Diatom responses to Holocene environmental changes in a small lake in northwest Spain

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Keywords: Diatoms, Holocene, sedimentary environments, palaeolimnology, northwest Spain

Abstract

The Holocene history of Lagoa Grande (1,360 m a.s.l; northwest Spain) has been investigated through the analyses of diatoms remains found in a sediment core. Changes in the lake have been interpreted in terms both of climatic variability and major changes in the catchment area. The diatom record begins at about 9800 yr BP and exhibits three marked changes at 8200, 6000, 4200 and at 2600 yr BP, which are interpreted as responses to climatic changes detected by marine and other terrestrial palaeoclimatic records. The initial lake was shallow and *Aulacoseira* species characteristic of acidic and oligotrophic waters were dominant. The early of Holocene is characterized by the presence of *Aulacoseira ambigua*, which suggests an increase in water depth and nutrient levels. Throughout the Holocene diatom assemblages underwent several changes linked to fluctuating limnological conditions. These changes in lake characteristics coincide with the regional succession of vegetation, suggesting that climate forcing initiated these limnological changes. During the last 2000 years catchment processes appear to be the major factor controlling lake characteristics in Lagoa Grande site. Diatom responses reflected the progressive peatland development and growth of littoral vegetation in the lake, and not only a change in the regional environment.

Introduction

Changes in lake water chemistry can be driven by many different factors either natural or human induced. Palaeolimnological investigations have shown the links between acid deposition of anthropogenic origin and surface water acidity (Battarbee and Renberg, 1990; Davis, 1987; Psenner, 1994; Renberg et al., 1993). Peat development and soil acidification have also been shown to lead to surface water acidification, especially where surface waters have low alkalinity (Brugam and Swain, 2000). Furthermore changes in climate affect many physical and chemical limnic properties, including nutrient availability and pH, all of which affect diatom community composition (Moser et al. 1996). In recent years, detailed studies in marine and other terrestrial palaeoclimatic records have shown that the Holocene climate variability has been wider and punctuated by cooling oscillations (Bond et al. 1997; 2001). The timing and frequency of these oscillations have already been established in different archives at least in the northern North Atlantic suggesting that solar activity played a major role (Bond et al. 2001). Little is still known, however, about the environmental effect of these climate oscillations on Southwest Europe (Desprat et al. 2003). This climatic variability, although weaker in amplitude than the shifts of the glacial cycles, has been large enough to have significant effects on lake ecosystems as indicated by the large fluctuations in hydrological conditions (Magny 1993, 2004). In addition, climate changes can trigger different processes and have varied patterns on a regional scale (Davies et al 2003; Magny et al. 2003). But, while vegetation response to climate changes through the Holocene are relatively well studied in Spain, their effects on aquatic environments have received much less attention. Compositional changes in the diatom remains found in sediment cores have been shown to represent a valuable indicator of past changes on lacustrine ecosystems and their catchment area (Prather and Hickman, 2000; Smol and Cumming, 2000). Observed variations of diatom-inferred pH with temperature (Psenner and Schmidt, 1992) represent a good example of how climate change indirectly affects diatom communities (Fritz, 1996).

The major aim of this study has been to examine which environmental factors are responsible for the observed changes in diatom communities and providing information on lake history in relation to palaeoenvironmental changes in the catchment during the Holocene. Most of the pollen records studied in Spain have been collected from lakes, so that they reflect changes in the catchment vegetation of those lakes that can influence lake characteristics through the retention of nutrients in the accumulating catchment biomass (Prather and Hickman, 2000). Catchment vegetation history was first assessed using pollen records from the same lake (Maldonado Ruiz, 1994) and then diatom analyses were made to study the effect of vegetation dynamics and other changes on the aquatic ecosystem. pH is usually one of the most important parameters determining the diatom assemblage composition in freshwaters, and diatom-inferred pH reconstructions have been shown to be generally reliable (Birks et al. 1990; Birks, 1995). Furthermore, this information has been compared with other palaeoecological and palaeoclimatic data from surrounding areas in an attempt to present possible palaeolimnological inferences related to climate.

Site description

Lagoa Grande is located in the Serra de Queixa (Galicia, northwestern Iberian Peninsula) (UTM 29TPG4479) at an altitude of 1360 m a.s.l. (Figure 1). Serra de Queixa is an upland area in the southeast of Galicia (Figure 1) with a quite uniform morphology. The highest altitude is Cabeza de Manzaneda (1778 m a.s.l.) and the lowest is Baños de Molgas (500-600 m a.s.l.). Glacial deposits lie on the upper levels of the range (Pérez Alberti et al. 1993; Vidal Romaní and Santos, 1994). Geology of the area is characterized by schist, sandstone and Cambrian-Ordovician quartzite southwards, and by Hercinian granite northwards (IGME, 1981). The common upland soils are ranker and lithosols (Aira Rodríguez, 1986). Vegetation is a mixed forest dominated by *Betula pendula*, *Acer pseudoplatanus* and *Quercus pyrenaica*, with a ground cover of *Saxifraga spathularis*, *Holcus mollis*, *Doronicum carpetanum*, *Dryopteris expansa* and *Poa nemoralis*. *Erica arborea* is also common (Izco Sevillano, 1987).

Lagoa Grande is an elliptical, shallow basin formed during the last deglaciation, which began as early as 17 500 yr BP (Muñoz Sobrino et al. 2001). It has a small catchment area and is only drained by a small creek. The underlying geology is composed of granite and gneiss.

Currently, the lake measures nearly 100 m in length and has a surface area of 0.5 ha. Most of the surface of the lake is less than 0.5 m deep. These shallow areas provide a good habitat for both submerged and emergent macrophytes, which are abundant throughout the lake. The vegetation in the surroundings of the lake is dominated by heathland, with *Halimiun alyssoides* and *Chamaespartium tridentatum*. *Quercus pyrenaica* is also abundant and in the near-shore areas *Betula pendula* is present. *Salix atrocinera*, *Prunus avium* and *Frangula alnus* are also present. Current diatom communities are chracterised by acidophilous taxa such as *Eunotia*, *Cymbella* and *Pinnularia*, which are common in peatbogs and occurr in oligotrophic and dystrophic waters.

Climatic conditions are characterized by an average annual temperature below 8ºC. Summers are cool with monthly mean temperature below 15ºC. Precipitation is concentrated in autumn and winter, and it ranges from 800 mm yr^{-1} in the lower region, to more than 2000 mm yr^{-1} in the upland area (Carballeira et al. 1982).

