Homage to Ramon Margalef; or, Why there is such pleasure in studying nature (J. D. Ros & N. Prat, eds.). 1991. *Oecologia aquatica*, 10: 127-135

FLUCTUATIONS, THE KEY ASPECT FOR THE ECOLOGICAL INTERPRETATION OF SALINE LAKE ECOSYSTEMS*

FRANCISCO A. COMÍN[1], RAMON JULIÀ[2] & PILAR COMÍN[1]

[1] Departament d'Ecologia. Facultat de Biologia. Universitat de Barcelona. Av. Diagonal, 645. 08028 Barcelona. Spain.
[2] Institut Jaume Almera (CSIC). Martí i Franquès, s/n. 08028 Barcelona. Spain.

Received: February 1991

SUMMARY

In Lake Gallocanta (Aragón, NE Spain) changes of the biological communities occur at different scales of time in accordance with physical and chemical characteristics of the water. Different stages of the lake can be defined by the values of abiotic and biotic variables. However, processes occurring at any time influence the characteristics of later stages, even after dry periods. Fluctuations of physical, geochemical and biological characteristics in Lake Gallocanta make clear this idea. Definition of the intensity and frequency of the fluctuations and their relationships with climatological and geomorphological characteristics of the watershed are the key aspects in understanding the ecological functioning of saline wetlands.

KEY WORDS: Saline lake ecosystems, fluctuations.

INTRODUCTION

Interpretation of the ecological characteristics of aquatic ecosystems requires definition of time and space scales because the significance of the data depends on the scale of observation (TURNER *et al*., 1989). This is particularly clear for ecosystems, such as saline wetlands, where salinity changes are related to water volume in a very wide range. The structure and functioning of the biological community changes in accordance with the intensity and frequency of the external disturbances (HARRIS, 1980; MARGALEF, 1986). The most conspicuous case is represented by ephemeral saline lakes.

The community fluctuations are strongly related to physical and chemical changes of the water, and these to climatological fluctuations (COMÍN *et al*., 1983). The succession resumes after every desiccated event. However, fluctuations of different lengths of time can take place between dry episodes, and during longer periods.

This paper presents an example of such a type of ecosystems: Lake Gallocanta, where some chemical and biological characteristics have been studied over a period of years, although not continuously (COMÍN *et al*., 1990). The major point

* Research supported by Diputación General de Aragón, Servicio de Conservación del Medio Natural.

here is to make it clear that observation of components and processes at different scales is necessary for any interpretation or applied interest of this type of ecosystems. Or, as previously mentioned by MARGALEF (1987), these ecosystems are better characterized by the type (intensity and frequency) of the fluctuations than by the values observed at any precise time and place.

GEOGRAPHICAL SETTING

Lake Gallocanta (40^o 50' N and 2^o 11' W) is the hydrological terminus of a 520 km^2 watershed in the Iberian Range (western limit of the Zaragoza and Teruel provinces, Aragón region). The geomorphological origin of the lake is a tectonic depression. Accumulation of eroded salts from the watershed and concentration by evaporation in this endorheic area is the origin of the present saline character of Lake Gallocanta.

The interesting point here is that Lake Gallocanta and its watershed are located at the boundary between semiarid and semihumid weather (COMÍN & ALONSO, 1988). The average annual rainfall varies widely from north to south in the Iberian Peninsula. This, with evaporation, determines wide spatial differences in the net annual rainfall-evaporation (r-e) budget. Because of the strong negative net annual r-e, every saline lake in Spain but one is ephemeral. Lake Chiprana is the only permanent saline lake in Spain. It is located very close to many other ephemeral lakes, under the same climatic conditions. The difference lies on the fact that Lake Chiprana is at relatively low altitude (150 m a.s.l.) and very close to the phreatic water table compared to other lakes.

