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Brief history of research on high mountain lakes in Sierra Nevada, Spain

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ABSTRACT

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In this article, we provide a concise overview of the history of limnological research in the Sierra Nevada lakes over the past fifty years. Particular emphasis is placed on the early stages of this research, including key events and circumstances that shaped its development and influenced its later evolution. The main lines of research carried out during the different stages we have distinguished are shown, highlighting the most relevant findings from each. In a sense, our article can be considered as an introduction to several contributions in this volume, which together present a comprehensive picture of the current state of the limnological studies in lakes of Sierra Nevada.

KEY WORDS: high mountain lakes, Sierra Nevada, Spain, brief limnological history

RESUMEN

Una breve historia sobre la investigación en lagos de alta montaña de Sierra Nevada, España

En este artículo presentamos brevemente la historia de la investigación sobre los lagos de Sierra Nevada durante los últimos cincuenta años, prestando especial atención a las primeras etapas e incluyendo información sobre algunos de los eventos y circunstancias que marcaron tales etapas y contribuyeron a explicar la evolución posterior de la investigación desarrollada. Mostramos las principales líneas de investigación llevadas a cabo a lo largo del tiempo, destacando los resultados más relevantes obtenidos en cada uno de los periodos que hemos considerado. En cierto modo nuestro artículo puede considerarse como la introducción a otros artículos, incluidos en este volumen, que ofrecen una visión general del estado actual de los estudios limnológicos realizados en lagos de Sierra Nevada.

PALABRAS CLAVE: *lagos de alta montaña, Sierra Nevada, España, breve historia limnológica.*

INTRODUCTION

At the time of writing this article, 50 years have passed since Rosa Martínez Silvestre published the seminal paper "*First report on the limnology of the alpine lake La Caldera, in the Penibetic Mountains (Sierra Nevada, Granada, Spain)*" in the Proceedings of the 19th Congress of the International Society of Limnology (Martínez-Silvestre, 1975). This work is regarded as the first to provide limnological data for a lake in the southernmost high mountain lake district in Europe. To commemorate this anniversary, this volume contains several articles that provide an overview of the current state of limnological research carried out in the Sierra Nevada, as well as the main scientific achievements reached to date.

In this introductory article, we briefly review the (short) history of limnological research in the lakes of Sierra Nevada, paying special attention to the early times. We deliberately include some of the events and circumstances that marked those early stages, which, although not strictly scientific, illustrate the working conditions and help to explain, at least partially, the subsequent evolution of the research.

In a retrospective view, without attempting an exhaustive analysis, we were able to identify several stages in this process:

THE SEVENTIES. FIRST STEPS

The beginnings of research on high mountain lakes in Sierra Nevada were largely linked to the University of Granada and Rosa María Martínez Silvestre, a young PhD in Chemistry from the University of Valencia, who joined the Department of Zoology at the University of Granada as an assistant professor during the 1971/72 academic year. At this university, and for a decade, she lectured on practical and theoretical ecology, promoted the creation of a Research Unit -the Laboratory of Ecology–seed of the later Department of Ecology. Very soon upon arrival, and, together with two biologists, Juan Carlos Canteras Jordana and Luis Cruz Pizarro, launched a line of research in freshwater ecology, which mainly focused on high mountain lakes.

Several interrelated reasons may largely explain our early interest in alpine lakes during those years. On one hand, high mountain lakes provided a valuable opportunity to start research on basic ecological questions. At this point, it is worth noting that, among lentic ecosystems, alpine lakes have traditionally attracted scientific attention due to their unique characteristics: they are typically isolated and remote environments, very often spatially related to glacial or periglacial landscapes, with little land cover, thin soil, and bedrock with low weathering rates. These features make them ideal natural laboratories for studying phenomena such as life under extreme conditions and the interactions between lakes and their surrounding watersheds (and airsheds). Moreover, the scarcity of natural lakes in Spain confers an additional value to high mountain lakes as they represent some of the few environments in which to explore these foundational ecological issues.

All the benefits previously outlined, combined with an exceptional geographical location, astride different biogeographical regions, are found in about thirty permanent lakes and several shallow ponds and pools that frequently dry up during summer at altitudes above 2500 meters, which largely explains their limnological importance.

