Lakes & Reservoirs: Research and Management 1999 **4**: 15–22

Limnological comparison of a new reservoir with one almost 40 years old which had been totally emptied and refilled

A. M. Geraldes and M. J. Boavida*

Departamento de Zoologia e Antropologia, Faculdade de Ciências da Universidade de Lisboa, Campo Grande C2 1749–016
Lisboa, Portugal

Abstract

In the present study, several limnological characteristics of a reservoir filled for the first time are compared with those of another reservoir totally emptied after being full for almost 40 years and then refilled. Three phases were considered during the study, determined by the filling and emptying in the oldest reservoir: (i) filling phase, from August to October 1994; (ii) regular water-level phase, from December 1994 to April 1995; and (iii) emptying phase, from May to July 1995. Several forms of phosphorus, phosphatase, chlorophyll *a*, and phytoplankton and zooplankton composition were determined. Trophic states of the two reservoirs were compared. Major limnological differences were not found between these two artificial lakes. In fact, physical factors such as temperature, chemical parameters such as the several forms of phosphorus measured, and biologically derived variables such as chlorophyll *a* and phosphatase activity exhibited similar patterns and values in both reservoirs, as well as practically the same relationships among those.

Key words

emptying reservoir, new reservoir, old reservoir, phosphatase, phosphorus, reservoir (re)filling.

INTRODUCTION

Reservoirs are special lacustrine environments in which physical, chemical and biological features are strongly conditioned by surface-level fluctuations caused by periodic, usually seasonal, natural filling, and from almost perennial, anthropogenic dewatering. These water movements are often dynamic, and therefore reservoirs are considered never to be in steady state (Wetzel 1990). Although reservoir management measures are needed to minimize the effects of water-level fluctuations, remarkably few studies have been undertaken to understand the mechanisms by which these singular hydrological patterns may influence reservoir dynamics. The literature mainly discusses the effects of hydrology on plankton communities (Rey 1984, 1988; Schmid-Araya & Zuñiga 1992; Barone & Flores 1994; Flores & Barone 1994) and on nutrient concentrations (Fabre 1988; Barone & Flores 1994). There are a few studies on filling processes in new reservoirs, focussing on zooplankton structure (Pinel-Alloul & Méthot 1984) and on both phytoplankton and zooplankton dynamics (Robarts *et al.* 1992) as well as on organic matter production and decomposition (Kimmel *et al.* 1988).

In Portugal, examples of complete emptying and refilling of reservoirs are also scarce. However, there are studies on the effects of reservoir emptying and subsequent refilling on the structure and dynamics of zooplankton communities (Boavida & Crispim 1993; Crispim & Boavida 1993) and on phosphorus dynamics (Marques & Boavida 1993, 1994). All these studies for Portugal concern the same large reservoir and it was concluded that both zooplankton communities and phosphorus dynamics were not much affected by the disturbing processes of reservoir emptying and refilling.

The present study was carried out on two small mountain reservoirs so far not studied. Vale do Rossim Reservoir (hereafter, Rossim Reservoir) was built in 1956, emptied in 1993 for repairs to the dam wall and refilled in 1994. Lagoacho Reservoir was built in 1993 and filled for the first time in 1994. Both reservoirs were almost completely emptied again at the end of May 1995 for further repairs. Since Lagoacho was built close to Rossim (approximately

---

*Author to whom correspondence should be sent.
Email: zboavida@fc.ul.pt

Accepted for publication 20 November 1998.

3 km away), both reservoirs are subject to the same climate. The aim of the present study is to compare the limnology of a recently inundated reservoir with one almost 40 years old, which had been completely emptied (and remained empty for about 2 years) and was refilled at the same time as the new reservoir was receiving water for the first time. The comparative limnology of the reservoirs was studied by measuring the concentrations of total phosphorus, total soluble phosphorus, and soluble reactive phosphorus, phosphatase enzyme activity, and phosphomonoesters concentrations in lake water, and chlorophyll *a* concentrations. Furthermore, the trophic state of the reservoirs was compared by the determination of Carlson's Trophic State Index for lakes (Carlson 1977) and the constitution of both phytoplankton and zooplankton communities was described for the two water-bodies.

MATERIALS AND METHODS

Both reservoirs are located at an altitude 1425 m a.s.l. in the mountainous system of Serra da Estrela, Portugal (Fig. 1), on granitic bedrock, within the boundaries of a natural park (Parque Natural da Serra da Estrela). Morphological and hydrological characteristics of the reservoirs, as well as data on temperature and dissolved oxygen in the water column, are shown in Table 1. The climate in Serra da Estrela is continental, with warm, dry summers and long, cold winters. Despite the cold winters, snow is not always abundant and consequently ice cover only seldom occurs in the deepest lakes and reservoirs. During the present study, winter was abnormally warm and there was no snow.

