

Article

The Evolution of an Ancient Coastal Lake (Lerna, Peloponnese, Greece)

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Abstract: Degradation of coastal environments is an issue that many areas in Europe are facing. In the present work, an ancient coastal lake wetland is investigated, the so-called Lake Lerna in NE Peloponnese, Greece. The area hosted early agricultural populations of modern Greece that started modifying their environment as early as the early–middle Neolithic. Two drill cores in the area of the ancient lake were analysed to establish the sedimentological succession and the depositional environments using sub-fossil assemblages (molluscs and ostracods). Three lithological and faunal units were recovered, the latter being confirmed by the statistical ordination method (non-metric multidimensional scaling). The usage of sub-fossil mollusc species for the first time in the region enriched the dataset and contributed significantly to the delimitation of the faunas. These consist of environments characterised by various levels of humidity (from stagnant waters to freshwater lake) and salinity, with ephemeral intrusions of salt water to the lake, documented by mollusc and ostracod populations. We conclude that the lake and its included fauna and flora were mostly affected by climatic fluctuations rather than human intervention in the area.

Keywords: molluscs; palaeoenvironment; ostracods; Holocene; biodiversity; sedimentology

1. Introduction

Coastal ecosystems are important for human activities [1] because most of human activities are connected to the sea [2]. In the region of modern-day Greece, coastal areas started hosting permanent human settlements as early as the Holocene Climatic Optimum (6000–5000 BP) [3]. In this context, coastal lakes, disconnected from the sea by barriers, together with the relevant ecosystems became affected by human presence [4,5]. As such, coastal lakes and wetlands are pockets of high biodiversity and they often host endemic species [6]. In addition, they constitute environments where non-marine molluscs thrive, mainly freshwater and other gastropods that can live in lakes, bogs and swamps, and can be important environmental indicators [7].

The focus of this work is on the so-called Lake Lerna, present in the Gulf of Argos during part of the Holocene, a region which has been exploited by humans since the Neolithic [8]. The area has been studied in the past through several perspectives, such as the reconstruction of palaeoclimates and the development of agriculture [8–10] or the study of legends that took place in the region (namely the myth of Hercules and the Lernaean Hydra [3]). Ancient Lake Lerna formed at about 8630 ± 100 BP [4], covering the south-western part of the Argolis Plain up until recent years [4]. The latter work was the first to describe in detail the structure of the plain, based on sedimentological results and ostracod assemblages. Another aspect that has been analysed by [11] concerns environmental destruction caused by early inhabitants of the area. Recent works [12] identified the climate changes happening in the area during the past 5000 years.

Here, we aim to understand the evolution of Lake Lerna (Figure 1) to examine the possibility of a human impact on the lake in comparison to climate fluctuations. Through the stratigraphic, sedimentological and palaeobiological analysis of two subfossil-rich shallow drill cores, we investigate the palaeoenvironmental evolution of the lake, regarding the alternation of swamp and shallow lake and terrestrial depositional environments.

