebst neuen Fundorten für ein paar im Süsswasser auftrettende Bangioideen. *Svensk Botanisk Tidskrift,* 5: 20–23.

LÓPEZ BERMÚDEZ, F. J. 1973. *La vega alta del Segura. Clima, hidrología y geomorfología*. Publicaciones del Dpto. De Geografía. Univ. Murcia. 288 pp.

MARCO, S. & M. ABOAL. 2008. *Batrachospermum arcuatum* (Batrachospermaceae, Floridophyceae) en el Parque Natural del Marjal de Pego-Oliva. Nueva cita para la flora algal de las aguas continentales españolas. *ALGAS. Boletín de la Sociedad Española de Ficología,* 39: 35–37.

NECCHI-JÜNIOR, O., L. H. Z. BRANCO & C. C. Z. BRANCO. 2003. Ecological distribution of stream macroalgal communities from a drainage basin in the serra da Canastra Nacional Park, Minas Gerais, Southeastern Brazil. *Brazilian. Journal of Biology*, 63(4): 635–646.

PREFASI, M. & M. ABOAL. 1994. Estudio del Género *Batrachospermum* Roth: *B. boryanum* Sirod. y *B. moniliforme* Roth en la provincia de Castellón, España. *Acta Botanica Malacitana,* 19: 45–50.

ROS, M. D., E. LÓPEZ-JIMÉNEZ & M. ABOAL. 1997. Primera cita de *Hildenbrandia angolensis* Welwitsch ex W. West & G.S. West (Hildenbrandiales, Rhodophyceae), para la flora algal epicontinental española. *Anales del Jardín Botánico de Madrid*, 55(2): 458–460.

SABATER, S., M. ABOAL & J. CAMBRA. 1989. Nuevas observaciones de rodofíceas en aguas epicontinentales del NE y SE de España. *Limnetica,* 5: 93–100.

SHEATH, R. G. & J. M. BURKHOLDER. 1985. Characteristics of softwater streams in Rhode Island. II. Composition and seasonal dynamics of macroalgal communities. *Hydrobiologia,* 128: 109–118.

SHEATH, R. G. & J. D. WEHR. 2003. *Freshwater Algae of North America: Ecology and Classification*. Academic Press. San Diego. CA. 918 pp.

SKUJA, V. H. 1926. Eine neue Süsswasserbangiacee *Kyliniella latvica* n.g., n. sp. *Acta Horti Botanici Universitatis Latviensis*, 1: 1–5.

VIS, M. L. & R. G. SHEATH. 1993. Distribution and systematics of *Chroodactylon* and *Kyliniella* (Porphyridiales, Rhodophyta) from North American streams. *Japanese Journal of Phycology,* 41: 237–241.

YOON, H. S., K. M. MÜLLER, R. G. SHEATH, F. D. OTT & D. BHATTACHARYA. 2006. Defining the major lineages of red algae (Rhodophyta). *Journal of Phycology,* 42: 482–492.

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- Relación de autores con indicación del autor responsable a efectos de la correspondencia. Se deberá indicar expresamente la dirección e-mail de dicho autor.
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La segunda página incluirá el Resumen en castellano, palabras clave, el *Abstract* en inglés y *keywords*. Tanto el Resumen como el *Abstract* no deberán sobrepasar las 400 palabras y deberán incluir el título del trabajo en el idioma correspondiente.

Las siguientes páginas se ordenarán en apartados que se estructurarán al estilo científico. Los apartados y párrafos del texto comenzarán sin sangrado. Se acentuarán las mayúsculas en todos los casos.

Los apartados se escribirán sin numerar y se escalarán según el siguiente formato:

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Apartado secundario.- **Minúsculas y en negrita.**

Apartado terciario.- *Itálica*.

Apartado de cuarto nivel.- Letra normal subrayada.

Siguientes niveles.- numéricos (1), (1.1), (1.1.1), etc.

Las Tablas constituyen una de las partes más costosas en tiempo y presupuesto por lo que se ruega se preparen procurando ocupar el mínimo espacio posible. Las tablas pueden tener la anchura de una columna (8 cm) o dos columnas (16 cm) y su longitud no puede exceder de 25 cm. Se incluirán al final del manuscrito y tendrán numeración arábiga. En el texto siempre se citarán de forma completa (p.e. Según se puede ver en la Tabla 6... o, Los datos (Tabla 6) indican que..., etc.) y nunca en forma abreviada –Tab. 6 o tab. 6. Las leyendas de las tablas se presentarán en castellano e inglés y se incluirán en el mismo apartado que el texto de las figuras. No deberán usarse líneas verticales y los encabezamientos de las columnas deberán ser breves. Se prestará particular atención en no publicar tablas que dupliquen información que ya está en forma de figuras.