Rossim Reservoir was built in 1956 to generate electrical power and supply water to surrounding villages. It was completely emptied for repairs in 1993, refilled in winter 1994, and partially emptied again in May 1995 for further repairs. During this period, the water was channelled to Lagoacho through a tunnel connecting the two systems. However, in spite of the tunnel, there was no water exchange between the two water-bodies beyond this water transference period. The direct influence of human activities on the impoundments is greater during summer when the reservoirs and surroundings are used for recreation such as fishing, boating, swimming and camping. At that time of the year

Enunciar + claro o clima
no trabalho.

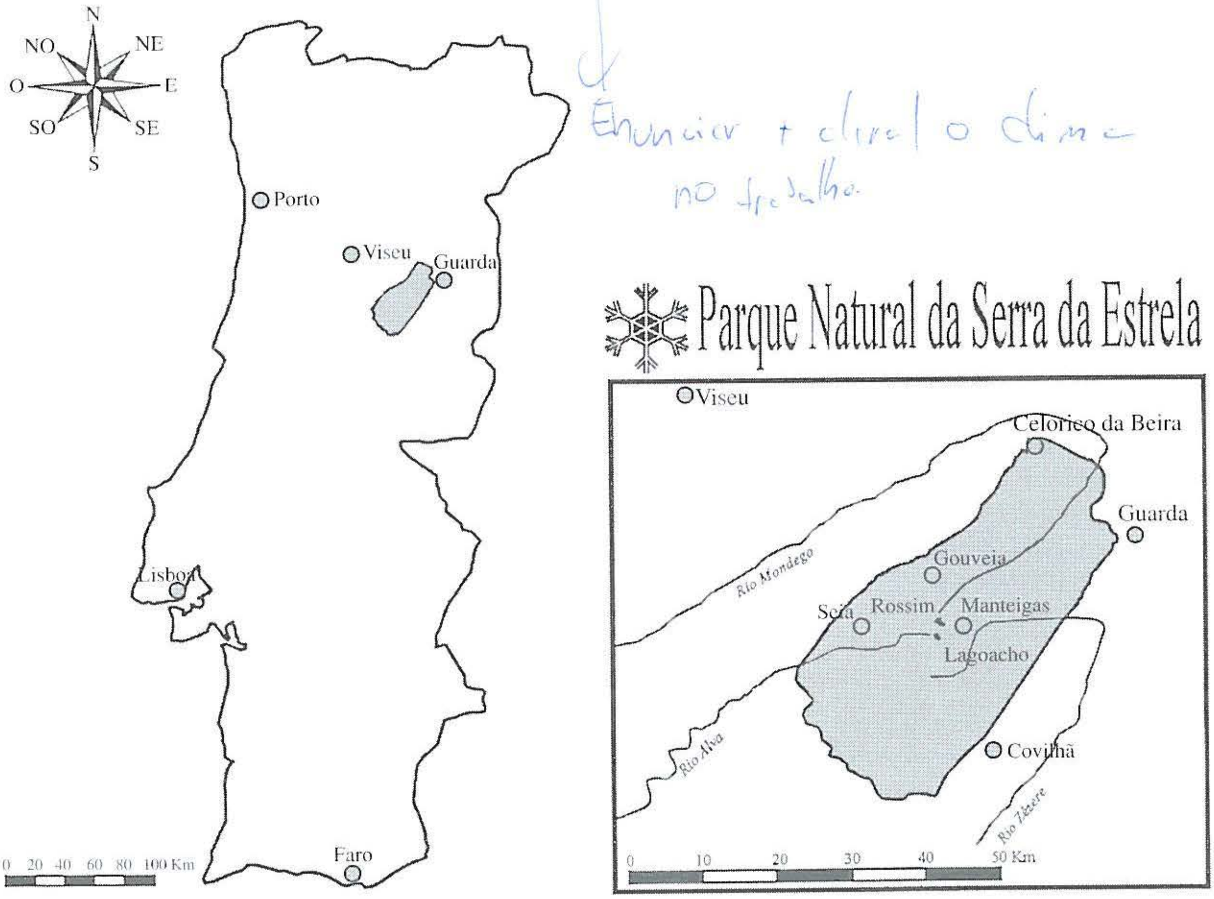

Fig. 1. Location of Rossim and Lagoacho reservoirs in Portugal.

it is also possible to find some domestic cattle (sheep and goat) grazing on the shores.

Lagoacho was built in 1993 and has the same uses as Rossim Reservoir. It was completely filled for the first time in December 1994. However, in May 1995 it was almost completely emptied for repairs. Nevertheless, the drawdown was not so extensive as in the same period in Rossim Reservoir. Since Lagoacho is of recent formation, was never used for recreation, and cattle grazing on the shores did not occur because of construction activities, human influence was considered negligible.