It is worth mentioning that, at the beginning of the 1970s, knowledge of lakes and ponds of Sierra Nevada was practically non-existent, even though since the mid-18th century scientists: Antonio Ponz, Simón de Rojas Clemente, Charles Edmond Boissier, Moritz Willkomm, Johan Lange, Frank Pfendler D´Ottensheim, Otto Quelle, Hugo Obermaier, Juan Carandell or Fidel Fernández, among others, had visited the Sierra and published monographs that included aspects related to its biophysical environment, particularly botanical and geological but also anthropological and social topics (for details see, for instance, Titos Martínez, 1991a,b, Gómez Ortiz, 2006, Castillo, 2009). Most of them refer to the water bodies they visit as "…*the Sierra's most interesting curiosity... true alpine ponds suspended in the mountains at heights unlike any other in Europe*..." in Pfendler´s words (Pfendler d´Ottensheim, 1848) although in most cases their descriptions do not go beyond highlighting their aesthetic and landscape value.

Only the studies by González Guerrero (1975, 1976), focusing on the "phycotopes" of Siete Lagunas Valley, and the unpublished manuscript by Francisca Caballero López (1945), very recently edited by Miguel Álvarez Cobelas (2021), which gathers algological results from samples taken by the end of September 1945 in Las Yeguas Lake, can in some way be considered as the protohistory of the limnological knowledge of lakes and ponds in Sierra Nevada.

Such a situation explains why, for example, Margalef and colleagues at the University of Barcelona, who in the mid-70s had just begun an ambitious project funded by the Spanish National Institute for Nature Conservancy whose main objectives were: "*...without neglecting the possibilities of obtaining varied information on the largest possible number of [Pyrenean] lakes, the research will be based on repeated visits to a small number of lakes, on the quantification of the observations and on their interpretation within a coherent ecosystem model that embodies the main characteristics of mountain lakes*", demanded the convenience of starting a program of research "*on the lake systems of other Spanish mountain ranges (Picos de Europa, Gredos, Montes de León, Sierra Nevada), as the basis for a comparative study*" (Margalef et al., 1975).

Martínez-Silvestre's 1975 study on Lake La Caldera provided information on the chemistry of the water and on the phytoplankton specific composition during the ice-free period of 1973. It also presented preliminary results on chlorophyll-*a* and primary production carried out in the summer of 1974. Her subsequent papers completed such an information as quantified the structure of its "stable" phytoplankton community (Martínez, 1977) and provided data on the vertical distribution and temporal variation of both phytoplankton biomass and primary production, including some measurements taken during the ice-covered period (Martínez, 1980a). Additionally, she published a note on the daily vertical migration of *Rhodomonas minuta* (Martínez, 1980b). In the late 1970s, Cruz-Pizarro (1978) published a paper showing comparative results on the diurnal vertical migration behavior of crustacean and rotifer species in this lake, marking the first published research on zooplankton ecology in lakes of Sierra Nevada. It is fair to add that such research lines could only be tackled thanks to the invaluable guidance and support of Margalef and his colleagues. Since 1973, when R. Martínez attended a course on "*Advanced Ecology for Postgraduates*" at the University of Barcelona (UB), a sustained collaboration was established, with PhD students from the University of Granada visiting and conducting research stays at the Department of Ecology in Barcelona, for many years thereafter.

The article by Martínez-Silvestre (1975) was not, however, the first work published on lakes of Sierra Nevada. Heinz Löffler, an outstanding specialist in the taxonomy of both planktonic and benthic limnetic entomostracean with significant contributions in the systematics, biogeography and paleoecology of *Copepoda*, *Branchiopoda* and *Ostracoda*, published a paper on Harpacticoids of Andalusian high mountain lakes [*Harpacticiden (Crustacea, Copepoda) der Hochgebirgsgewässer Andalusiens (Sierra Nevada, Spanien)*]. This work was published in a journal of very limited diffusion and difficult to access during those days: *Sitzungsberichte der Akademie der Wissenschasften Mathematisch-naturwissenschaftliche klasse (Meeting reports of the Austrian Academy of Sciences)* (Löffler, 1974).

It was not until 1977 that we heard about the existence of this article when one of us (L. C-P), during the 20th SIL Congress in Copenhagen, met Heinz Löffler and, talking about our work in Sierra Nevada, he mentioned his paper on the littoral crustacean fauna in La Caldera, Río Seco and Las Yeguas lakes from samples collected in August 1972.