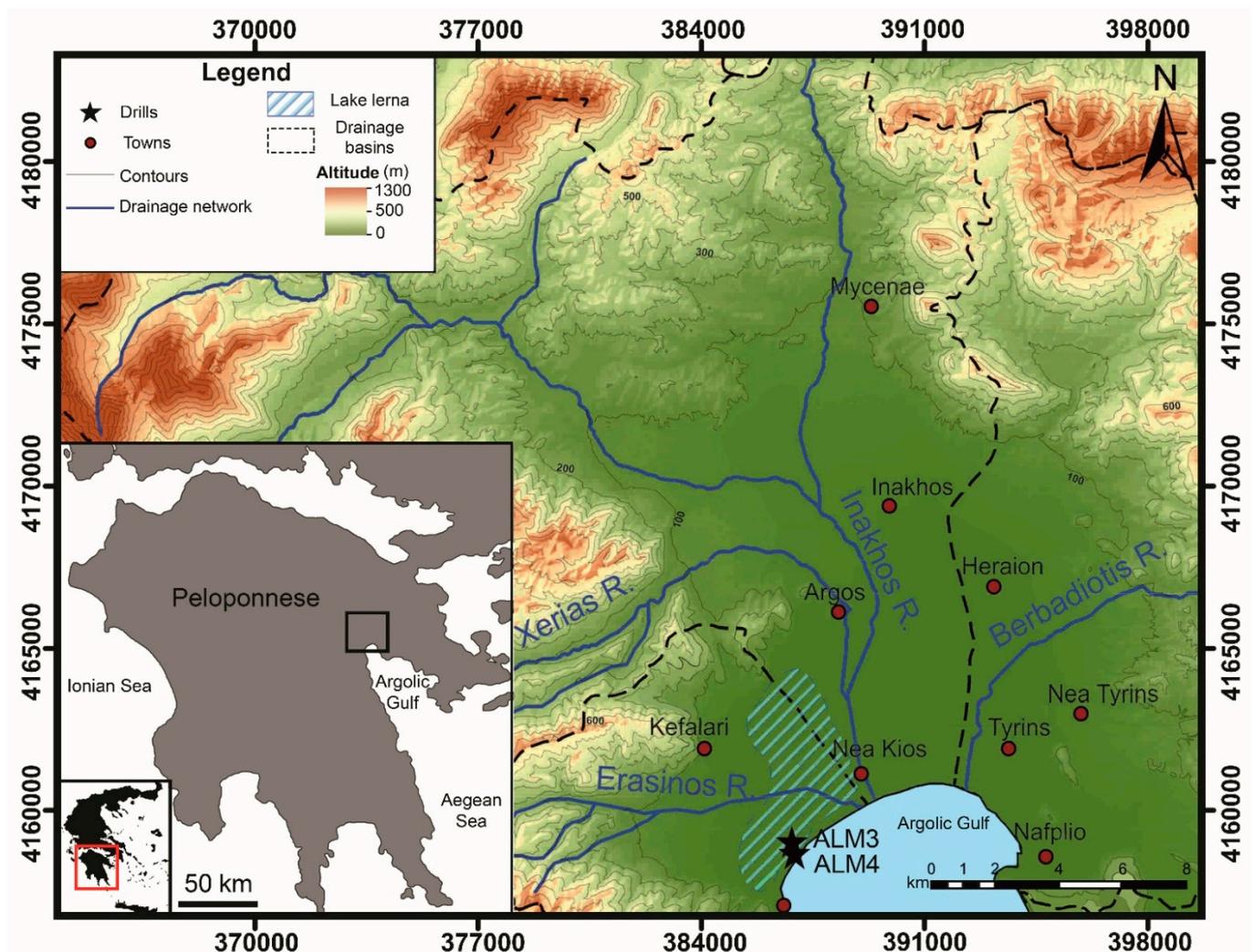


Figure 1. The study area, along with the main morphological structures and the sampling localities in the Argolis Plain, Peloponnese, Greece. Made with the geographical coordinate system: Greek Grid, EGSA 87.

Coastal environments are amongst the most disturbed by human activities, especially coastal lakes and wetlands, which are particularly affected by humans [13]. Furthermore,

non-marine molluscan faunas have faced a decline in diversity in recent years, as recorded in Europe [14]. The results of the present work contribute to the investigation of coastal environmental and ecological parameters that could potentially affect coastal wetland ecosystems of the past, present and future.

2. Geology and Geomorphology

The wider area of the Argive Plain has been of interest to both archaeologists and natural scientists for the past 50 years [15–23]. Geologists and geoarchaeologists have studied the area focusing on its geomorphological evolution both during the geological time and in prehistorical to historical times.

The Argive Plain consists of alpine formations that appear in its mountainous parts, as well as Upper Pliocene to Upper Pleistocene deposits found in low topographic areas around the Argos basin. The relatively modern Upper Pleistocene-Holocene deposits cover the low elevation and the coastal areas [24–27].