Vegetation is similar in the surroundings of both reservoirs and is composed largely of *Juniperus communis* L. ssp. *nana*, *Cytisus* sp., *Erica* sp. and *Halimium alyssoides*. Phytoplankton in both reservoirs consisted mainly of species of *Cosmarium*, *Botryoccocus*, *Dictyosphaerium*, *Pectodictyon*, *Scenedesmus*, *Ankistrodesmus*, *Dinobryon* and *Mallomonas*. Zooplankton in both reservoirs included the rotifers *Polyarthra dolichoptera*, *Conochilus* sp., *Synchaeta* sp., *Keratella reticulata*, *Keratella serrulata*, and *Keratella valga*. *Tropocyclops prasinus*, *Eucyclops* sp., *Megacyclops viridis*, *Alona costata*, *Alona quadrangularis*, *Chydorus spaericus* and *Bosmina* sp. were the most abundant crustacean zooplankton species common to both reservoirs.

Table 1. Morphometric, physical, and chemical characteristics of Rossim and Lagoacho reservoirs. Values other than morphometric and on water temperature and dissolved oxygen were obtained in June 1994

	Rossim Reservoir	Lagoacho Reservoir
Area (ha)	37.0	23.7
Total capacity (m^3)	3 567 440	1 052 000
Max. depth (m)	17.46	29.00
Alkalinity (meq/L)	0.03	0.05
Cl^- (mg/L)	1.90	1.60
SO_4^{2-} (mg/L)	0.95	0.83
N-NO_3 (μg/L)	0.00	0.00
N-NH_4 (μg/L)	29.0	38.0
Ca^{2+} (mg/L)	0.61	0.86
Mg^{2+} (mg/L)	0.16	0.18
Na^+ (mg/L)	1.41	1.24
K^+ (mg/L)	0.14	0.22
TN (mg/L)	0.12	0.22
Si (mg/L)	1.15	1.27
pH	6.28	6.42
Conductivity (μS/cm at 18°C)	11.4	11.7
Water temperature range (°C)	2.0–21.5	3.0–22.0
Dissolved O_2 range (mg/L)	8.5–13.0	8.0–12.5

Samples were taken monthly in both reservoirs from August 1994 to April 1995. From May to June, samples were taken weekly. A final sample was taken in July 1995. Water samples were collected close to the shore from the upper 30–40 cm stratum directly into acid-rinsed polyethylene bottles and were transported to the laboratory in a cold container (about 8°C) within 24 h. Seasonal temperature profiles were recorded. Water temperature and dissolved oxygen were measured by meter (YSI 5075; Yellow Springs Instrument Co., OH, USA). Readily available phosphorus was estimated as soluble reactive phosphorus (SRP). Soluble reactive phosphorus concentrations were estimated spectrophotometrically by the method of Murphy and Riley (1962). Total phosphorus (TP) was determined after acid hydrolysis with persulfate for 60 min under high temperature and pressure (American Public Health Association 1989). The same procedure was carried out to determine total soluble phosphorus (TSP) after filtering the water (0.45 μm membrane filter). For all SRP, TP and TSP determinations, five replicates were run. Phosphomonoesters (PME) concentration and acid phosphatase (APA) activity of lake water were determined as described in Boavida and Heath (1988). Acid phosphatase and PME determinations were performed on three replicates. Chlorophyll *a* values were obtained from 150 to 300 mL of water filtered through a Whatman GF/A filter no more than 2 h after collection. Concentrations were determined spectrophotometrically after overnight extraction in 90% acetone, according to American Public Health Association (1989). All concentrations were expressed in μg/L except APA activities which were expressed in enzyme units (e.u.). One e.u. was defined as the amount of enzyme which hydrolyses 1 μmol/L of substrate (pNPP, Sigma, Sigma-Aldrich Co., MO, USA) in 4 h. A Bauch and Lomb Spectronic 710 digital spectrophotometer (Bauch & Lomb GMBH, Munich, Germany) was used to measure absorbance.

The strength of relationships between variables, including both water temperature and dissolved oxygen concentration, was examined by Spearman's rank correlation coefficient analysis followed by multiple stepwise linear regression analysis (Sokal & Rohlf 1981). To summarize the relationships between the studied parameters and the variation in water-levels, principal components analysis (PCA) was performed on the data set for all sampling dates (Gaugh 1982). Cluster analysis using Euclidean distance as a measure of dissimilarity was used as an adjunct to PCA, and to help identifying the different groups (Digby & Kempton 1987). Data were normalized when necessary by means of a log (x + 1) transformation. Statistical tests were performed using SPSS (Chicago, USA; Norusis 1992). Trophic state was assessed by calculating phosphorus and chlorophyll components (TSI (TP) and TSI (Chl), respectively) of Carlson's Trophic State Index (Carlson 1977).

Four seasonal samples were obtained in order to determine phytoplankton and zooplankton composition. Samples were taken and analyzed according to American Public Health Association (1989).

RESULTS

During the study period neither reservoir stratified. Homeothermy was observed for the whole period, with water temperature ranging from 2.0 to 21.5°C in Rossim Reservoir and from 3.0 to 22.0°C in Lagoacho Reservoir (Table 1).