Between the ephemeral Spanish saline lakes, Gallocanta is noteworthy because its water level shows very distinct seasonal and longer period fluctuation (Fig. 1), while the other saline lakes in Spain dry every year in response to very strong negative rainfall- evaporation budgets (COMÍN & ALONSO, 1988).

The peculiar location of Lake Gallocanta explains the water level fluctuations. Interannual differences of the rainfall cause mid-term trends in the water level fluctuations superimposed on the seasonal fluctuations. Fluctuations at any organizational level of the ecosystem are supposed to follow those of water level in saline lakes because salinity changes are wide enough to affect physical, chemical and biological characteristics. This is the uniqueness of Lake Gallocanta. Very few other examples like this are available. In saline lakes which dry every year and in permanent saline lakes the biological components do not show such clear

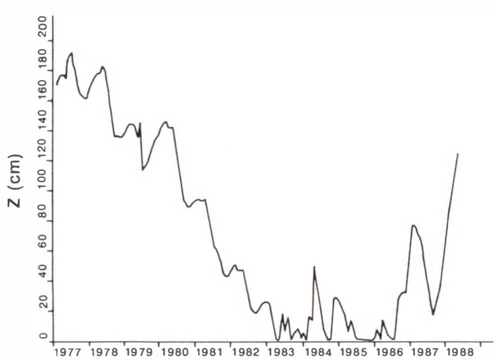

FIGURE 1. Recorded changes of the water level in Lake Gallocanta

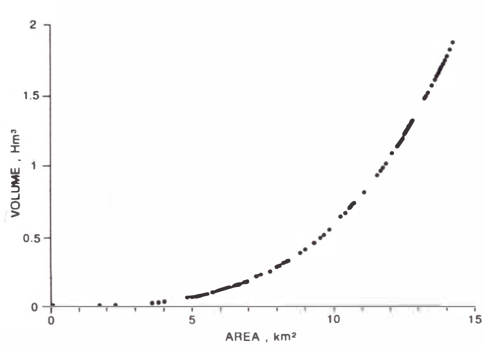

FIGURE 2. Relationship between area covered by the water and water volume in Lake Gallocanta.

fluctuations in water level or in related characteristics (physical, chemical and biological).

The average annual rainfall in Gallocanta is 488 mm. This is the average of annual rainfall measured every day at five meteorological stations located in the watershed. No significant differences were observed between the five stations. A rough calculation of the net annual evaporation from the lake, taking into account changes in water volume during months with no rainfall at all, gives a figure of 750 mm. The volumes of different vertical sections of the lake were calculated as the product of the water height by the simultaneous change of area. The areas were estimated from aerial photographs at precise dates in 1977 and 1983, when lake water was at different levels, and these were recorded. The relationship between water volume and area covered by the water is quite linear for a part of the graph (Fig. 2). However, water level and rainfall are far from a direct relationship.

The water volume in the lake is the result of the balance inputs-outputs. Rainfall on the lake, run-off and groundwater constitute the inputs. Outputs consist, basically, of evaporation from the lake. Most of the Gallocanta watershed is occupied by cereal fields. Considering a long enough period of time, inputs equal outputs. In this steady-state condition, $V_i = V_0$, V_i and V_0 being the volumes of water entering and going out of the lake. Following BOWLER (1981), in an endorheic area this expression can be written as:

$$A_l P + (A_c - A_l) P_f = A_l E \qquad (1)$$

where A_l and A_c are, respectively, the areas (m^2) of the lake and the watershed. P is the rainfall ($l\ m^{-2}$), E the evaporation ($l\ m^{-2}$) and P_f is the water volume entering to the lake per square meter of watershed.

Reordering the elements in (1),

$$A_c/A_l = [(E-P)/P_f] + 1 \qquad (2)$$

This equation includes morphometric parameters in the first part and climatic parameters in the second part. In this equation $P_f = P\ c$, where c is the equivalent to a run-off coefficient or a coefficient to transform from rainfall in the watershed to water entering the lake.