Tectonic action has shaped and still shapes the landscape in the wider area. The western margins of the Argolic Gulf and the Argive Plain are delimited by faults in the direction NW-SE to NW-NNE, in a staggered arrangement (Kiveri-Lerni-Kefalari). The eastern margins of the Argive Plain are also bordered by regular faults, direction NW-SE, which are intersected by faults with a main direction of NE-SW. The arrangement of the Upper Pliocene to Holocene deposits creates a main NW-SE direction of the ruptured structures in the area, with small deviations to the west and east. Regarding the geomorphology, the study area is surrounded by mountain ridges (from W-N-E), with the most important drainage basins being that of Inakhos and Xovriou, which are crossed by the homonymous rivers [28].

The drainage network of the wider area is dendritic and the flow is transient, with small or no runoff quantities most of the hydrological year. Inakhos is an important river, with the highest contribution to the study area. A characteristic landscape often found in the area consists of karstic, dissolving forms, in carbonate formations, seen as dolines and caves. Lake Lerna belongs to a large karstic system that was isolated at about 7000 years BP from the open sea by a beach barrier [4].

3. Materials and Methods

In order to reconstruct the palaeoenvironment, two shallow boreholes were made at the locality of the ancient Lake Lerna, in the area of Almyros, Argive Plain, Peloponnese, for the extraction of two cores: ALM3 (x: 386840.032, y: 4159040.203, 0.862 m.a.s.l.) and ALM4 (x: 386916.843, y: 4158686.257, 0.376 m.a.s.l.) (Figure 1). Sampling was carried out using a portable vibracoring sampler (Cobra) with a diameter of 50 mm, and the sediment was encased inside 1 m closed plastic tubes. The boreholes reached a depth of 400 cm (ALM3) and 398 cm (ALM4).

The cores were analysed at the Laboratory of Physical Geography, Faculty of Geology and Geoenvironment of the National and Kapodistrian University of Athens. The plastic tubes with the cores were split lengthwise, leaving the sediment sequence undisturbed. A stratigraphic analysis was accomplished by studying the sedimentary sequence through visual inspection. Photographs of the retrieved macrofauna were taken under a LEICA M165 C stereoscope, with a LEICA IC90 E camera.

To determine the cores' chronostratigraphy, five samples were prepared for accelerator mass spectrometry (AMS) radiocarbon dating on bulk sediment samples, some containing shell shards and peat. The dating was carried out at Centro di Datazione e Diagnostica dell'Università del Salento (CECAD), Lecce, Italy. The results of AMS dating were calibrated using standard materials supplied by IAEA (International Atomic Energy Agency) and NIST (National Institute of Standard and Technology) (Table 1). The "conventional radiocarbon age" was calculated with a $\delta^{13}\text{C}$ correction based on the $^{13}\text{C}/^{12}\text{C}$ ratio measured directly with the accelerator. For the estimation of the measurement uncertainty (standard deviation), both the radioisotope counting statistics and the scattering of the data have

been taken into account. The larger of the two is given as final error (see Table 1). As such, the values of the carbon stable isotopes fractionation term ($\delta^{13}\text{C}$) measured by AMS can differ from the natural fractionation and from those measured by IRMS. Moreover, due to the hard water effect or any inwash of detrital organic matter [12], the bulk samples containing low organic material but many shell shards yielded inaccurate dates and were not taken into account.

Table 1. Absolute ages of dated samples.