Methods

A 630 cm long sediment core was taken in summer 1995 using a Russian corer (Jowsey, 1966) close to the centre of the lake. Coring was done continuously in 50 cm sections. The lithology was described using the Troels-Smith system (1955). Subsamples of 1 cm^3 were taken from the centre of the core for diatom and chrysophyte stomatocyst analyses at 10 cm intervals. The proportion of diatom frustules to chrysophyte cysts can be a useful index of trophic status in temperate lakes (Smol, 1985). Chrysophytes are generally associated with low total phytoplankton biomass and trophic status and oligotrophic phases in temperate lakes. Samples for diatom and total stomatocyst analyses were prepared according to Renberg (1990). Aliquots of evaporated suspensions were embedded in Naphrax (R.i. = 1.74). When possible, at least 500 diatom valves per sample were counted on random transects in the light microscope (Nikon Optiphot II) with phase-contrast oil immersion objectives at a magnification of x1000. At some levels, however, diatom preservation was very poor. Counting techniques followed Battarbee (1986). Diatom concentration was estimated using microsphere markers (Battarbee and Kneen, 1982). Taxonomic identifications were mainly based on Krammer and Lange-Bertalot (1986-1991). Critical identifications were confirmed using a scanning electron microscope (JEOL JSM-6400 SEM). Total stomatocysts were enumerated simultaneously with diatoms.

The absolute chronology used is based on radiocarbon dating of 2 bulk samples taken at 55cm and 285cm depth (Table 1). At 500 and 610 cm depth, dates were estimated through correlation of a pollen profile of the studied core (Santos, unpublished data) with the chronology obtained by Maldonado Ruiz (1994). Linear interpolation was used to develop the chronological model, assuming present day for the core top.

Diatom stratigraphic diagrams were drawn using the PSIMPOLL computer program (Bennett, 1992). The main zones of change in the diatom data were identified by classification; the method applied was binary splitting by information content, as implemented in the PSIMPOLL program. Square root transformation was used in order to optimise the signal to noise ratio. The "broken-stick" model was used to assess the significance of the diatom assemblage zones (Bennett, 1996).

Diatoms have often been used to reconstruct lake acidification in water quality studies (Battarbee et al. 1990). Although there are several published diatom-based transfer functions for reconstructing pH in Europe (e.g. Birks et al. 1990; Korsman and Birks, 1996; Juggins et al. 1996), none of these functions were derived from lakes located near the studied area. In this paper diatom-inferred pH was derived using EDDI software for palaeoenvironmental reconstructions (Juggins, 2001). Lake-water pH values were reconstructed using weighted averaging (WA) (Birks et al. 1990) with inverse de-shrinking because the reconstructed values lay closer to the mean of the training set values (Juggins, 2001). The reliability of each reconstructed pH value was assessed using the percentage of taxa in the fossil sample not present in the modern calibration dataset. Experiments with simulated data (Birks, 1998) suggest that a reconstruction with <25% of fossil taxa not found in the modern dataset is reliable. The diatom taxa present in the Lagoa Grande core are all common and well represented in the European combined pH training set.

Multivariate ordination techniques were performed using CANOCO (version 3.10) (ter Braak, 1988, 1990). To establish whether species responses were linear or unimodal, floristic variations in the diatom data were assessed using detrended correspondence analysis (DCA; ter Braak, 1987). Unimodal ordination analysis was used because the gradient on the first axis was longer than 2 standard deviation units (3.353). Therefore, DCA (Hill and Gauch, 1980), a unimodal technique ordination, was used to identify the main gradients in the species data. This technique assumes that any structure within the data is a response to changes in a few unknown environmental variables (latent variables). This method also maximizes species dispersion along a hypothetical environmental gradient (ter Braak, 1987). All taxa with more than 2% abundance in at least two samples were used in the statistical analyses (see species list and codes used in the ordination plot in Table 2).

Results

Core lithology and chronology

The sediment core is homogeneous in colour with no abrupt transitions. A detailed sediment lithology of the Lagoa Grande sequence is shown in Figures 2 and 3. The upper sediment is predominantly organic, while the lower part contains silt and clay. The estimated age for the bottom of the sequence is ca. 9850 yr BP indicating that the record spans nearly the entire Holocene period. The boundaries of the zones in years BP were estimated from these dates by linear interpolation.

Diatom and chrysophyte stomatocyst stratigraphy

Diatom remains are absent between 190 and 220 cm depth, and badly preserved in the most superficial sediments of Lagoa Grande. One hundred thirty-three diatom taxa, belonging to 17 different genera, were identified from the core material. The most significant features in the diatom stratigraphy are the high percentages of *Aulacoseira* species, particularly *Aulacoseira nygaardii*; the rise of *Aulacoseira valida* at 510 cm; and the dominance of *Aulacoseira tethera* between 130 and 60 cm. Another conspicuous feature is the peak in abundance of *Aulacoseira ambigua* and *Navicula* *leptostriata* between 450 and 260 cm. Eight diatom assemblage zones were distinguished using cluster analysis (Figure 2). A brief description of diatom assemblage zones is given in Table 3.

Inferred pH

The diatom-inferred pH value at the beginning of the profile is around 6 and increased slightly over zone GDE2 reaching values above 6 pH units (Figure 2). The inferred pH varies between 6 and 7 during zones GDE2 and GDE3. There is, however, a small drop below pH 6 at 450 cm. Diatom-inferred pH experiences small excursions along zone GDE4 and GDE5, but the overall pH value reconstructed for these zones keeps around 6. The lowest inferred pH values of the whole record occurs in the uppermost three zones, with a drop at the beginning of zone GDE7 to a value around 5 pH units.

Statistics

Indirect ordination, DCA detrended by segments, was used to analyze the species variation in Lagoa Grande core samples (Figure 4a, b). DCA axis 1 (λ_1=0.333; 29.5%) and DCA axis 2 (λ_2=0.160; 14.1%) explain a total of 43.6% of the variance in the diatom percentage data (Figure 4a). The underlying environmental variables are interpreted from the species distribution within the DCA first two axes (Figure 4b). The first axis represents a pH gradient, with increasing pH to the left. Species at the low end of the axis include alkaliphilous species such as *Aulacoseira valida*, *Aulacoseira ambigua*, and *Navicula atomus*. At the high end of the first axis *Eunotia diodon*, *Eunotia paludosa*, *Eunotia incisa* and *Cymbella hebridica* all typify acid conditions in the lake.

The second DCA axis is interpreted to represent nutrient levels. The higher scoring species for the second axis include *Aulacoseira lirata*, *Cymbella perpusilla*, *Aulacoseira alpigena* and *Aulacoseira distans*. These diatom species are associated with oligotrophic conditions. Species indicating eutrophic conditions such as *Aulacoseira ambigua* are located at the low end of the second axis. The first axis is inferred to indicate a pH gradient with the lowest values represented by high, positive scores and the highest pH values represented by negative scores. The inferred underlying gradient for DCA axis 2 is nutrient level with inferred increasing values to the left.

Discussion

Changes in the composition of the diatom community can be interpreted in terms of lake history, catchment processes and climate. The estimated basal date indicates that almost the whole Holocene was retrieved. A longer sedimentary record was expected because a previous work on the same lake reveals that environmental conditions at this site were favourable for sediment deposition to occur before 12 790 yr BP (Maldonado Ruiz, 1994). This palynological study provides useful information about the history of catchment vegetation during the Holocene to establish the linkage between aquatic and terrestrial systems (Figure 5).