Equation (2) is useful to define the conditions for the hydrological balance of a terminal lake in a closed basin. In the case of Gallocanta,

$$520/20 = [(720\text{-}500)/\ 500\ c] + 1$$

From this, a value of 0.019 is obtained. This is the value of the run-off coefficient which equals the second part of the equation, named the climatic function, to the first part, the morphometric function.

Then, under the present conditions, the water level of the lake will remain in steady state when the value for both functions is 26.

This model can be applied only to closed basins. In the case of Gallocanta, some corrections should be introduced if direct measurement of the hydrological balance gives support to the idea that groundwater relation exists with other close aquifers (CRUZ *et al.*, 1979).

Another important criticism of the model proposed refers to the run-off coefficient, which is estimated from the other parameters in the equation and not measured directly. The value of the coefficient can change at least one order of magnitude depending on the rainfall intensity and the land state, among other factors (BOWLER, 1981). So, it can change during the period of time of a fluctuation in the lake water level. However, for the period of time between identical water levels, an average could be used if direct estimates are not available.

The combination of the climatic and the morphometric parameters define the state of any saline lake (Fig. 3). For those lakes where great changes of water volume occur, an oscillating area, rather than a point in that space, could be defined.

In the case of Lake Gallocanta, the value of A_c/A_l was 26 in 1981, when the water level was relatively high. Depending on the parameters in the climatic function, the lake will change from an ephemeral condition to either of the other two possibilities in figure 3. For example, a rainfall decrease to 250 mm will transform the lake into an evaporitic saltern, that is, dry or with huge amounts of salt precipitates. This change would be forced if outgoings from the watershed (e.g., use of groundwater for irrigation, extraction from connected watersheds) increase. Just a 6.6% increase of the evaporation, combined with a low rainfall, gives an Fc = [(800- 250)/(250 x 0.02)] + 1 = 111, characteristics with which the lake would change to the evaporitic stage (Fig. 3).

THE RESPONSE TIME OF THE LAKE TO CLIMATIC CHANGES

The water volume in the lake does not change immediately after changes in the parameter which constitute inputs and outputs from the watershed. So, changes