Sample	Age (BP)	$\delta^{13}\text{C}$ (‰)	Code	Core Depth	Bulk Sediment Colour
LTL19897A	3200 ± 45	11.3 ± 0.4	ALM3 1–2 3.8 α	154 ± 0.5 cm	Brown
LTL20303	1515 ± 45	27.1 ± 0.5	ALM3 190–193.5	190–193.5 cm	Brown-Grey
LTL19748A	5640 ± 45	26.9 ± 0.5	ALM3 2–3 88.5	288 ± 0.5 cm	Grey-Black
LTL20301A	596 ± 45	21.0 ± 0.5	ALM4 203–205	203–205 cm	Brown
LTL20302	4610 ± 45	28.8 ± 0.6	ALM4 328–330	328–330 cm	Black

The stratigraphy of the sedimentary material from the two cores was examined using sedimentological and micropalaeontological techniques. Samples were taken from each core every 7 cm. Parts of the cores that were deemed displaying a change in the sequence were sampled every 2 cm. Each sample (20 g dry-weight) was treated with H_2O_2 (30%) to remove the organic material and agglomerates. The samples were washed using six mesh sizes to separate gravel (>2 mm), sand subdivisions (1 mm, 500 μm , 250 μm , 125 μm , 63 μm) and silt/clay particles (<63 μm). The samples were then dried in an oven at 80 °C.

The acquired data from sieving were used to provide evidence about the depositional environment. The sediments are characterised following Folk and Ward [29]. Sediment texture determination, transport processes and deposition environment were classified using the software GRADISTAT statistical package [30]. The software calculated the sediment distribution and particle size statistics (mean size (Mz), sorting (σ), skewness (Sk), kurtosis (Ku)) using alternative equations expressing values in ϕ units [29]. The GRADISTAT analysis produces triangular diagrams showing the relative proportion of sand, silt and clay (Figures S1–S8). From the values of one parameter or the combination of many, the depositional environments are determined, and transport and deposition mechanisms are interpreted. Mean size Mz represents the size of the granules of which sediment is composed (fine-grained or coarse-grained), and the type of energy that caused the transport (i.e., water, ice or wind). Grain concentration is measured by σ of the sample around its mean. High σ values mean that the classification in terms of grain size is poor, i.e., during the transport and deposition of the sediment, a limited sorting of its grains took place. Small σ values mean good gradation and therefore good classifications, i.e., the grains of the sediment have been well sorted from the means of transport and storage. The parameter Sk refers to the presence of coarser or finer grains. Curves with excess fine-grained material have a positive value, while those with excess coarse-grained material have negative values. The Ku parameter is a quantitative expression used to describe the deviation from normality. In other words, it measures the ratio between the gradation in the tail of the curve and the gradation in its central part. They are divided into leptokurtic, mesokurtic and platykurtic. Leptokurtic distribution corresponds to a large concentration of grains close to the mean, mesokurtic distribution refers to a normal grain distribution around the mean and platykurtic distribution refers to a large dispersion of grain distribution relative to the mean [31].

All samples were prepared for palaeoenvironmental analyses; molluscs (gastropods and bivalves), ostracods, charophytes and pollen were used for palaeoenvironmental reconstructions. For taxonomic analysis, recovered specimens were separated into morphospecies and were identified to the lowest taxonomic level possible. Selected specimens were photographed under the stereoscope. With an aim of visualising groupings of the data, we performed a non-metric multidimensional scaling (NMDS) using the Bray–Curtis

dissimilarity index. All analyses were carried out in RStudio version 3.5.2 and Vegan package 2.5-4, and stratigraphic plots were made with package rioja version 0.9-26. Relative abundances were used for each species in percentages for all stratigraphic plots.

Palynological samples were prepared using standard procedures. Palynomorphs were investigated by extraction with wet sieving through 125 μm and ultrasonic 10 μm mesh sieves. Briefly, samples were treated according to the following procedure: sediment samples underwent carbonate and silicate removal with 10% HCl, they then were decanted three times and 30% HF, neutralised with KOH (10%) and subsequently washed with deionised water and sieved over a precision sieve with 10 μm pore size. Finally, one *Lycopodium* spore tablet was added to each sample to ensure estimation of the absolute abundances and reliability of quantitative data. The residues were mounted in glycerine gel on microscope slides for analysis under a binocular NIKON transmission microscope, and one or two slides of each processed sample were analysed.