Early Holocene: GDE1, GDE2 and GDE3 (9850-7200 yr BP; 11 300-8000 cal yr BP)

The basal sediments of the core represent the early Holocene period. The diatom assemblage in the bottom sediments was dominated by acidophilous *Aulacoseira* species (*A. lirata*, *A. alpigena*, *A. tethera*, *A. distans* and *A. nygaardii*), indicating slightly acidic, oligotrophic conditions in Lagoa Grande. *Aulacoseira* species have been considered as planktonic, facultative and opportunist (Willén, 1991). Siver and Kling (1997) noted that these taxa are abundant in waters with pH between 5 and 6, low specific conductivity and low nutrient concentration. Given that *Aulacoseira* species are poor competitors for silica, their growth is favoured during periods of low diatom production (Wolfe et al. 2000). The underlying gradients in the species data suggest low pH and nutrient-poor water. These diatom assemblages suggest cold climatic conditions (Wolfe and Härtling, 1996).

After 9100 yr BP the planktonic taxon *Aulacoseira ambigua* became abundant. *A. ambigua* is the dominant euplanktonic diatom in many shallow lakes (Gasse, 1986) and has been considered to be characteristic of relatively warm waters (Denys, 1991-1992). Therefore, its presence suggests increased water temperature. The increase in the abundance of planktonic species also suggests higher nutrient concentrations and pH. The scores on both DCA axis point to high pH and nutrient-rich water. Associated with the development of aquatic vegetation (Maldonado Ruiz, 1994), the appearance of *A. ambigua* likely reflected a climatic warming and improved conditions for the growth of planktonic diatoms.

At about 8200 yr BP shifts in the composition of diatom assemblages occurred concurrently with a drop in diatom concentrations, indicating low productivity in the lake. *Aulacoseira ambigua* declined and was replaced by *Aulacoseira valida*. *A. ambigua* is a species favoured by high light conditions, blooming in spring and early summer in many temperate lakes (Brugam, 1983). On the other hand, *A. valida* develops in low temperature environments (Denys, 1991-1992). This would suggest colder temperatures that would have supressed the development of euplanktonic *A. ambigua*. This event is also coincident with a drop in total pollen concentrations (Maldonado Ruiz, 1994). A drop in pollen concentrations could be related to shifts in sedimentation rate. However sedimentation rates calculated for this part of the core don't show an increase that could have result in low pollen concentration values. Therefore, although this drop cannot be unequivocally related to regional climatic change, overall evidences suggest colder conditions.

Other palaeoenvironmental studies in Iberia (Pons and Reille, 1988; Peñalba, 1994; Allen et al. 1996; Julià et al. 1997) have hypothesised a climatic deterioration during the Early Holocene between 8000 and 9000 yr BP throughout the whole Iberian Peninsula. Diatom and pollen data from Lagoa Lucenza, a site close to Lagoa Grande but in a different catchment, exhibit a similar cold fluctuation coinciding temporally with the event recorded in Lagoa Grande (Leira and Santos, 2002). A major change occurred in the North Atlantic Ocean dated at c. 8600 yr BP. Sea Surface Salinity (SSS) and Sea Surface Temperature (SST) have been reconstructed from a marine core off Portugal. A significant reduction in both salinity and temperature took place during the Early Holocene as a result of an important flux of freshwater into the northwestern ocean (Duplessy et al. 1992). This water influx would be sufficient to weaken the thermohaline circulation, resulting in a reduced heat transport and cold conditions over the North Atlantic and the European continent (Duplessy et al. 1992; Bond et al. 1997; Mayewski et al. 2004). This climate cooling event appears to be reflected in a marked hydromorphological change characterised by colder and drier conditions in southern Europe (Magny et al. 2003). A shorter growing season and/or a lengthening of the period of winter cold, would result in low diatom productivity and nutrients. However, planktonic species continue to be abundant suggesting that this cooling might not imply a significant change in moisture conditions.

Mid Holocene: GDE4 (7200-3600 yr BP; 8000-4100 cal yr BP)

After ca. 7300 yr BP *Aulacoseira valida* disappeared from the record just as *Aulacoseira ambigua* reappeared and became relatively abundant. This may reflect the transition to a warmer and humid climate, with an increase in limnetic nutrient concentrations. The peak of *Aulacoseira ambigua* suggests higher water levels likely in response to increased precipitation. This euplanktonic species is characteristic of eutrophic to mesoeutrophic lakes (Lepistö, 1990; Siver and Kling, 1997). The underlying environmental gradients inferred from the species data also suggest that nutrient status was high during most of the mid-Holocene. Milder conditions would enhance catchment processes, promoting leaching and nutrient availability. The increased nutrient availability stimulated the development of *Aulacoseira ambigua*. Climatic reconstructions based on pollen and palaeohydrological data indicate that during this period summer temperatures were warmer than today (Huntley and Prentice, 1988) along with wetter conditions (Harrison et al. 1996). Other palaeoenvironmental data for the northern Iberian Peninsula also suggest higher temperatures and more precipitation during the mid-Holocene (Ramil Rego et al. 1998; Sánchez Goñi and Hannon, 1999; Santos et al. 2000).

At ca. 6000 yr BP a number of high-altitude pollen records reflect a slight cooling of the climate (Maldonado Ruiz, 1994, Santos et al. 2000), which was also inferred based on astronomical calculations (Berger and Tricot, 1986). The ratio of chrysophyte cyst to diatom frustules was exceptionally high during this period, increasing up to 0.21 by 390 cm (ca. 6000 yr BP). In many temperate lakes chrysophytes are often less abundant following nutrient inputs and the ratio appears to follow these patterns (Siver, 1991). Thus, high chrysophyte cyst to diatom ratios can be used as an indicator of oligotrophic conditions in waterbodies (Smol, 1985). Furthermore, as a group, the chrysophytes have been reported to be more abundant at low temperatures (Siver, 1991). Inferred values from the pH model and the DCA sample scores on axis 1 indicated a drop in pH at 380 cm. Likewise, planktonic *Aulacoseira ambigua* declined by 400 cm, reflecting decreased productivity and possibly shallower conditions.

The benthic *Navicula leptostriata* also increased and fluctuated during this period. This species, primarily episammic, is considered acidophilous and indicative of oligomesotrophic waters with low total organic carbon (TOC) content (Anderson et al. 1986). But *N. leptostriata* peaks were not coincident with significant changes in DCA samples scores or in the abundance of *A. ambigua*. Furthermore, there were enough fluctuations and overlaps during this period to suggest an overall compatibility of these species that could have dominated during different parts of the growing seasons and therefore did not directly compete. These changes in diatom composition may be attributed to changes in catchment vegetation and soils that had caused variations in TOC content in the lake.