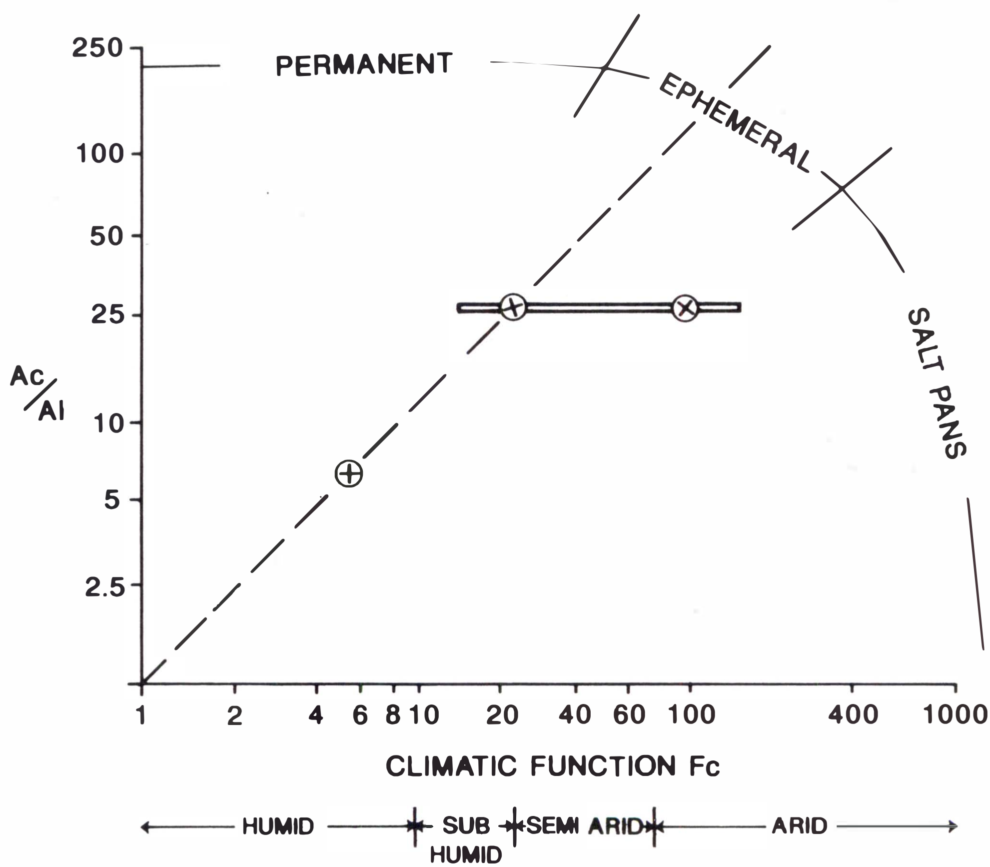

FIGURE 3. Change in Lake Gallocanta as a consequence of increased water extraction and decreased rainfall in the space defined by the relationship between the morphometric function (A_c/Al) and the climatic function (Fc).

TABLE I. Values of the response time (years) of different saline lakes (Data from LANGBEIN, 1961, except for those of Gallocanta).

Lake	k, year^{-1}
Pyramid	65
Redberry	50
Dead Sea	35
Basin	25
Quill	20
Great Salt Lake	9
Eyre	1.5
Elton	1
Gallocanta	2.4-0.3

from year to year in the water inputs and outputs are not paralleled by changes of the same volume in the lake water. In some terminal lakes, water level hardly changes in spite of great year to year changes of rainfall. In other lakes, great changes of water level are observed from one year to the next, although rainfall hardly changes. The point is that the geomorphological structure of the basin deviates the relationship between the input-output balance of the watershed and lake water volume from linearity.

The response time of the lake water volume as affected by changes in the water inputs to the watershed can be calculated following LANGBEIN (1961). A change of the lake water volume (V), will occur if there is a difference between inputs (I) and outputs (O):

$$\Delta V = I - O \quad (3).$$

In a terminal lake the water outflow

$$Q = EA_l = (V + b) / k,$$

where E is the net evaporation, A_l the lake area, V the lake water volume, and b and k are constants for every lake. Then, in equation (3)

$$\Delta V = I - (V/k) - (b/k).$$

If the time intervals are short enough,

$$V_t - V_{t-1} = I_t - (V_t/k) - (b/k) \quad (4)$$

where t and t-1 refer here to consecutive years. After n years,

$$V_n = I_n \ K/(1+k) + I_{(n-1)} \ k/(1+k) + I_{(n-2)} \ k/(1+k) + ...$$

This equation indicates that the volume of water in the lake is a weighted average of the inflows during the preceding years. The effect of the inflows of a determinate year on lake volume decreases geometrically with time.

The values of k, the solutions of equation (4), are the response times of the lake water volume to the inflows of the previous year. For Gallocanta, these response times for consecutive years during the period 1976-87 fluctuate between 0.3 and 2.4 years. That is, the lake water volume takes between 3.6 and 28.8 months to change in response to the changes in the water volume inflowing to the lake from one year to the next which occurred in Gallocanta during that decade.

Table I lists the response times, k, of several saline lakes. In Gallocanta, the lowest values of k correspond to great changes in the water level between consecutive years (1980-1981, 1981-1982, 1986-1987, 1987-1988). The highest values of the response time correspond to the lowest differences in water level between two consecutive years (1977-78, 1979-80).