Las figuras tendrán numeración arábiga con el texto explicativo en el pie. El texto incluirá la versión en castellano y en inglés. Las figuras pueden ir a tres tipos de caja de texto: 8, 12.5 y 16 cm. Los autores procurarán que los originales tengan el tamaño de letra y el grosor de línea necesario para que al reducirse puedan ser interpretables y legibles. No se aceptarán figuras que no cumplan este requisito.

Los pies de figura, junto con los encabezamientos de las tablas, estarán en una página aparte situada inmediatamente después de la bibliografía y antes de las tablas y figuras.

Las citas de las figuras en el texto se harán de forma completa y en minúscula cuando se inserte dentro del texto de un párrafo (p.e. En la figura 1 se indica la situación de los puntos de muestreo). Por el contrario, se citará de forma abreviada y en mayúscula cuando esté entre paréntesis y no relacionada directamente con el texto del párrafo [p.e. Las muestras se han recogido en cinco estaciones distribuidas a lo largo del río (Fig. 1) y con una periodicidad mensual].

Las unidades se expresarán preferiblemente en el Sistema Internacional (SI) con los símbolos en forma abreviada cuando vayan precedidos de una expresión numérica. Cuando se exprese un valor como combinación de dos unidades éstas se indicarán con el signo aritmético correspondiente p.e. m/s, mol/m^3, pero para más de dos unidades se usarán exponentes, p.e. $mgC\ m^{-2}\ h^{-1}\ \mu mol\ m^{-2}\ s^{-1}$.

Las cantidades con decimales se expresarán con un punto (4.36), los miles con cuatro números, sin ninguna separación o símbolo (4392) y para valores iguales o superiores a las decenas de mil se intercalarán blancos separando los miles (13 723 o 132 437). Siempre que sea posible se indicarán los números con notación exponencial decimal con el mínimo posible de decimales ($13.7 \cdot 10^3$, $13.2 \cdot 10^4$).

La BIBLIOGRAFÍA se ordenará al final del texto, alfabéticamente y cronológicamente para cada autor, según las pautas siguientes:

- Revistas:

RUEDA, F. J., E. MORENO-OSTOS & J. ARMENGOL. 2006. The residence time of river water in reservoirs. *Ecological Modelling*, 191: 260-275.

IBISATE, A., A. OLLERO & J. DÍEZ. 2011. Influence of catchment processes on fluvial morphology and river habitats. *Limnetica*, 30 (2): 169-182.

Titles of journals should not be abbreviated.

- Libro:

KALFF, J. 2002. *Limnology*. Prentice Hall. NJ. USA.

- Capítulo de libro:

SEAR, D. A. 2010. Integrating science and practice fro the suitable management of in-channel salmonid habitat. In: *Salmonid Fisheries: Freshwater habitat management*. P.S. Kemp (ed.): 81-119. Wiley-Blackwell, Chichester. UK.

CASTRO, M., J. MARTÍN-VIDE & S. ALONSO. 2005. El clima de España: pasado, presente y escenarios de clima para el siglo XXI. In: *Evaluación preliminar de los impactos en España por efecto del Cambio Climático*. J. M. Moreno Rodríguez (ed.): 113-146. Ministerio de Medio Ambiente, Madrid, Spain.

- Congresos:

GEORGE, D. G. 2006. Using airborne remote sensing to study the mixing characteristics of lakes and reservoirs. Proceedings of the 10th European Workshop on Physical Processes in Natural Waters. June 26-28, 2006. Granada, Spain: 2001-207.

- Informes:

DOLZ, J. & E. VELASCO. 1990. *Análisis cualitativo de la hidrología superficial de las cuencas vertientes a la marisma del Parque Nacional de Doñana* (Informe Técnico). Universidad Politécnica de Cataluña. Barcelona, Spain.

- Tesis y Maestrías:

MORENO-OSTOS, E. 2004. *Spatial dynamics of phytoplankton in El Gergal reservoir (Seville, Spain)*. Ph.D. Thesis. University of Granada, Spain.

THOMPSON, K. L. 2000. *Winter mixing dynamics and deep mixing in Lake Tahoe*. Master's Thesis, University of California, Davis.