Late Holocene: GDE5, GDE6, GDE7 and GDE8 (3600-0 yr BP; 4100-0 cal yr BP)

After 4500 yr BP there was a general reduction in the arboreal cover in the north of the Iberian Peninsula (Watts, 1986; Turner and Hannon, 1988; Peñalba, 1989; Santos et al. 2000), which has been linked to the start of anthropogenic activity. It is, however, very difficult to distinguish between the effect of climate and that of human impact on vegetation. In addition, extensive deforestation could have concealed the effects of any climate change in the palaeorecord (Maldonado Ruiz, 1994). Furthermore, it has been suggested that agricultural activity did not reach the high altitude areas of the northwestern Iberian Peninsula until c. 1000 yr BP (Allen et al. 1996; Santos, 1996). Changes in the diatom assemblages spanning between 4200 and 3200 yr BP suggest lower lake depths and change in nutrient concentration because of the disappearance of *Aulacoseira ambigua*, although the dominance of *Aulacoseira nygaardii* is still indicative of acidic water and relatively deep lake conditions (Gasse and Van Campo, 1998). The drop in the inferred pH values between 300 and 250 cm was also due to the disappearance of *A. ambigua*. In the absence of any clear evidence of anthropogenic influence on the catchment area, these changes in the diatom assemblages may be considered consistent with an increasing duration of winter cold. This conclusion is supported by data from peatbogs in northern Galicia that suggest cold climatic conditions at about 4000 yr BP (Martínez-Cortizas et al. 1999). An area of the core is then encountered that is deficient in diatoms. Trophic and hydrological changes might have accounted for the low abundance and/or absence of diatom remains between 3200-2700 yr BP. In this part of the Lagoa Grande core, diatom assemblages appear to record a change in the lake trophic status with increases in oligotrophic taxa, indicating a decrease in nutrients and productivity.

At the beginning of 2600 yr BP the diatom record underwent another major change. Epiphytic acidophilous taxa (*Eunotia serra* and *Tabellaria flocculosa*) dominated the Lagoa Grande record. The underlying nutrient gradient along DCA axis 2 increased during this event. As such, a decrease in nutrients could be expected along with natural acidification. The high values of the chrysophyte cyst to diatom ratio during this event also suggest nutrient-poor conditions. These data coincide with a northern European cooling event traditionally known as the Subatlantic period recently documented in southern Europe (Desprat et al. 2003). The diatom assemblages indicated a progressive shallowing and low pH. These changes in diatom assemblages might be indirectly related to climate but probably directly related to changes in the nutrient level conditions due to peat development on the catchment. Peat accumulation began as early as ca. 3000 yr BP in the Lagoa Grande site (Maldonado Ruiz, 1994). Peatland development has been reported to be a cause for natural acidification of lakes (Prather and Hickman, 2000). Hence, low pH would be expected due to the decomposition of littoral vegetation and the production of humic acids. These changes are likely to reflect local factors such as the lake-level lowering due to sediment inputs and the development of littoral vegetation, and not only change in the regional climate characterised by an atmospheric climate cooling.

After 2000 yr BP *Aulacoseira tethera* became very abundant along with periphytic assemblages. *Aulacoseira tethera* is a facultative planktonic diatom indicative of oligotrophic conditions, and has been reported from waters with pH values ranging between 4.4 and 5.3 in upland lakes of Cumbria (United Kingdom) (Haworth et al. 1986). This diatom assemblage indicates shallow water, but with enough open water habitats for seasonal phytoplankton development. Relatively high lake levels are indicated by pulses of *Aulacoseira tethera*, while dry seasonal episodes are indicated by assemblages dominated by *Eunotia* spp. These episodes are probably related to the filling of the lake basin and the seasonality of the water level. Simultaneous high values of Cyperaceae pollen (Maldonado Ruiz, 1994) probably also relate to fluctuating lake levels that made suitable habitats for littoral vegetation during the dry season.

The most recent part of the record is characterized by low concentrations and poor diatom preservation. Epiphytic and acidophilous taxa such as *Eunotia*, *Cymbella* and *Pinnularia* are more abundant. These species are common in peatbogs and occurr in oligotrophic and dystrophic waters (Krammer and Lange-Bertalot, 1986-1991). This suggests that modern conditions have existed since ca. 1000 yr BP in Lagoa Grande. The chrysophyte cyst to diatom ratio is high during this zone, although this also may be related to the better preservation of these more heavily silicified algal remains.

Conclusions

The diatom record presented here can be directly correlated with pollen derived climate changes, and therefore it is possible to draw the following conclusions concerning the response of the lake to climatic changes.

The diatom record suggests that the lake was originally acidic and oligotrophic due to cold climatic conditions. *Aulacoseira ambigua* increase indicates periods of high water levels and increased productivity in response to a warmer and more humid climate. Milder conditions would enhance catchment processes, promoting leaching and nutrient availability.

Changes in diatom assemblages during the Holocene indicate fluctuating limnological conditions. These oscillations in Lagoa Grande record have been dated at ca. 8200, 6000, 4200 and 2600 yr BP. At these times diatom assemblages reflect fairly low lake productivity and cold water. Similar events within the Holocene have been observed in pollen profiles from the region, but there is no chronological coincidence in all sequences. (Allen et al. 1996; Sánchez Goñi 1999; Sánchez Goñi and Hannon, 1999).

At Lagoa Grande the changes in the diatom record were contemporaneous with the shifts in vegetation communities, indicating that external forcing factors initiated these changes. These external factors may be local catchment processes or regional climatic cooling. Catchment processes have influenced Lagoa Grande over most of the Holocene, but only during the Late Holcene catchment changes played a controlling role in the lake development and concealed the effects of climate. Despite that, at present it is not possible to exclude rigorously the influence of local catchment processes as an explanation of these oscillations in lake history.

Acknowledgements

The lake sedimentary core was taken by J.R. Vidal, L. Santos and M.L. Caeiro. I thank R. Bao and L. Santos for helpful discussions and comments on the manuscript. Radiocarbon dates on the sediment samples were provided by Beta Analytic Inc. Miami (Florida) and funded by R. Bao. The Electron Microscopy Service of the

University of A Coruña provided facilities and technical help. This paper profited from the reviews by M.F. Sánchez Goñi and H.J.B. Birks.