4. Results

4.1. Radiocarbon Dating

The results of the radiocarbon dating are presented in Table 1. The ages of the samples vary considerably, most likely due to the hard water effect or any inwash of detrital organic matter [12]. Due to the presence of molluscs along the cores, we are hesitant to take into account most of our dated samples, except the sample LTL20302 (Table 1), which has enough plant remains (seen as a black-coloured layer) to produce a clearer result (see discussion of [12] for details).

4.2. Cores' Lithostratigraphy

Based on the analysis of both cores, four units of depositional environments were distinguished (units A to D). Combined results of lithostratigraphy, biostratigraphy and dating were acquired from both ALM3 and ALM4 cores. Each sedimentological unit (SU) is described starting at the bottom of each core, following the deposition sequence (Figure 2).

4.2.1. Fluvial Deposits—Sedimentological Unit A (SUA)

Sedimentological Unit A corresponds to the base of the ALM3 core and ranges from 400 cm to 350 cm. It is characterised by brown-grey, slightly gravelly mud sediment (Figure 2); the gravelly fraction represents 3%, the sandy one 7% and the silt/clay 90%. The sediments were characterised as slightly gravelly mud with unimodal distribution, and are moderately well sorted.

The sediment sorting ranges from 0.45ϕ to 0.7ϕ , and is classified as moderately well sorted. Skewness (Sk) values range from -0.24ϕ to -0.36ϕ , defined as negative to very negative asymmetry. Kurtosis (Ku) values range from 1.4ϕ to 2.7ϕ and are classified as leptokurtic to very leptokurtic (Figure S1).

4.2.2. Shallow Lake Swamp Deposits—Sedimentological Unit B (SUB)

This unit covers the largest parts of both ALM3 and ALM4. Characterised by grey and dark brown sediments, with very fine granulometry (silt/clay almost 95%), it is rich in molluscs and organic material. Furthermore, SUB is divided into two sub-units, B1 and B2, with a smooth transition between the two. SUB1 is dominated by grey clay/sandy clay sediments rich in organic material, shells and includes layers of peat and gyttja. A whitish-grey layer of ash was observed at 290 cm SUB2 and is characterised mostly by brown sandy clay (silt/clay 90% and sand 10%).

More specifically, in core ALM3, SUB1 ranges from 350 cm to 250 cm. In this organic-rich, one-meter thick sedimentary sequence, two peat layers were present at 292–290 cm (sample ALM 3-21) and 275–273 cm (sample ALM 3-18) depth. Additionally, at 290–287 cm (sample ALM 3-20), a clay layer, rich in white-grey ash, was observed. Most of the sediments in SUB1 were characterised as slightly gravelly mud to mud [30], with a unimodal distribution, and are well to very well sorted, except for the sample at 275–273 cm depth,

which was characterised as sandy mud [30] with a unimodal distribution, and is well to moderately well sorted. SUB2 (250 cm to 180 cm) is characterised by slightly sandy clay sediments, and organic material, such as the peaty layers of B1, are absent. SUB2 is characterised as slightly gravelly mud to sandy mud [30] with a unimodal distribution and is well to moderately sorted.