Because of its exceptional geographical location, as one of the most interesting areas at the crossroads of distinct biogeographic regions, Löffler granted a key value to the results from Sierra Nevada as came to reinforce his hypothesis that the crustacean fauna of high mountain lakes in Central and South America, as well as in Africa, was often represented by psychrophilic species that spread from the north during the Quaternary. Also, based on comparative studies of the species distribution in mountain lakes of Central America and Central and Southern Europe (Sierra Nevada), he proposed a broader explanation for the general biogeographic distribution of Harpacticoids.

Let´s take a quick look at the "*state of the art*" in limnological knowledge across other lake districts during the 1970s:

A concise review on the status of high mountain lakes research in the 1970s.

High mountain lakes, mainly because of their unique characteristics, have attracted interest from scientists for a long time. Limnological studies of alpine and subalpine lakes, especially from Central Europe and the Pyrenees, can be traced back to the beginning of last century and even earlier, before limnology was formally established as a scientific discipline. Much of this pioneering work mainly addressed descriptive aspects related to the physiographic characteristics of lake catchments, the physical and chemical conditions and resources of the water, and the structure of littoral/planktonic biocenosis (Delebecque & Rittero, 1898, Huber-Pestalozzi, 1926, Monard, 1928, Pelosse, 1927, Pesta, 1929, ...).

Scientific expeditions, especially those carried out during the interwar years, greatly contributed to complete the scarce knowledge at that time available on alpine lakes from other mountain regions throughout the world. These efforts helped to reveal their unique features and singularities and to enable comparisons between different lake systems. Notable examples include the Yale North India Expedition to the Himalayan Mountains (de Terra, 1933, Hutchinson, 1933, 1934, 1937, Löffler, 1969), the Cambridge Expedition to East African Lakes (Worthington, 1931), the German-Austrian Limnological Sunda (Indonesia) Expedition (Brehm, 1933, Ruttner, 1931), and the Percy Sladen Trust Expedition to the Lake Titicaca (Rich, 1934, Gilson, 1938).

During the 1960s and 1970s research on high-mountain lakes shifted from being largely descriptive to being more systemic and aimed at understanding the ecological structure and functioning of those systems. The UNESCO International Biological Program (IBP, 1964-74), the most thriving scientific program of its kind at that time, largely contributed to this change. Within the IBP, research teams investigated lake productivity in a series of lakes across Europe and North America, gaining valuable insight into links among functional components of aquatic ecosystems in alpine and arctic lakes (e.g. Capblancq & Laville, 1972, Ferrari, 1976, Findenegg, 1964, Lair, 1975, Larson, 1973, Löffler, 1972, Nauwerk, 1968, Pechlaner, 1971, Pechlaner et al., 1972, Rey & Capblancq, 1975, Rhode et al., 1966, Rigler, 1972, Tilzer, 1972, Vollenweider, 1969, and *references cited therein*).

In the case of Spain, research on high-mountain lakes during the 1970s remained very limited. Until the 1930s, it was almost limited to pioneering work stemming from a couple of scientific expeditions to Lake San Martín de Castañeda (Lago de Sanabria), the largest lake of glacial origin in Spain. The first expedition was led by the geographer Wilhelm Halbfass during August and September of 1912, followed several weeks later by a second expedition led by José Taboada Tundidor, a High School Natural History teacher and Assistant Professor (Catedrático Auxiliar Numerario) at the Faculty of Sciences of the University of Granada. Halbfass (1913), Bachmann (1913), and Burckhardt (1920) published most of the results obtained from the first expedition, while those from the second expedition were published by Taboada Tundidor (1913), considered as the first truly limnological papers published in Spain. The paper by González Guerrero (1927) stands as an early example of the relatively few specific works on botany carried out in wetlands and lakes of the Pyrenees. During the 1940s and 1950s, alpine limnology in Spain was mainly linked to the early work of Margalef in the Pyrenees (Margalef, 1948, 1949a, 1953), Picos de Europa (Margalef, 1950) and Sierra de Guadarrama (Margalef, 1949b), and that of Caballero (1944) in Sierra de Gredos. Later significant contributions include González Guerrero (1965) in Sierra de Guadarrama and Margalef et al. (1975), Miracle (1978a, 1978b) or Campas & Vilaseca (1979) in the Pyrenees.

FIRST EXTENSIVE SURVEYS. FIRST DOCTORAL THESES.