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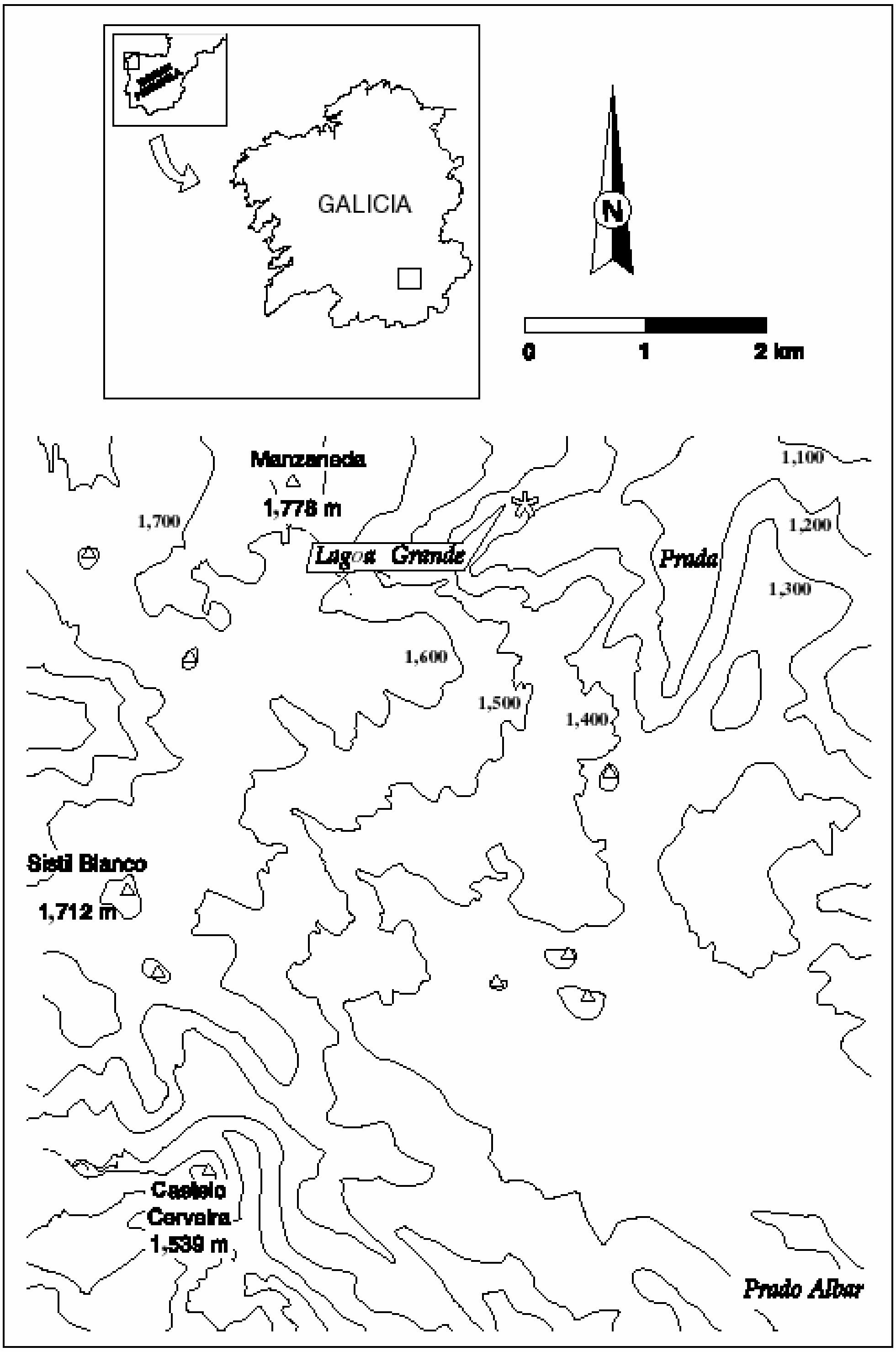