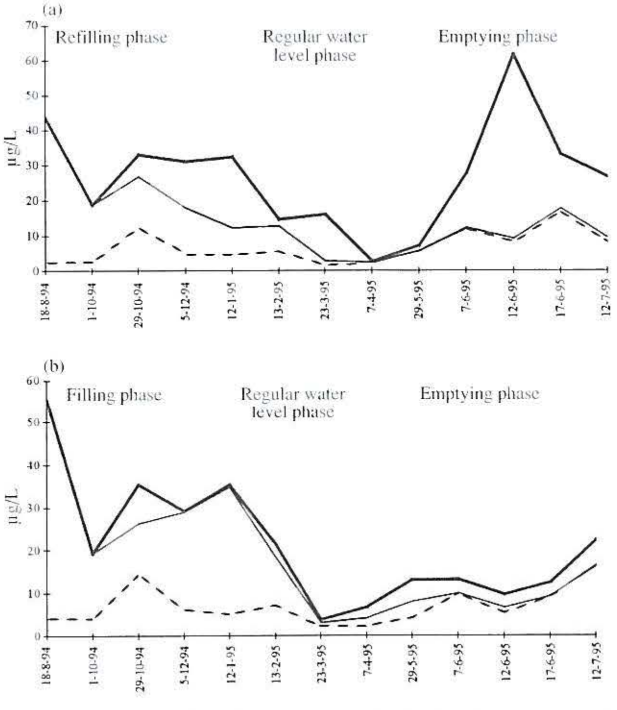

Fig. 2. (▬), total phosphorus; (—), total soluble phosphorus and (– – –) soluble reactive phosphorus concentration in (a) Rossim and (b) Lagoacho reservoirs.

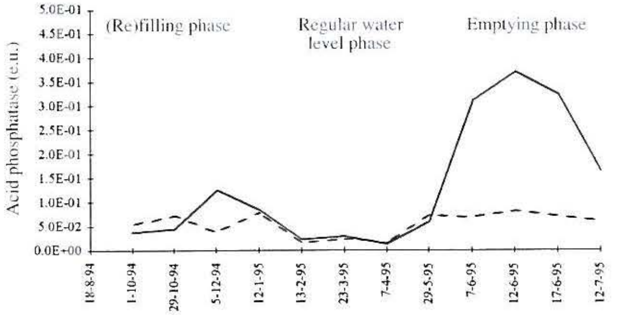

Fig. 3. Changes in acid phosphatase activity in (—) Rossim and (– – –) Lagoacho reservoirs.

Trends in TP, TSP and SRP concentrations were similar in both reservoirs (Fig. 2). However, during the first phase the highest concentrations were obtained in Lagoacho Reservoir. In Rossim Reservoir, TP concentrations ranged between 33.00 and 43.65 μg/L during this period, while in Lagoacho Reservoir the variation was between 35.41 and 55.37 μg/L. Total phosphorus and TSP concentrations decreased until the end of the (re)filling phase in both systems (Fig. 2). Soluble reactive phosphorus ranged between 2.34 μg/L (18 August 1994) and 12.23 μg/L (29 October 1994) in Rossim Reservoir, and between 4.02 μg/L (18 August 1994) and 14.54 μg/L (29 October 1994) in Lagoacho. According to these low and high limits for both TP and SRP, available phosphorus in Rossim Reservoir varied between 7 and 28% of TP, and between 11 and 26% in Lagoacho Reservoir. The concentrations of all measured phosphorus fractions decreased to minimum values during the regular water phase (Fig. 2).

During the emptying phase, concentrations of these parameters increased again. In Rossim Reservoir, TP concentrations rose to 61.30 μg/L and SRP values to 16.30 μg/L. During this phase, a large concentration of suspended particles was observed. This could have resulted from increased water turbulence during emptying, and could have caused the return of complex phosphorus to the water, thus contributing to the observed high TP concentration. In Lagoacho Reservoir, the concentration of all forms of phosphorus slightly increased. The biggest increase was observed at the end of the emptying process. Phosphomonoesters were below detection levels in both systems in all periods. In both Rossim and Lagoacho, significant correlations were found between TP and TSP ($r = 0.56$; $P < 0.05$) and ($r = 0.94$; $P < 0.05$), respectively. In Lagoacho Reservoir, a significant correlation was found between TP and SRP ($r = 0.61$; $P < 0.05$). Variables selected by multiple stepwise linear regression analysis are shown in Table 2. Because both TSP and SRP are fractions of TP, these correlations have no particular ecological interest.

During the (re)filling phase in Rossim Reservoir, APA activity increased slightly, ranging from 3.80×10^{-2} to 4.56×10^{-2} e.u.. The same pattern was observed in Lagoacho Reservoir, where APA values varied between 5.47×10^{-2} and 7.19×10^{-2} e.u. (Fig. 3).