GEOCHEMICAL RELATED BIOLOGICAL FLUCTUATIONS

The model of salinity versus water volume changes proposed by LANGBEIN (1961) is common for every ephemeral saline lake (Fig. 4). The time necessary for a lake to show the complete fluctuation will depend on the particular climatic circumstances. For Gallocanta in recent times, at least twelve years have been necessary lately (COMÍN *et al.*, 1990). The lake has also dried up on at least three other occasions during the present century (GUIRAL, 1981). HERNÁNDEZ & ARANEGUI (1926) referred to another dry period at the end of nineteenth century during which cartloads of salt were collected.

The physical, chemical and biological characteristics of the lake change as the water level fluctuates within the area defined in figure 4. Several phases can be distinguished bearing in mind geochemical and biological features observed in Lake Gallocanta from 1980 to 1987. During 1980-81, at a relatively high water level, a seasonal fluctuation was observed, e.g.: small changes in the amounts of different dissolved ions and biological populations occurred (COMÍN *et al.*, 1983). From mid 1981 to 1983 a dominant water level decrease and salt concentration increase took place. The saturation points were reached for most of the ion couples and precipitation of salts proceeded intensively

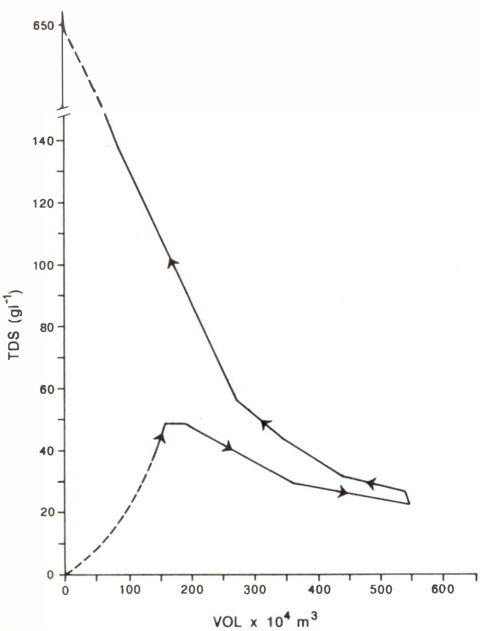

FIGURE 4. Salinity versus water volume in Lake Gallocanta, 1986-87. The dashed lines complete an hypothetical emptying-drying- refilling fluctuation.

TABLE II. Amounts of salts lost from the water of Lake Gallocanta during the dry period 1983-86.

Ion	tm
Cl^-	66,435
SO_4^{2-}	35,965
CO_3^{2-} + HCO_3^-	1,941
Na^+	20,811
Mg^{2+}	9,134
Ca^{2+}	2,192
K^+	539

(Fig. 5). The lake dried up after a period of brines. During the years 1983-86 the lake remained dry or with very low water levels.

A refilling period was initiated in 1986. The water level increased and, since 1988,

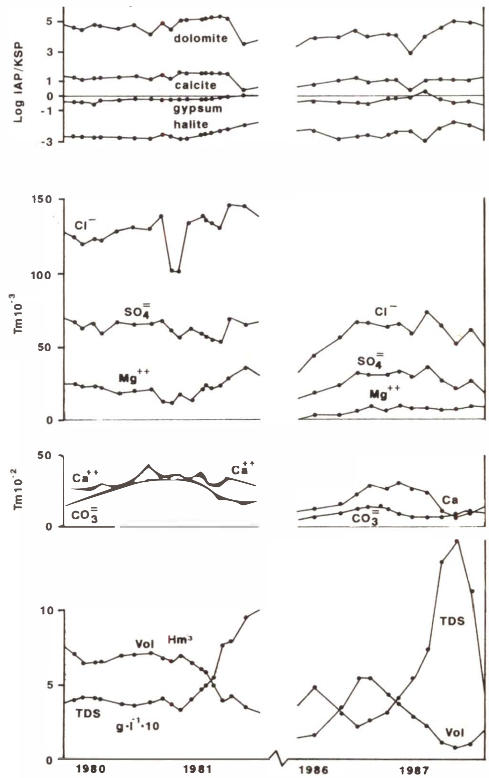

FIGURE 5. Changes in total dissolved solids (g l^{-1}), water volume (hm^3), absolute amounts of the most abundant anions and cations (tm) and the saturation coefficient (lg AP/kt) of the most abundant salts in the water of Lake Gallocanta during two annual cycles (1980-81 and 1986-87). A dry period occurred in between (1983-86).