In the 1980s, two projects were funded by the Spanish Ministry of Education and Science (MEC) to study lakes in Sierra Nevada: "*Estudio limnológico de las lagunas de alta montaña de*

Sierra Nevada, Granada" (1981-1983), granted to R. Martínez and "*Ecología del zooplancton en lagos de alta montaña*" (1984-1986), led by L. Cruz-Pizarro. Extensive surveys were conducted over numerous lakes in those projects which provided data on the taxonomic composition and structure of the littoral and planktonic communities, and the factors controlling species distribution and community assemblages. This research enabled faunal and floristic comparisons between lakes in Sierra Nevada and those from other geographical areas. The data collected formed the basis for the PhD Thesis of Morales-Baquero (1985) "*Estudio de las comunidades de Rotíferos Monogonontes de lagos de alta montaña de Sierra Nevada*", that of Sánchez-Castillo (1986) "*Estudio de las comunidades fitoplanctónicas de las lagunas de alta montaña de Sierra Nevada*", and the BSc Memory of Hernández-Marquez (1986) "*Crustáceos planctónicos y béntico-litorales de las lagunas de Sierra Nevada: Taxonomía, Distribución y Ecología*". The findings of these PhD theses were later published in a series of papers (Morales-Baquero, 1987, 1988, Morales-Baquero et al.,1989, Sánchez-Castillo, 1987a, 1987b, 1988, Sánchez-Castillo et al., 1989, Cruz-Pizarro & Morales-Baquero, 1987).

Cruz-Pizarro (1981a, 1981b) and Morales-Baquero et al. (1988) published the first data on biomass and production of *Mixodiaptomus laciniatus* and of *Euchlanis dilatata*, the most abundant copepod and rotifer species in the plankton of Sierra Nevada lakes. Similarly, Canteras & Pérez (1987) were also the first to publish results on the biomass and production of the heterotrophic bacterial communities in eleven of these lakes.

Towards the end of this period, Carrillo (1989), in her PhD Thesis "*Análisis de las interacciones tróficas en el plancton de un sistema oligotrófico*", started a novel research line. Through *in situ* experiments, she sought to understand the fate of energy in food webs and to evaluate the interactions that shape the structure of plankton communities in high-mountain lakes.

After the doctoral theses of Sánchez-Castillo (1986) and Carrillo (1989), studies of the diversity and taxonomy of microalgae regained interest, focusing on benthic and epizoic species (Sánchez-Castillo & De la Rosa-Álamos, 1993, Pérez-Martínez et al., 2001). Special mention should be made on the extensive studies of diatoms carried out in most Sierra Nevada lakes and ponds (Linares-Cuesta, 2003, Sánchez-Castillo et al., 2008) that sought an integrative approach to the analysis of algal communities that would improve understanding of how freshwater algae respond to environmental variables, as previously suggested by Tolotti (2001).

In recent years, progress has been made in understanding the phycological components of high-altitude lake and stream meadows, locally referred as to *borreguiles* (González Díaz, 2011). These are suitable habitats for the development of unicellular and filamentous microalgae, which are thought to be early indicators of mild eutrophication, an aspect that has not been adequately studied in these systems.

PROCESSES-ORIENTED APPROACHES. LARGE INTERNATIONAL PROJECTS.

At the turn-of-the- twenty-first-century, research on Sierra Nevada lakes is aimed at studying processes and theoretical questions, including (1) the search and quantification of mechanisms that generate plankton community structure, (2) the analysis of food web complex interactions from an energetic perspective, and (3) the exploration of the connections between energy flow and nutrient recycling (e.g. Reche, 1995, Reche et al., 1993, 1994, 1996, 1997, 1998, 2005, Villar-Argaiz, 1999, Medina-Sánchez et al., 1999, Pérez-Martínez & Barea-Arco, 2000, Barea-Arco et al., 2001). In all these studies, *in situ* experimental approaches and high frequency sampling were used. The lakes were treated as true natural laboratories, where biotic interactions (direct and indirect) could be studied by tracking signals generated by changes (disturbances) in some of the components of the system that can be easily distinguished from background noise (Neill, 1988). For example, studies by Carrillo et al. (1990 a, 1995, 1996 a, 1996 b), Cruz-Pizarro & Carrillo (1991), Villar-Argaiz et al. (2000), among others, are based on experimental manipulations in mesocosms to monitor both individual species and whole-assemblage responses of phytoplankton to

varying grazing pressure and to quantify the specific release rates of ammonium and phosphorus by zooplankton.