During the regular water-level phase, APA activity decreased to the minimum values recorded: 1.52×10^{-2} e.u. in Rossim Reservoir and 1.82×10^{-2} e.u. in Lagoacho Reservoir. During the emptying phase APA activities increased again in both systems. However, in Rossim Reservoir the increase was higher and activity rose to 3.75×10^{-1} e.u., while in Lagoacho Reservoir the highest observed value was 8.46×10^{-2} e.u.. By the end of the

Table 2. Variables selected by multiple stepwise linear regression analysis in Rossim and in Lagoacho reservoirs

	r^2	F	P
Rossim Reservoir			
log TSP = 0.674 log TP + 0.174	0.69	8.974	<0.05
log SRP = 0.451 log APA + 0.292	0.71	10.155	<0.01
log TP = 0.428 log APA + 0.509 log TSP + 0.320	0.74	10.433	<0.01
log APA = 0.629 log TP + 0.761 log SRP − 0.340	0.87	12.360	<0.01
Lagoacho Reservoir			
log TSP = 1.105 log TP + 0.687 log DO − 0.943	0.99	338.873	<0.01
log TP = 0.891 log TSP − 0.602 log DO + 0.846	0.99	318.775	<0.01

TSP, total soluble phosphorus; TP, total phosphorus; SRP, soluble reactive phosphorus; APA, acid phosphatase; DO, dissolved oxygen.

emptying period APA activity slightly decreased again. In Rossim Reservoir, significant correlations were found between APA and TP (r = 0.73; $P<0.01$), between APA and SRP (r = 0.66; $P<0.05$) and between APA and water temperature (r = 0.63; $P<0.05$). The latter has no ecological meaning. The positive correlation between enzyme activity and SRP is different to expected (significant, though negative) when planktonic organisms produce phosphatase in response to the scarcity of available phosphorus in the water; this probably means that phosphatases are produced in a constitutive way in Rossim Reservoir, i.e. independently of the phosphorus concentration in the reservoir's water. A correlation between APA and TP is often found; for a correct interpretation of this relationship, however, other correlations with ecological meaning should have been found. Multiple stepwise linear regression analyses are presented in Table 2. In Lagoacho Reservoir, no significant correlations were found between APA and other parameters.

During the (re)filling phase, chlorophyll *a* concentrations varied between 5.57 and 12.47 μg/L in Rossim Reservoir, and between 15.15 and 16.93 μg/L in Lagoacho Reservoir (Fig. 4). During the filled phase, chlorophyll *a* concentrations were low in both reservoirs. During the emptying phase chlorophyll *a* concentrations significantly increased in Rossim Reservoir, while in Lagoacho they remained similar to those observed during the regular water-level phase. In Rossim Reservoir a significant correlation was found between chlorophyll *a* and TP (r = 0.66; $P<0.05$) meaning that most phosphorus was in the algal biomass. In Lagoacho Reservoir, no significant correlation was found between chlorophyll *a* and other variables.

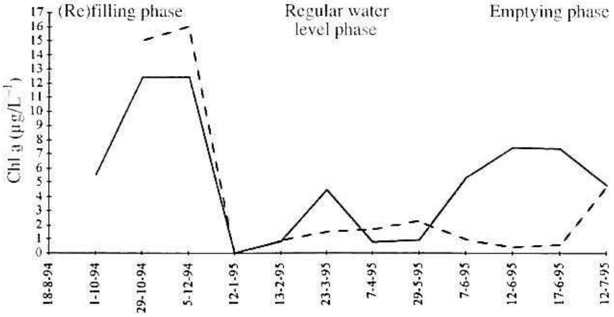

Fig. 4. Chlorophyll *a* concentrations in (—) Rossim and (---) Lagoacho reservoirs.

Principal components analysis and cluster analysis applied to data from Rossim Reservoir indicated the existence of two groups, one of samples obtained during the end of the refilling phase and during the regular water-level phase, and one

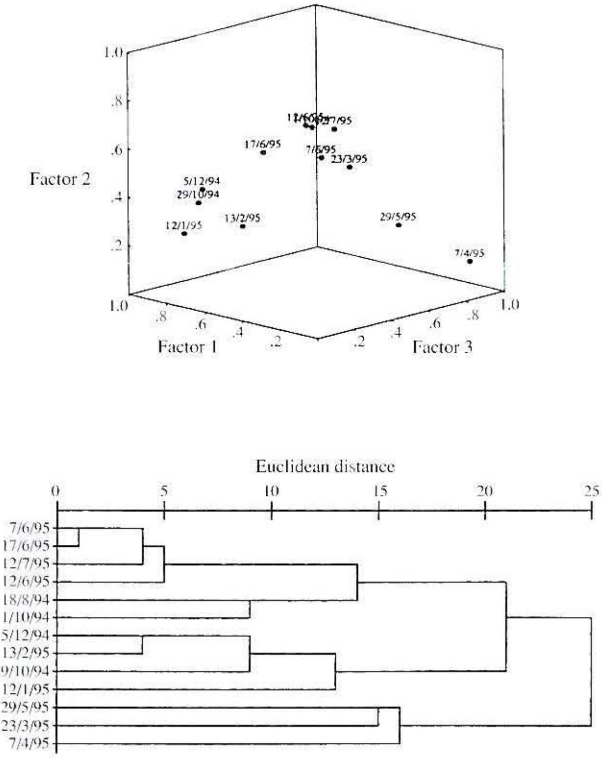

Fig. 5. Principal components analysis and cluster analysis of data from Rossim Reservoir.