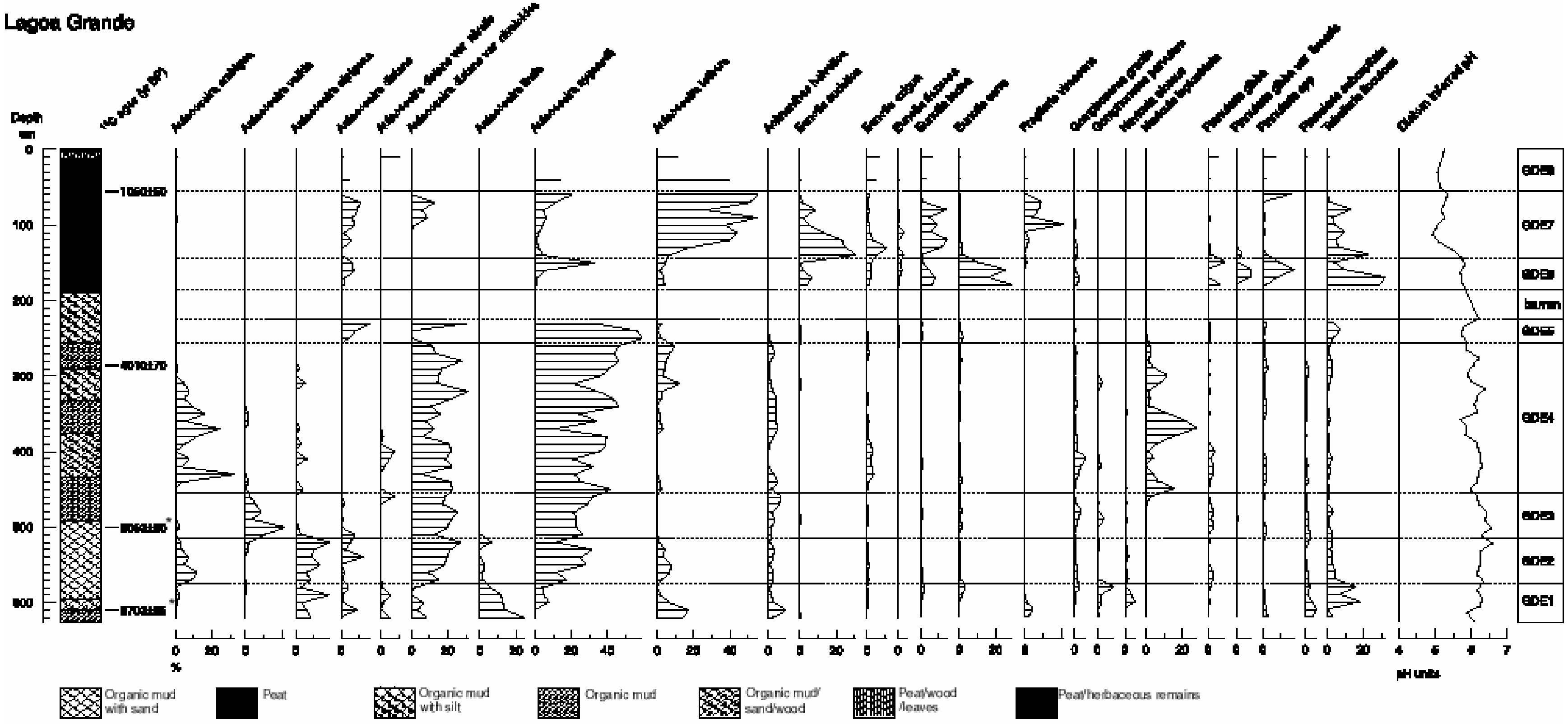
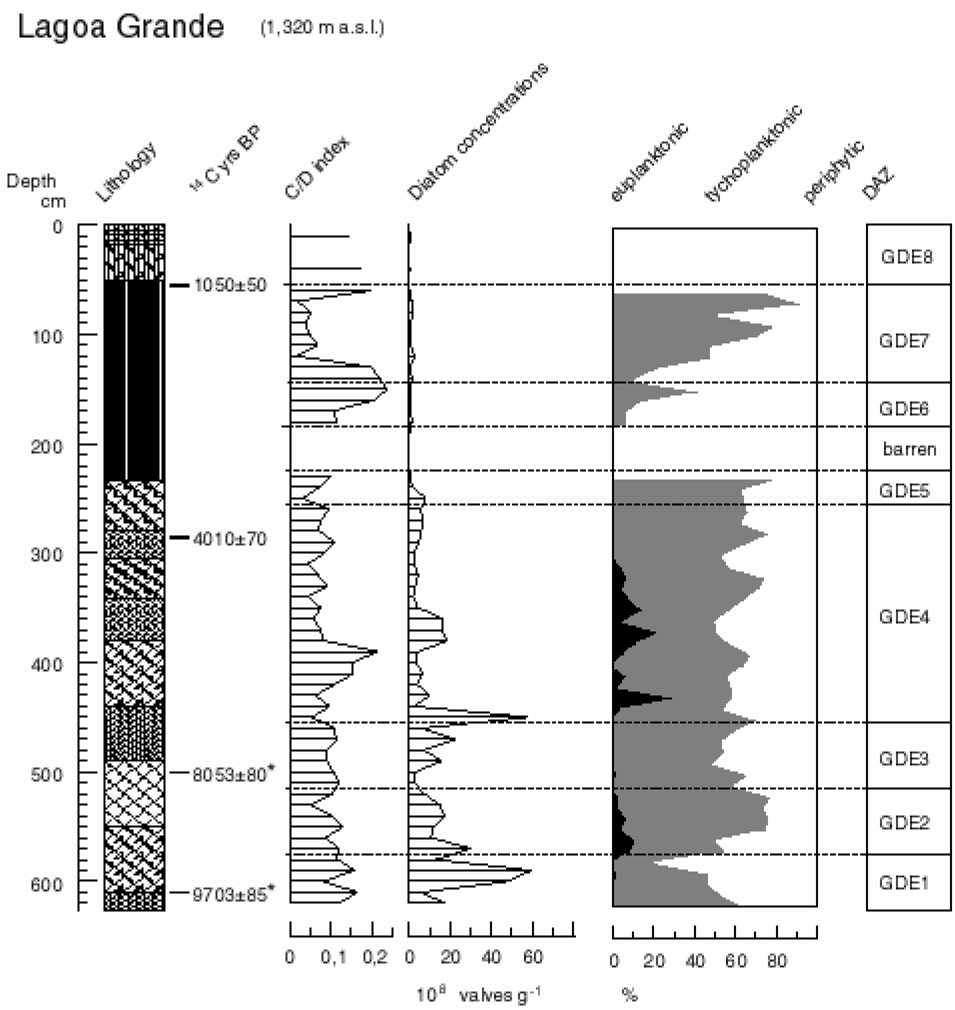
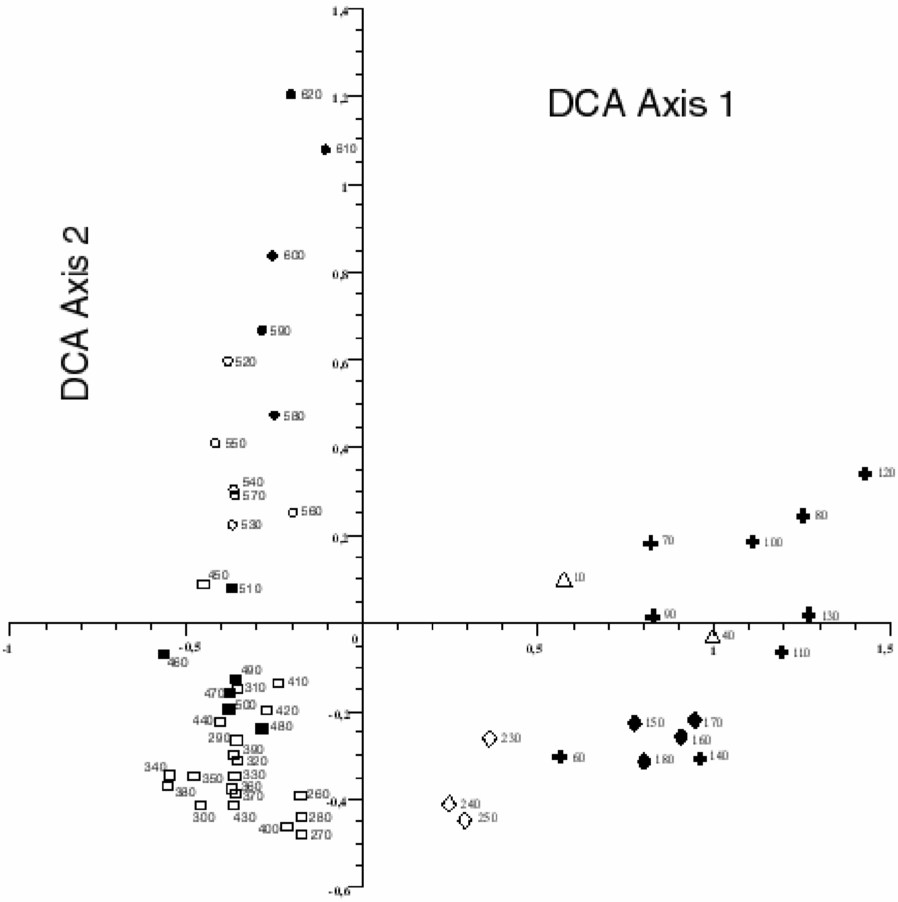