Carrillo et al. (1990 b) were the first to describe and quantify the effects of an unpredictable atmospheric allochthonous input (Saharan dust) on the vertical light climate of Lake La Caldera, giving rise to a new and still-ongoing research line. Morales-Baquero et al. (1992) provided a regional limnology overview of the singular characteristics of Sierra Nevada lakes, based on the studies carried out by the limnology group of the University of Granada during the 70s and 80s, and pointed out the significance of these systems for climate change monitoring.

During this period, new researchers joined the research team, and the rate of production of publications exhibited a significant increase. This allowed for the development of new and more ambitious projects and above all, for the participation of the University of Granada, as contractor, in several international initiatives funded by foreign Institutions (e. g. The Open Society Foundation of the Central European University; The Hungarian Scientific Research Found…). Notably, the University of Granada participated in two major European co-operative projects: the AL:PE 2 project, the first comprehensive study of remote mountain lakes at a European level, and the MOLAR project, built upon AL:PE 2 success.

The AL:PE 2 project "*Acidification of mountain Lakes: Palaeolimnology and Ecology. Remote Mountain Lakes as Indicators of Air Pollution and Climate Change*" involved 17 Institutions. Its goals were to (1) evaluate the response of remote mountain lakes to varying levels of long range transported air pollution components (including acid deposition, total phosphorus, persistent organics and trace metals), and (2) identify unpolluted remote lakes within Europe that could be used as reference sites for climate change research. A range of remote lakes in different European countries, from the Svalbard Island to Sierra Nevada in Spain, were sampled and studied in the project.

The MOLAR project "*Measuring and modelling the response of remote mountain lakes ecosystems to environmental changes: a programme of Mountain Lake Research*" (1996-99) involved 24 Institutions and focused on 23 remote lakes (for details, see Patrick et al., 1998, Straskrabová et al., 1999a, 1999b, The MOLAR Water Chemistry Group, 1999, Battarbee et al., 2001). The project's goal was to quantify and model atmospherically transported pollutant fluxes and pathways to the lakes, and their temporal responses to climate variability at seasonal, inter-annual and decadal time scales.

The achievement of these objectives represents a large part of the scientific effort carried out in the study of high mountain limnology in the Sierra Nevada during the second half of the 1990s. A deeper understanding of these goals constitutes the base of much of the research developed throughout the present century.

The results of the AL:PE and MOLAR projects were published in Camarero et al. (1995), Cruz-Pizarro & Carrillo (1996), Carrillo et al. (1995, 1996 a), Reche et al. (1998), Morales-Baquero & Conde-Porcuna (2000) or Villar-Argaiz et al. (2000), among many other articles.

SIERRA NEVADA LAKES AND GLOBAL CHANGE

Mountain lakes, mainly due to their extreme climatic conditions and low buffering capacity, are widely recognized as the finest sensors available for the detection of past and present global changes. They effectively reflect alterations in their surrounding watersheds and airsheds, earning them the designation "*eyes on global environmental change*" by many researchers (Adrian et al., 2009, Moser et al., 2019). Because of that, high mountain lakes (1) offer ideal conditions for the study of climate change; (2) can enhance our understanding of global climate effects, and (3) serve as valuable models for predicting future changes (Sommaruga-Wögrath et al., 1997).

Throughout the present century, research on high mountain lakes in the Sierra Nevada has deepened in the knowledge of their internal dynamics (especially physical) and the role of their sediments in the biogeochemistry of the systems (e.g. Rodríguez-Rodríguez et al., 2004, Rueda et al., 2007, de Vicente et al., 2010a, 2010b, García-Jurado et al., 2011, 2012). In addition, research has been aimed at detecting and monitor-

ing the effects of global warming at the ecosystem scale in an area highly influenced by other local and regional climate-driven changes, such as the atmospheric deposition of aerosols (particles and organisms) transported by Saharan dust storms (Morales-Baquero et al., 2006).

The main research lines developed during this stage focus on:

Climate reconstruction, Palaeolimnology, Trophic web processes, The impact of multiple stressors, and the Biogeochemical consequences of Saharan dust.

A comprehensive review and update of the key findings in these areas is presented in several articles included in this volume.

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AUTHOR CONTRIBUTIONS

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