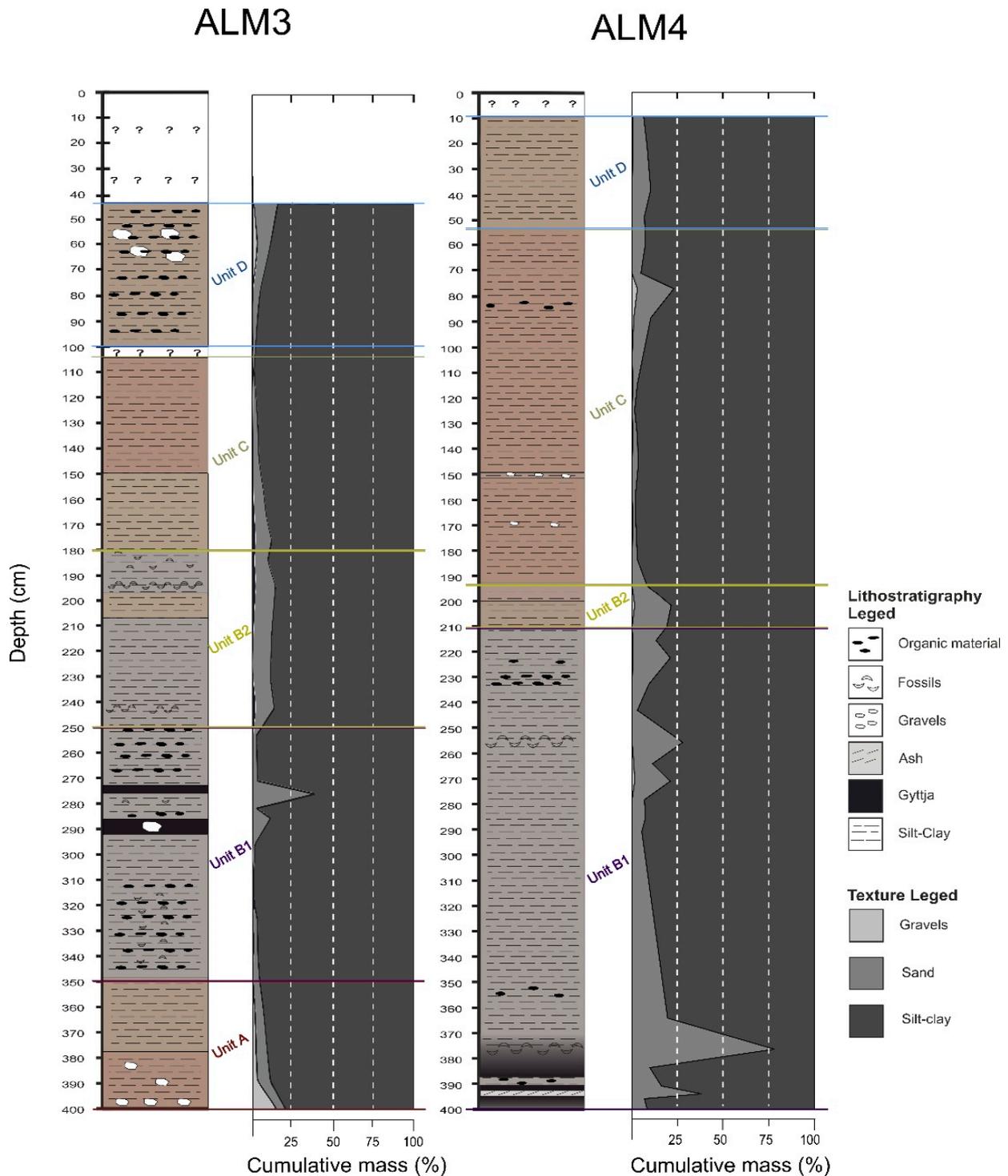


Figure 2. Cores ALM3 and ALM4 lithostratigraphy along with the corresponding sediment texture graphs. The sedimentological units are indicated on each core. The question marks (?) are indicative of disturbed material during coring.

The sediment sorting ranges from 0.3ϕ to 0.86ϕ , classified as very well to moderately sorted. Skewness (Sk) values are from -0.38ϕ to 0ϕ , which vary from very negative to almost normal asymmetry. Kurtosis (Ku) values range from 0.74ϕ to 3.16ϕ , and most of the sediments at sub-unit B1 are classified as platykurtic and as very platykurtic at SUB2 (Figures S1–S3).