En el manuscrito se listarán únicamente los trabajos citados en el texto; en éste, las referencias se harán en minúsculas (Kalff, 2002; Dolz & Velasco, 1991; Rueda *et al*., 2006). En ningún caso se aceptarán como referencias trabajos no publicados (p.e. en preparación) o aún no aceptados (p.e. enviado). Sí se podrán incluir citas de trabajos aceptados para su publicación (en prensa). Se recuerda la conveniencia de reducir al máximo las referencias bibliográficas de difícil consulta como informes, resúmenes a congresos, etc.

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Scope

Limnetica publishes original research papers on ecology of continental waters. Its scope includes ecology of rivers, lakes, reservoirs, lagoons and wetlands, biogeochemistry, paleolimnology, development of new methods, taxonomy, biogeography, and all aspects of theoretical and applied continental aquatic ecology, like management and conservation, impact assessment, ecotoxicology and pollution. *Limnetica* will accept for publication scientific papers presenting advances in knowledge or technological development, as well as papers derived from new practical approaches on the topics covered by the journal.

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Manuscript will be typed at double space on A-4 sheets. Papers can be written in Spanish or English, and must not exceed 6000 words of text nor 25 printed pages (figures and tables included). Exceptionally, and after consulting the Editor, long lists, annexes and additional information can be published in the web site of the journal. Papers that do not follow the present instructions will be rejected.

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The first page must include:

- Title in upper case.
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The second page will include Abstract and key words, both in English and Spanish. Abstracts must start with the title and not exceed 400 words.

Following pages must be structured in sections following the scientific style. Section headings and text will have no left indent.

Sections and subsections will not be numbered, and must adjust to the following format:

Main section. Bold, upper case (**INTRODUCTION**).

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Lower-level sections. They will go numbered (1), (1.1), (1.1.1), etc.

Tables are one of the most costly parts, both in terms of time and money; therefore, they must be drawn as compact as possible. Tables can be 1-column (8 cm) or 2-column (16 cm) wide, and their length cannot exceed 25 cm. They will be included at the end of the manuscript and numbered in Arabic numbers. In the text they will be written in complete form (e.g., as can be seen in Table 6. . . , or Data (Table 6) show that. . .), never in abbreviated form (neither Tab. 6 nor tab. 6). Table captions will be written in both English and Spanish, and will be included in the text in the same section than Figure legends. No vertical lines can be drawn in tables, and column headings must be short. No table will be published that shows information presented in figures.

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Figures can fit three box-sizes: 8 cm, 12.5 cm, or 16 cm. Authors must make sure that font size and line thickness can be easily read after reduction, otherwise figures will be rejected.

Figure legends and table captions will go in a page after Literature Cited and before Tables and Figures.

Figure calls must be made in complete, lower case form when in the text (e.g., Location of sampling sites is shown in figure 1), in abbreviated, upper case when going in a parenthesis and not directly related to the text [e.g., Samples were taken monthly at five sites along the river (Fig. 1)].

Units must be expressed preferably following the International System (I.S.), with abbreviated symbols when preceded by numeric expressions. Values combining two units must be expressed with the corresponding arithmetic sign, like m/s, mol/m^3, ind/l, but when there are more than two units exponentials must be used, like in mgC m^{-2} h^{-1}, µmol m^{-2} s^{-1}.

Decimal numbers will be expressed with a dot (4.36), thousands with 4 digits, with no blank space or symbols (4392), and figures over ten thousand will have blank space markings (13 723 or 132 437). Whenever possible the scientific notation will be used, with the smallest possible number of decimals ($13.7 \cdot 10^3$, $13.2 \cdot 10^4$).

BIBLIOGRAPHY should be listed at the end of the paper in alphabetical order and chronologically for each author, in the following standard form:

- Journals:

RUEDA, F. J., E. MORENO-OSTOS & J. ARMENGOL. 2006. The residence time of river water in reservoirs. *Ecological Modelling*, 191: 260-275.

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- Books:

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CASTRO, M., J. MARTÍN-VIDE & S. ALONSO. 2005. El clima de España: pasado, presente y escenarios de clima para el siglo XXI. In: *Evaluación preliminar de los impactos en España por efecto del Cambio Climático.* J. M. Moreno Rodríguez (ed.): 113-146. Ministerio de Medio Ambiente, Madrid, Spain.

- Conferences:

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- PhD and Master Dissertations:

MORENO-OSTOS, E. 2004. *Spatial dynamics of phytoplankton in El Gergal reservoir (Seville, Spain).* Ph.D. Thesis. University of Granada, Spain.

The Bibliography will only contain papers cited in the text, where they must go in lower case (Margalef, 1975; Wetzel & Likens, 1991; Riera *et al*., 1992). Unpublished papers should not be included among the references. References to materials hard to get (reports, conference abstracts, etc.) must be limited to the minimum possible.