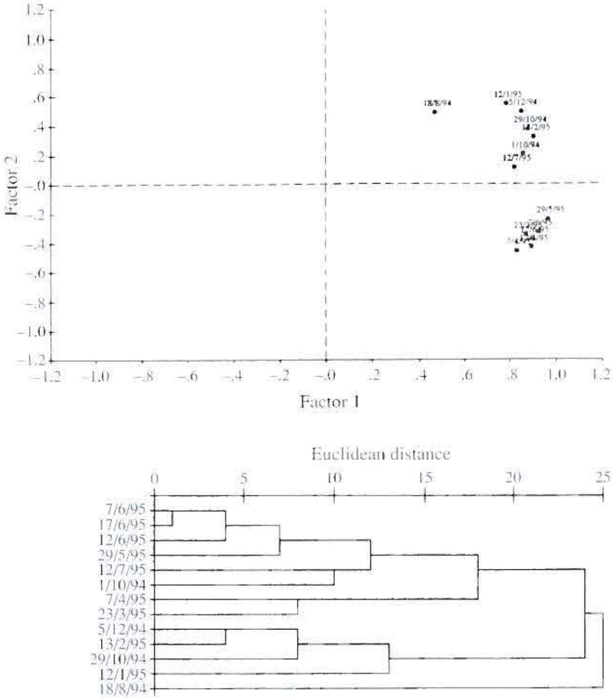

Fig. 6. Principal components analysis and cluster analysis of data from Lagoacho Reservoir.

of samples obtained at the beginning of the refilling phase and during the emptying phase (Fig. 5). In contrast, for Lagoacho Reservoir data, a clear definition between samples was not obtained in PCA analysis. However, cluster analysis separated samples obtained in the filling/regular water-level phase from those of the emptying phase (Fig. 6).

According to Carlson's Trophic State Index, both reservoirs were classified as eutrophic until 12 January 1995. In Rossim Reservoir, TSI (TP) varied between 53 and 58, and TSI (Chl) between 47 and 55. In Lagoacho Reservoir, TSI (TP) ranged between 52 and 62, and TSI (Chl) between 57 and 58. From 13 February 1995 to 23 March 1995 these systems were considered as mesotrophic (Rossim Reservoir: TSI (TP), 42–44; TSI (Chl), 28–45; Lagoacho Reservoir: TSI (TP), 22–55; TSI (Chl), 29–35). During the emptying phase, Rossim Reservoir became eutrophic again; TSI (TP) ranged between 51 and 63 and TSI (Chl) between 47 and 50, while Lagoacho Reservoir remained mesotrophic; TSI (TP) ranged between 35 and 48 and TSI (Chl) between 29 and 45.

DISCUSSION

The relatively high concentrations of TP, TSP and SRP recorded during the (re)filling phase in both reservoirs might have been caused by the leaching of nutrients, particularly phosphorus, from flooded terrestrial vegetation and soil. In addition, in Rossim Reservoir, the resuspension of sediments as the water rose could have contributed to observed concentrations (Fabre 1988). The nutrient release in Lagoacho Reservoir might have been higher than in Rossim as a consequence of the existence of larger amounts of terrestrial vegetation on this previously non-inundated reservoir. Similar results were obtained for other reservoirs during the filling phase by Pinel-Alloul and Méthot (1984), Kimmel *et al.* (1988), Robarts *et al.* (1992), who referred to this phenomenon as a 'trophic upsurge'. A significant increase of primary production as a result of high nutrient concentrations during the 'trophic upsurge' was also observed by these authors. The increase in chlorophyll *a* during the (re)filling phase in both reservoirs could reflect the raising primary production ascribed to this phenomenon. According to Pinel-Alloul and Méthot (1984), the 'trophic upsurge' is followed by a decline, referred to as a 'trophic depression', and a return to a stabilized trophic state; this would be the result of the exhaustion of the available nutrients from the flooded land and the gradual flushing of the reservoirs towards a steady lake-type system (Pinel-Alloul & Méthot 1984; Kimmel *et al.* 1988; Robarts *et al.* 1992). This phenomenon may have occurred in the reservoirs studied. The decrease in phosphorus concentrations during the regular water phase could be related to an increase in sedimentation rates as well as to the exhaustion of the available nutrients by phytoplankton (Boström *et al.* 1988; Wetzel 1993). Thus, the differences in the studied reservoirs could be explained by different sedimentation rates, which in turn are explained by intrinsic morphological and hydrological characteristics. In Rossim Reservoir, nutrients might have been used more quickly as a consequence of higher phytoplankton biomass derived from recolonization from resting forms, commonly produced in situations of stress such as emptying.