TABLE III. Outstanding processes and components of the biological facies which occur in Lake Gallocanta at different phases.

	DESICCATION	BRINE	DRY	FLOODING	REFILLING	HIGH LEVEL
TDS ($g\ l^{-1}$)	60-200	200-600		35-50	40-20	15
WATER LEVEL (cm)	50-20	20-0	0	0-75	75-100	150
PRECIPITATING SALTS	Calcite Dolomite Gypsum Halite Bischofite					
BIOGEOCHEMICAL PROCESSES	Denitrification Fermentation Sulfate reduction Methane formation			Aerobic respiration Sulfide oxidation Mn, Fe oxidation Nitrification		
PHYSICAL PROCESSES	Washing margins		Wind deflation			
PHYTOPLANKTON	*Dunaliella salina* *Nannochloris* *Spirulina* Floating mats		Cysts	*Lobocystis dichotoma* *Oocystis solitaria* *Tetraselmis* *Gymnodinium*		*Rhodomonas* *Monoraphidium*
ZOOPLANKTON	*Arctodiaptomus* *Brachionus* *Fabrea*		Resting eggs	*Daphnia mediterranea* *Moina mongolica* *Branchinella*		*D. dolicocephala*
MACROPHYTES	Benthic microbial mats (decomposing)		Resting seeds (drying)	*Ruppia drepanensis* *Lamprothamnion papulosum* *Cladophora*		*Chara galioides*
OTHER FACIES	Insects colonizing margins Anoxic sediments		Terrestrial plants	Sediment disturbance		Flooded margins Highly dense bird populations

it has remained fluctuating around 100 cm. Huge amounts of salts were lost from the lake during the dry and low level periods (Table II) as can be seen by comparing the total concentration of dissolved solids in the same water volume at different times at the drying phase in 1981 and the refilling phase in 1987. Therefore the amount of salts during the latter are much lower than during the former. In addition to this, the molar ratios of the major ions changed, and ions were lost from the lake waters selectively by different processes.

Precipitation of salts is very important. The sediments of the lake contain different mineral components (COMÍN *et al.*, 1990), mainly carbonates (aragonite, high and low magnesium, calcite, dolomite) and sulphates (gypsum). In order to determine the relationship between the ionic composition of the water and the saturation point, after which precipitation takes place, the IAP/KSP ratio (the product of the free activities of the ions divided by the constant of the solubility product at 25 °C) for each mineral form was calculated using a computer program (KHARAKA *et al.*, 1988).

In Lake Gallocanta the pattern of change of ionic combinations over the saturation point during 1980-1981 is similar to that occurring in hypersaline marine environments while water evaporates. Carbonates precipitated first (10 times oversaturation for calcite and aragonite, and 100,000 times oversaturation for dolomite was observed during most of the 1980-81 period). The ratio for aragonite is very similar to calcite and is not represented in figure 5. Gypsum and halite increased the ratio IAP/KSP by mid-1981, paralleling the water volume decrease and TDS increase. Gypsum reached the equilibrium point at the end of 1981 while halite precipitated later on (COMÍN *et al*., 1990).

The high dolomite oversaturation is related to the high magnesium concentration (200-800 meq l^{-1}). It is probably related to gypsum precipitation, which favors dolomite precipitation because this mineral salt needs a high nuclear energy and is controlled by kinetics inhibition mechanisms (BERNER, 1971). Dolomite, calcite and gypsum hardly redissolve during the refilling period. Hence, the mineral composition of the water is extremely influenced by water level fluctuations.