GALICIA
N
0
1
2 km
Manzaneda
1,778 m
1,700
Lagoa Grande
Prada
1,100
1,200
1,300
1,600
1,500
1,400
Sistil Blanco
1,712 m
Castelo
Cerveira
1,539 m
Prado Albar


Lagoa Grande
Depth
cm
0
100
200
300
400
500
600
%
Diatom inferred pH
pH units
GDE8
GDE7
GDE6
barren
GDE5
GDE4
GDE3
GDE2
GDE1
Organic mud with sand
Peat
Organic mud with silt
Organic mud
Organic mud/ sand/wood
Peat/wood /leaves
Peat/herbaceous remains


Lagoa Grande
(1,320 m a.s.l.)
Depth cm
Lithology
^{14}C yrs BP
C/D index
Diatom concentrations
euplanktonic
tychoplanktonic
periphytic
DAZ
0
100
200
300
400
500
600
1050±50
4010±70
8053±80*
9703±85*
GDE8
GDE7
GDE6
barren
GDE5
GDE4
GDE3
GDE2
GDE1
0
0,1
0,2
0
20
40
60
10^8 valves g^{-1}
0
20
40
60
80
%

Leira, 1998

a)


DCA Axis 1
DCA Axis 2
1,4
1,2
1
0,8
0,6
0,4
0,2
0
-0,2
-0,4
-0,6
-1
-0,5
0,5
1
1,5
620
610
600
590
520
580
550
540
570
560
530
450
510
120
80
70
100
10
90
130
40
110
460
490
410
470
310
500
420
440
480
290
390
320
340
350
330
360
370
380
300
430
260
280
400
270
230
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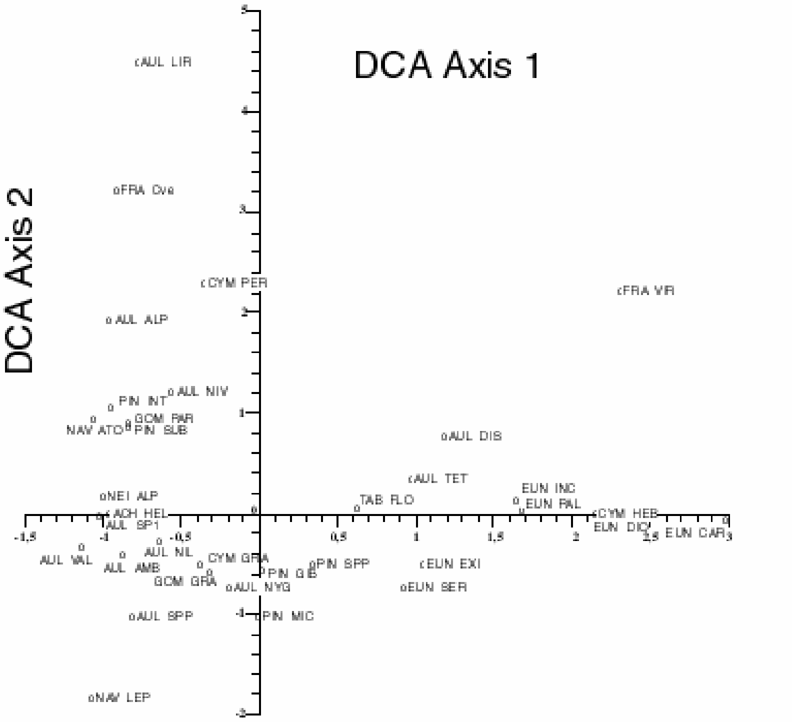
250
150
170
160
180
140
60

b)


DCA Axis 1
DCA Axis 2
5
4
3
2
1
0
-1
-2
-1,5
-1
-0,5
0,5
1
1,5
2
2,5
3
AUL LIR
FRA Ove
CYM PER
FRA VIR
AUL ALP
AUL NIV
PIN INT
GOM PAR
NAV ATO
PIN SUB
AUL DIS
AUL TET
EUN INC
TAB FLO
EUN PAL
NEI ALP
ACH HEL
CYM HEB
AUL SP1
EUN DIO
EUN CAR
AUL NIL
AUL VAL
AUL AMB
CYM GRA
PIN GIB
PIN SPP
EUN EXI
GOM GRA
AUL NYG
EUN SER
AUL SPP
PIN MIC
NAV LEP

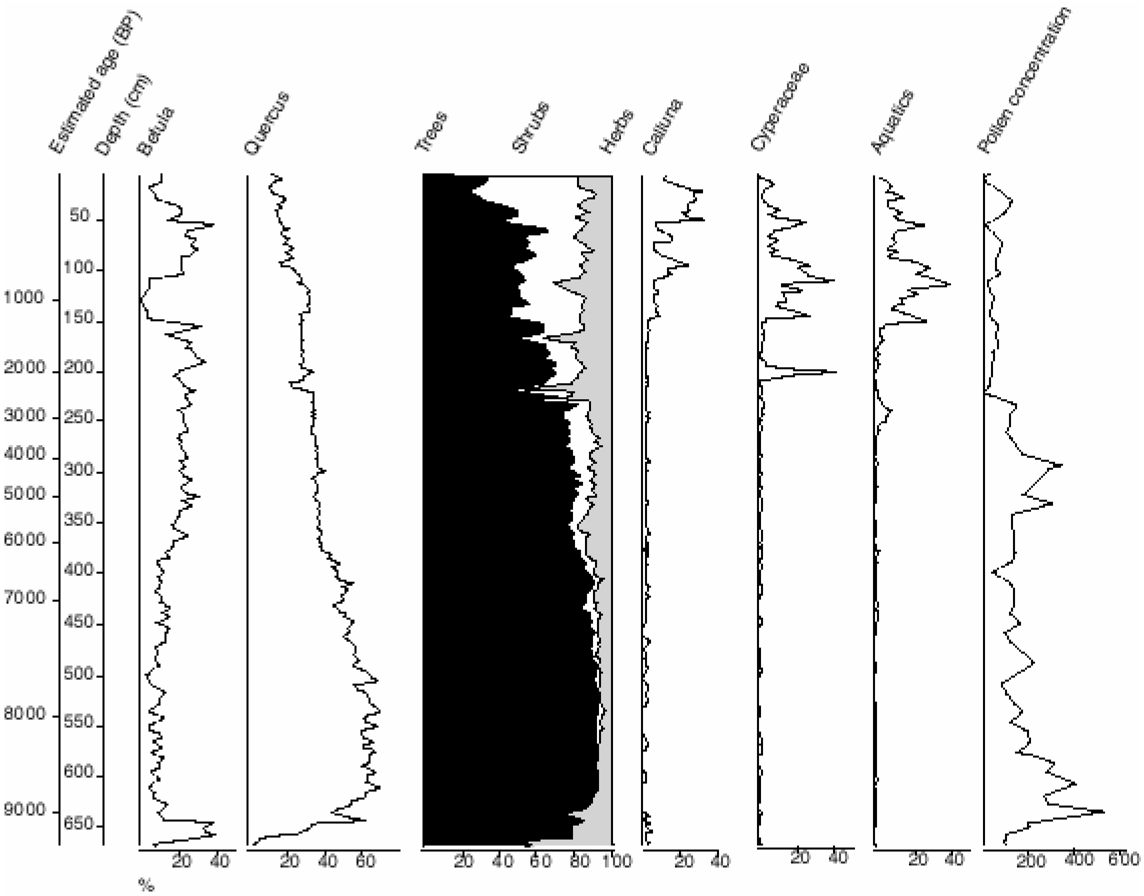

Estimated age (BP)
Depth (cm)
Betula
Quercus
Trees
Shrubs
Herbs
Calluna
Cyperaceae
Aquatics
Pollen concentration
1000
2000
3000
4000
5000
6000
7000
8000
9000
50
100
150
200
250
300
350
400
450
500
550
600
650
20
40
60
80
100
200
400
600
%

FIGURE CAPTIONS

Figure 1.- Map of Spain showing the geographical position of the Serra de Queixa. The detailed map shows the location of Lagoa Grande sequence and its catchment.

Figure 2.- Diatom summary diagram of the core from Lagoa Grande. Only selected taxa are shown (taxa>2%) along with a plot showing the diatom-inferred pH. Diatom assemblages zones (DAZ) and lithology are also shown. Asterites indicate the ages attributed by correlation with another core analysed by Maldonado Ruiz (1994).

Figure 3.- Diatom concentrations expressed as total number of diatom valves per gram of sediment and stomatocyst to diatom ratio (C/D). Percentage of euplanktonic, tychoplanktonic and benthic taxa in Lagoa Grande core are also shown. Asterites indicate the ages attributed by correlation with another core analysed by Maldonado Ruiz (1994).

Figure 4.- Plot of the DCA scores for the first two ordination axis for Lagoa Grande record samples. The samples of the different diatom assemblages zones are indicated with different symbols (GDE1 ●, GDE2 ○, GDE3 ■, GDE4 □, GDE5 ◇, GDE6 ◆, GDE7 ✚, GDE8 △) (a).Plot of the DCA scores for the first two ordination axes for the Lagoa Grande record species. Corresponding taxa names are given in Table 2 (b).

Figure 5.- Summarised Holocene pollen diagram from Lagoa Grande (Laguna de Las Lamas) of Maldonado Ruiz (1994), redrawn.

Table 1.- Radiocarbon dates from the Lagoa Grande sequence. The calibrated age range (Stuiver & Reimer, 1993) was calculated with a probability of 95.4% (two sigma).