The increased TP, TSP and SRP concentrations in Rossim Reservoir during the second emptying episode could have been caused by high turbulence after the opening of the gates located at the bottom of the dam; turbulence might have contributed to the increase in phosphorus by resuspension from the sediments (Wetzel 1993). This pattern is similar to that observed in other reservoirs by Marques and Boavida (1993, 1994), by Barone and Flores (1994), and by Flores and Barone (1994) during the emptying phase. Likewise, small TP, TSP and SRP increases observed in Lagoacho Reservoir during the emptying period could be related to the small intensity of the same kind of process. However, Salmoiraghi (1984) and Palau (1991) observed that in two reservoirs with hydraulic connections, the exchange of water from the first reservoir caused an increase of turbulence leading to sediment resuspension in the second recipient reservoir. In the reservoirs being studied here, morphometry and the fact that Lagoacho Reservoir (recipient) was also being emptied could have 'smoothed' the process; the water coming from Rossim Reservoir was rapidly removed and did not cause a significant increase in turbulence.

The increase in chlorophyll *a* concentrations during the emptying phase in Rossim Reservoir could have been related to the occurrence of a bloom of small *Cosmarium* sp. in this period (Geraldes, unpubl. data).

Phosphomonoesters were not found, either because they did not exist in the lake or because they were not detected due to rapid hydrolysis as they were released into the water (Boavida 1991). Acid phosphatase activity in Lagoacho Reservoir was higher than in Rossim Reservoir. Part of the APA activity detected in Lagoacho Reservoir could have been of terrestrial origin, resulting from the first flooding of soil (Jansson *et al.* 1981). The lowest APA activity was observed in both reservoirs during the regular water-level phase. This might have been because this phase occurred between winter and spring when phytoplankton biomass was low (Berman 1970; Boavida & Heath 1988; Wetzel 1993). In fact, Boavida and Heath (1988) noted that phosphatase activity and phytoplankton biomass were correlated. However, in these reservoirs, no significant correlations were found. This might be attributed to the large disturbance that occurred in both systems. The increase of APA activity in Rossim Reservoir during the emptying phase could be explained by the bloom of small *Cosmarium*. According to Jansson *et al.* (1981), Olsson (1983) and Rai and Jacobsen (1993), a major part of sestonic phosphatases is associated with small algae (<10 μm) and probably with bacteria. In contrast, the emptying process might have caused high plankton mortality; generally, phosphatase activity is highest when high rates of plankton decomposition occur (Halemejko & Chróst 1984; Boavida & Marques 1995). In Lagoacho Reservoir, the small increase in APA activity during this period could be explained by the lowest biomass of *Cosmarium* recorded.

Reduction of APA activity at the end of the emptying phase in both reservoirs might be related to progressive inactivation of the enzyme. Phosphatases found in natural environments persist for about 2 months with no appreciable loss of activity (e.g. Boavida 1991). If no more enzymes were produced to replace that inactivated, phosphatase activity of lake water would certainly decrease. The positive correlation and the functional relationship in Rossim Reservoir, or their absence in Lagoacho Reservoir, between APA and SRP, might suggest that APA is constitutively produced in both systems.

The effects of emptying/refilling hydrological patterns seemed not to be important. No important difference was found between the new reservoir and the one that has been filled for almost 40 years before being emptied and dried for about 2 years. The conclusion is that for structural/functional characteristics brought about by ageing to dominate more than 40 years are needed. It seems that the strongest influence in these reservoirs was that of climate and soil (in this case the same influence, given the vicinity of the waterbodies) which lead to similar limnological characteristics.

ACKNOWLEDGEMENTS

We would like to thank B. Paulo and P. Geraldes for their assistance in the field. AMG was supported by M.S. grant PRAXIS XXI/BM/1299/94, Junta Nacionale de Investigação Cientifica e Tecnológica, Portugal. Chemical analyses other than chlorophyll, phosphorus and phosphatase determinations were kindly performed at the Istituto Italiano di Idrobiologia, Pallanza, Italy. Pertinent comments and suggestions by an anonymous referee are appreciated. This paper is a contribution from Centro de Biologia Ambiental, Universidade de Lisboa, Portugal.

REFERENCES

American Public Health Association (1989) *Standard Methods for the Examination Of Water and Wastewater*. APHA, Washington.

Barone R. & Flores L. N. (1994) Phytoplankton dynamics in a shallow, hypertrophic reservoir (Lake Arancio, Sicily). *Hydrobiologia* **289**, 199–214.

Berman T. (1970) Alkaline phosphatases and phosphorus availability in Lake Kinneret. *Limnol. Oceanogr.* **25**, 663–74.

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

Boavida M. J. & Crispim M. C. (1993) Study of zooplankton populations as a 30-year old reservoir is being emptied. *Verh. Internat. Verein. Limnol.* **25**, 1204–6.

Boavida M. J. & Heath R. T. (1988) Is alkaline phosphatase always important in phosphate regeneration? *Arch. Hydrobiol.* **111**, 507–18.