In core ALM4, SUB1 was identified between 400 cm and 210 cm. Peat deposits were found at depths of 398–395 cm (sample ALM 4-36) and 385–370 cm (sample ALM 4-31, 32), with a gyttja layer occurring at 392–390 cm (sample ALM 4-34). A light grey material which corresponds to burned organic material (ash) was observed between the gyttja and the lower peat deposit at 395–392 cm (sample ALM 4-35). Further organic material and layers of shells were observed at depths 360–350 cm (sample ALM 4-30), 295–286 cm (sample ALM 4-29, 28), 255 cm (sample ALM 4-24), 245 cm (sample ALM 4-23) and 233–225 cm (sample ALM 4-22, 21). In core ALM4, the sediments of SUB1 are characterised as slightly gravelly sandy mud to mud with a unimodal distribution, and are poorly to very well sorted. Sub-unit B2 ranges from 210 cm to 193 cm depth. This unit is characterised by the smooth transition of the sediment from grey sandy/silty clay to grey-brown silty clay, with the absence of any organic material. Sub-unit B2 is characterised as slightly gravelly sandy mud to mud, with a unimodal distribution, and is well to moderately sorted.

The sediment sorting ranges from 0.3ϕ to 0.84ϕ , which is considered as very well sorted to moderately sorted, except for the samples at the depths of 391, 374, 362, 272 and 257 cm, which are characterised as poorly sorted. Skewness (Sk) values range from -0.7ϕ to 0ϕ , varying from very negative to almost normal asymmetry. Kurtosis (Ku) values range from 0.74ϕ to 3ϕ and most of the sediments of SUB1 and B2 are classified as very leptokurtic, with a few as platykurtic (Figures S5–S7).

Overall, SUB points to a shallow lake swamp depositional environment.

4.2.3. Lake Deposits—Sedimentological Unit C (SUC)

Next in the stratigraphic sequence, SUC consists of grey-brown to brown sandy/silty clays, with some gravel.

In core ALM3, SUC is found between depths of 180 cm and 102 cm. For the first 30 cm, the material consists of grey-brown clay, with a mean percentage of 92% silt/clays and 8% sands. There is a change in colour at 150 cm to brown silty clay, with mean values of silt/clays at 97.5% and sands as low as 2.5%. Granulometric data of SUC are characterised as slightly gravelly mud to mud with a unimodal distribution, and are moderately to very well sorted (Figures S3 and S4).

The same unit is also observed in core ALM4, from 193 cm to 53 cm depth. The dominant material is a brown mud, with a silt/clay value of 98%. Gravels were found occasionally at depths of 170 cm and 150 cm, while brown sandy mud (silt/clays 93% and sands 7%) with layers of organic material was observed from 110 cm up to 53 cm. Granulometric analysis shows that the sediments are characterised as slightly gravelly mud to mud, with mud predominating.

Most values of the statistical parameters of granulometry, as far as sorting is concerned, range from 0.3ϕ to 0.7ϕ , characterised as moderately well to very well sorted, except one sample at 84 cm depth of ALM 4, which was characterised as poorly sorted ($\sigma = 1.39\phi$). Most of the skewness (Sk) values range from -0.3ϕ to 0ϕ , varying from negative to almost normal asymmetry, except one sample at 84 cm depth of ALM 4, which is characterised as very negative asymmetry (Sk = -0.71ϕ). Kurtosis (Ku) values range from 0.74ϕ to 3.5ϕ ; most of the sediments are classified as platykurtic while the others are classified as very leptokurtic (Figures S7 and S8).

4.2.4. Anthropogenic Deposits—Sedimentological Unit D (SUD)

The last unit of the Almyros cores contains brown-grey silty clays, with the dominating silt/clays reaching a mean value of 90% with the sands at 9% and 1% of gravels. More

specifically, in core ALM3, SUD ranges from 100 cm to 43 cm. This sedimentary sequence contains sporadic organic material while gravels were observed at 68 cm until 51 cm.

The granulometric analysis of SUC data characterised the sediments as slightly gravelly sandy mud to slightly gravelly mud [28] with a unimodal distribution, and are moderately to very well sorted.