Depth (cm)	Laboratory reference	Years ^{14}C (BP)	Years cal. (BP)	Years cal. AD(+) BC (-)	δ13 C (‰)
55-56	ß-134913	1050±50	1060-910	890, 1040	-26.1
285-286	ß-134914	4010±70	4640-4280	-2690, -2330	-24.7

Table 2.- Diatom taxa used in the statistical analysis and the corresponding codes used in the ordination plot.

Code	Species Name
ACH HEL	*Achnanthes helvetica* (Hustedt) Lange-Bertalot
AUL ALP	*Aulacoseira alpigena* (Grunow) Krammer
AUL AMB	*Aulacoseira ambigua* (Grunow) Simonsen
AUL DIS	*Aulacoseira distans* (Ehrenberg) Simonsen
AUL LIR	*Aulacoseira lirata* (Ehrenberg) Ross
AUL NIL	*Aulacoseira distans* var. *nivalis* (W. Smith) Haworth
AUL NIV	*Aulacoseira distans* var. *nivaloides* Camburn
AUL NYG	*Aulacoseira nygaardii* Camburn
AUL SP1	*Aulacoseira* sp 1
AUL SPP	*Aulacoseira* spp.
AUL TET	*Aulacoseira tethera* Haworth
AUL VAL	*Aulacoseira valida* (Grunow) Krammer
CYM GRA	*Cymbella gracilis* (Ehrenberg) Kützing
CYM HEB	*Cymbella hebridica* (Grunow) Cleve
CYM PER	*Cymbella perpusilla* var. *striator* (Kalbe) Krammer
EUN CAR	*Eunotia carolina* Patrick
EUN DIO	*Eunotia diodon* Ehrenberg
EUN EXI	*Eunotia exigua* (Brébisson) Rabenhorst
EUN INC	*Eunotia incisa* Gregory
EUN PAL	*Eunotia paludosa* Grunow
EUN SER	*Eunotia serra* Ehrenberg
FRA COv	*Fragilaria construens* f. *venter* (Ehrenberg) Hustedt
FRA VIR	*Fragilaria virescens* Ralfs
GOM GRA	*Gomphonema gracile* Ehrenberg
GOM PAR	*Gomphonema parvulum* (Kützing) Kützing
NAV ATO	*Navicula atomus* (Kützing) Grunow
NAV LEP	*Navicula leptostriata* Jørgensen
NEI ALP	*Neidium alpinum* Hustedt
PIN GIB	*Pinnularia gibba* Ehrenberg
PIN INT	*Pinnularia interrupta* W. Smith
PIN MIC	*Pinnularia microstauron* (Ehrenberg) Cleve
PIN SPP	*Pinnularia* spp
PIN SUB	*Pinnularia subcapitata* Gregory
TAB FLO	*Tabellaria flocculosa* (Roth) Kützing

Table 3.- Description of the local diatom assemblage zones in Lagoa Grande.

DAZ	Depth (cm) Age (yr BP)/(cal yr BP)	Description
GD1	*620-575* *9850- 9200* *11300-10450*	The first three zones represent the early Holocene. Diatom concentration is relatively low in the beginning (0.56 x 10^9 valves g^{-1} of dry matter) although it increases rapidly. Small acidophilous tychoplanktonic *Aulacoseira* including *A. lirata* (24%) *A. alpigena* (18%) *A. tethera* (17%) *A. distans* (9%) and *A. nygaardii* (8%) dominate the assemblage. The mesotrophic acidophilous taxon *Tabellaria flocculosa* is also well represented in this initial flora with an abundance of 16%. The chrysophyte cyst to diatom frustule (C/D) ratio ranges from 0.08 to 0.16.
GDE2	*575-515* *9200- 8300* *10450-9250*	Facultative planktonic species continue to dominate. *Aulacoseira nygaardii* and *Aulacoseria distans* var. *nivaloides* account for 50% of the assemblage at 530 cm depth. The euplanktonic *Aulacoseira ambigua* became more abundant (12%). This mesotrophic alkaliphilous species is the only euplanktonic taxon observed throughout the record. Diatom concentrations decrease sharply down to 0.7 x 10^9 valves g^{-1}.
GDE3	*515-455* *8300-7200* *9250-8000*	*Aulacoseira distans* var. *nivaloides* and *Aulacoseira nygaardii* continue to dominate the assemblage. There is significant change in the diatom flora with the decline of *Aulacoseira ambigua* which disappears while *Aulacoseira valida* increases up to 21% at 500 cm. Diatom concentrations drop to 0.2 x 10^9 valves g^{-1} at the beginning of this zone and increase again towards the end. The cyst to diatom ratio remains low and relatively constant ranging from 0.9 to 0.11.
GDE4	*455-255* *7200-3600* *8000-4100*	This zone represents the mid-Holocene period. It is defined by an increase of the euplanktonic *Aulacoseira ambigua*, and the decrease and disappearance of *Aulacoseira valida*. *Aulacoseira distans* var. *nivaloides* and *Aulacoseira nygaardii* remain the dominant species. The acidophilous and meso-oligotrophic species *Navicula leptostriata* is also abundant. After an initial increase at 450 cm depth (5.8 x 10^9 valves g^{-1}) diatom concentrations decrease coinciding with the highest sediment accumulation rate. The cyst to diatom ratio is fairly constant throughout this zone peaking at 390 cm (0.21).
GDE5	*255-225* *3600–3200* *4100-3650*	This zone represents the latter half of the mid-Holocene. Diatom abundances are very low. *Aulacoseira ambigua* has disappeared at the end of the previous zone and the benthic *Navicula leptostriata* decreases to less than 2% while the tychoplanktonic and oligomesotrophic *Aulacoseira nygaardii* increase to represent nearly 59% of the assemblage.
	225-185 *3200-2700* *3650-3050*	Diatoms are absent or too sparse too count.
GDE6	*185-145* *2700-2200* *3050-2400*	Diatom abundance and preservation is very poor. The chrysophyte cyst to diatom ratio increases from 0.11 to 0.24. It is characterized by a relatively high diversity of periphytic acidophilous taxa (*Eunotia* spp. *Cymbella* spp. and *Pinnularia* spp.) while tychoplanktonic species decreased to 7% at the start. Epiphytic *Tabellaria flocculosa* and *Eunotia serra* dominate the assemblages. At the end of this zone a peak of *Aulacoseira nygaardii* is also noticeable.
GDE7	*145-55* *2200-1000* *2400-1000*	The most abundant species is *Aulacoseira tethera* followed by *Eunotia carolina Tabellaria flocculosa* and *Fragilaria virescens*. *A. distans* var. *distans A. distans* var. *nivaloides* and *A. nygaardii* are also abundant in the uppermost part of this zone. Overall cyst to diatom ratio decreases.

GDE8	*55-0* *1000-0* *100-0*	Diatom concentration is the lowest of the whole record and diatom valves are badly preserved. The diatom flora is dominated by the acidophilous taxa *Eunotia* spp. *Cymbella* spp. and *Pinnularia* spp. The chrysophyte cyst to diatom valves ratio increases.