Eolic deflation contributes directly to the export of salts from the lake. Strong winds affect Gallocanta. Evaporation is increased by the wind. The water mass is displaced in the wind direction, sometimes increasing the water level in the leeward shore by 20 cm, which means flooding of a large land area where water is adsorbed onto clays.

Biogeochemical processes occurring in the sediments of wetlands include aerobic and anaerobic processes (i.e.: denitrification, fermentation, sulphate reduction, methanogenesis) which affect the carbonate and sulphate concentrations in the water (Table III). For example, a sulphate reduction rate of 9.5 mmol SO_4^{2-} m^{-2} d^{-1} was estimated in a coastal marine sediment (JØRGENSEN, 1977). If this, quite acceptable activity took place in Lake Gallocanta, 20 tm SO_4^{2-} per day could be reduced in the sediments during the low water level periods.

The specific composition of the biological communities also changed during the same period. Populations characteristic of the different phases can be proposed (Table III). However, it is not possible to define rigid limits between phases. Moreover, the main point we want to make here is the idea of continuity in saline lakes; over a period of time very different geological and biological facies can appear at successive times of a fluctuation.

The great spatial heterogeneity described before (DE DECKKER, 1988) is also a substantial characteristic of saline lakes. For example, the branchiopod *Branchinella spinosa* is present in the waters of Gallocanta after a dry period and under a combination of salinity, temperature and probably other factors. During the other phases, this population is also present in the lake sediment, like many other animals and plants, in the form of resistance organs (eggs, ephippia, cysts, seeds). Those species which are not able to persist under unfavorable conditions migrate (e.g.: birds) or die. Migration or exportation of organic matter, also of salts, has a buffer effect on the ecology of saline lakes. Accumulation of salts and dead organic matter has a stress effect.

MARGALEF (1987) proposed a mathematical model which considers the biological production depending on the change of both the inputs of external energy and the covariance of the production factors. He derived the original expression

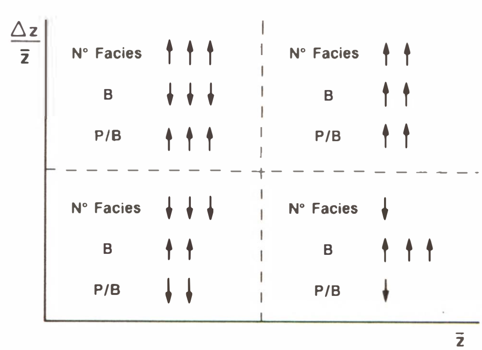

FIGURE 6. Relative intensities of synthetic characteristics in saline wetlands at different stages defined by water level and changes of the water level (Δ Z/z).

dB/dt = A C (where B is biomass, t is time, A is external energy and C is covariance of production factors) into

$$d^2B / dt^2 = C (dA/dt) + A (dC/dt)$$

and named the three terms, respectively, deceleration, energy degradation and ecological segregation in reference to general trends occurring during the ecological succession.

The application of models of this type to saline lakes is not possible yet because of the lack of data. However, endorheic wetlands areas like Gallocanta, where the water level fluctuates at different time scales, seem promising for providing sufficient reliable data to test some of the theoretical models proposed for fluctuating ecosystems.

A simplified graphic representation can relate the changes in the relationship between salinity and water volume to the community changes through time and space. In the case of most saline wetlands the change in time of external energy inputs can be represented by water level fluctuations (changes through time, vertical axis in figure 6). The ecological segregation, mostly horizontal heterogeneity in wetlands, can be represented by the water level (changes through space, horizontal axis in figure 6). Validation of this type of relationship requires data at different time scales (LIKENS, 1987), which will provide tools for a better knowledge of the way aquatic ecosystems work (MARGALEF, 1986).

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