Boavida M. J. & Marques R. T. (1995) Low activity of alkaline phosphatase in two eutrophic reservoirs. *Hydrobiologia* **297**, 11–16.

Boström B., Persson G. & Broberg B. (1988) Bioavailability of different phosphorus forms in freshwater systems. *Hydrobiologia* **170**, 21–34.

Carlson R. E. (1977) A trophic state index for lakes. *Limnol. Oceanogr.* **22**, 361–9.

Crispim M. C. & Boavida M. J. (1993) Study of zooplankton in Maranhão Reservoir after refilling (in Portuguese). *Bol. UCA* **1**, 140–63.

Digby P. G. N. & Kempton R. A. (1987) *Multivariate Analysis in Ecological Communities*. Chapman & Hall, New York.

Fabre A. (1988) Experimental studies on some factors influencing phosphorus solubilization in connection with the drawdown of a reservoir. *Hydrobiologia* **159**, 153–8.

Flores L. N. & Barone R. (1994) Relationship between trophic state and plankton community structure in 21 Sicilian dam reservoirs. *Hydrobiologia* **275/276**, 197–205.

Gaugh H. G. (1982) *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge.

Halemejko G. R. & Chróst R. J. (1984) The role of phosphatases in phosphorus mineralization during decomposition of lake phytoplankton blooms. *Arch. Hydrobiol.* **101**, 489–502.

Jansson M., Olsson H. & Broberg O. (1981) Characterization of acid phosphatases in the acidified Lake Gardsjön, Sweden. *Arch. Hydrobiol.* **92**, 377–95.

Kimmel B. L., Soballe D. M., Adams S. M., Palumbo A. V., Ford C. J. & Bevelhimer M. S. (1988) Inter-reservoir interactions: Effects of a new reservoir on organic matter production and processing in a multiple-impoundment series. *Verh. Internat. Verein. Limnol.* **23**, 985–94.

Marques R. T. & Boavida M. J. (1993) Effects of water level fluctuation on the forms of phosphorus in mesotrophic Maranhão Reservoir. *Verh. Internat. Verein. Limnol.* **25**, 1207–9.

Marques R. T. & Boavida M. J. (1994) Environmental impact of the emptying of Maranhão Reservoir (in Portuguese). *Proceedings of the 4th National Conference on Environmental Quality*, E63–E73. Mirasete Artes Gráficas Loda, Lisboa.

Murphy J. & Riley J. P. (1962) A modified single solution method for the determination of phosphate in natural waters. *Annals Chem. Acta* **27**, 31–6.

Norusis M. J. (1992) *SPSS For Windows: Base System User's Guide*. SPSS Inc., Chicago.

Olsson H. (1983) Origin and production of phosphatases in acid Lake Garsjön. *Hydrobiologia* **101**, 49–58.

Palau A. (1991) Evolution of annual chlorophyll concentration in a high mountain pump storage reservoir. *Verh. Internat. Verein. Limnol.* **24**, 1401–4.

Pinel-Alloul B. & Méthot G. (1984) Analyse multidimensionnelle de l'évolution du zooplancton durant la mise en eau de trois reservoirs du Nord du Québec. *Can. Verh. Internat. Verein. Limnol.* **22**, 1444–55.

Rai H. & Jacobsen R. (1993) Dissolved alkaline phosphatase activity (APA) and the contribution of APA by size fractionated plankton in Schöhsee. *Verh. Internat. Verein. Limnol.* **25**, 164–9.

Rey J. (1984) Export de matériel zooplanctonique dans l'exutoire d'une retenue des Pyrénées. *Verh. Internat. Verein. Limnol.* **22**, 1493–7 (in French).

Rey J. (1988) Impact de la vidange sur le developpement des populations zooplanctoniques dans une retenue des Pyrénées. *Ann. Limnol.* **23**, 235–41 (in French).

Robarts R. D., Zohary T., Jarvis A. C., Pais-Madeira C. M., Sephton L. M. & Combrink M. (1992) Phytoplankton and zooplankton population dynamics and production of a recently formed African reservoir. *Hydrobiologia* **237**, 47–60.

Salmoiraghi G. (1984) Limnology of Suviana-Brasimone man-made lakes. Influence of pumped storage operations on physical, chemical and biological characteristics. *Verh. Internat. Verein. Limnol.* **22**, 1550–7.

Schmid-Araya J. M. & Zúñinga L. R. (1992) Zooplankton community structure in two Chilean reservoirs. *Arch. Hydrobiol.* **123**, 305–35.

Sokal R. R. & Rohlf F. J. (1981) *Biometry*. Freeman and Co., San Francisco.

Wetzel R. G. (1990) Reservoir Ecosystems: Conclusions and Speculations. In: *Reservoir Limnology: Ecological Perspectives* (eds K. W. Thornton, B. L. Kimmel & F. E. Payne). Wiley, New York.

Wetzel R. G. (1993) *Limnologia*. Fundação Calouste Gulbenkian, Lisboa (in Portuguese).