Regarding core ALM 3 and the samples at depths of 95 and 78 cm, their sorting is 0.3ϕ , which are very well sorted. Skewness (Sk) values are 0ϕ , which are considered as almost normal asymmetry. Kurtosis values are 0.74ϕ and are classified as platykurtic. For samples at depths of 61 and 45 cm, the sorting ranges from 0.87ϕ to 0.94ϕ and are characterised as moderately sorted. Skewness (Sk) values range from -0.38ϕ to -0.4ϕ , identified as very negative asymmetry. Kurtosis (Ku) values are 3.14ϕ and 3.7ϕ , classified as very leptokurtic (Figure S4).

In core ALM4, SUD is observed from the depth of 53 cm up to 10 cm. In contrast to ALM3, the sediment lacked organic material and gravel. The granulometric analysis of SUD in core ALM 4 also shows sediments characterised as slightly gravelly mud to sandy mud by [29], with a unimodal distribution and being very well sorted. The values of the statistical parameters as far as sorting is concerned are 0.45ϕ , which corresponds to well-sorted material. Skewness (Sk) values are -0.25ϕ , identified as negative asymmetry, while kurtosis (Ku) values range from 1.3ϕ to 1.6ϕ and are classified as leptokurtic to very leptokurtic (Figure S8).

4.3. Palaeobiological Analysis

4.3.1. Palaeofauna

Taxonomic analysis yielded 25 species of molluscs (23 gastropod species and two bivalve species) and 24 species of ostracods. All the molluscan fauna (Figure 3) is characteristic of freshwater environments, whereas in the ostracod assemblages, some species that tolerate higher salinities and low oxygen levels [32] are present. Molluscs and ostracods were analysed qualitatively and quantitatively to extract information relative to environmental changes. The analysis of the two cores ALM3 and ALM4 placed the faunas in three different molluscan–ostracod units (MOU) based on the prevailing environmental conditions. These three units reflect similar environments for both mollusc and ostracod faunas (Figures 4–6). The molluscan species and their habitats are presented in Table 2.

The first unit, MOUA, includes samples 18–26 of ALM 3 (Figure 4, 275 to 344 cm) and samples 31–33 of ALM 4 (Figure 5, 374 to 388 cm), and the dominance of a stagnant to slow-moving freshwater environment, where *Gyraulus crista* is the most abundant gastropod. Taxa that inhabit woodland ponds, marshlands and require humid conditions, such as *Hippeutis* sp. [33] and *Carychium* sp., are found in MOUA as smaller variations within the environment. In addition, a taxon that is mostly found in caves or in karstic crevices, *Zospeum* sp., is found in both cores of MOUA in association with other terrestrial molluscs such as *Vallonia* sp. and *Vertigo antivertigo*. The ostracods of MOUA correlate well with the environment that is revealed from the molluscan fauna, and give additional information about the salinity oscillations and the very low levels of dissolved oxygen of the swamp (*Cyprideis torosa*, *Heterocypris salina*) [34].

The second unit, MOUB, represents a swamp environment found in the stratigraphic sequence (lighter-coloured grey sediments) that includes samples 8–17 of ALM3 (Figure 4, 155 to 270 cm) and 18–30 of ALM4 (Figure 5, 205 to 362 cm). MOUB has the characteristics of a shallow permanent to slow-moving water body marked by the presence of *Planorbis* cf. *atticus*. Dense vegetation is inferred by the increased number of Bithyniidae, whereas elevated salinity is inferred by ostracod assemblages for all units of both cores. A synchronous abundance of the gastropods Bithyniidae and Planorbidae, along with the ostracods *Cyprideis* and *Heterocypris*, is evidence of high-salinity events (Figures 4 and 5). The ostracod fauna of MOUB includes the largest numbers and taxonomic diversity of Candonidae, Cyprididae and Cytherideidae. In MOUB of ALM3 core, a relative reduction in the ostracod population is observed in its upper part (Figure 4, samples 11–8), were

Candona sp. is the dominant taxon. In between this unit, several samples were barren (Figures 4 and 5).

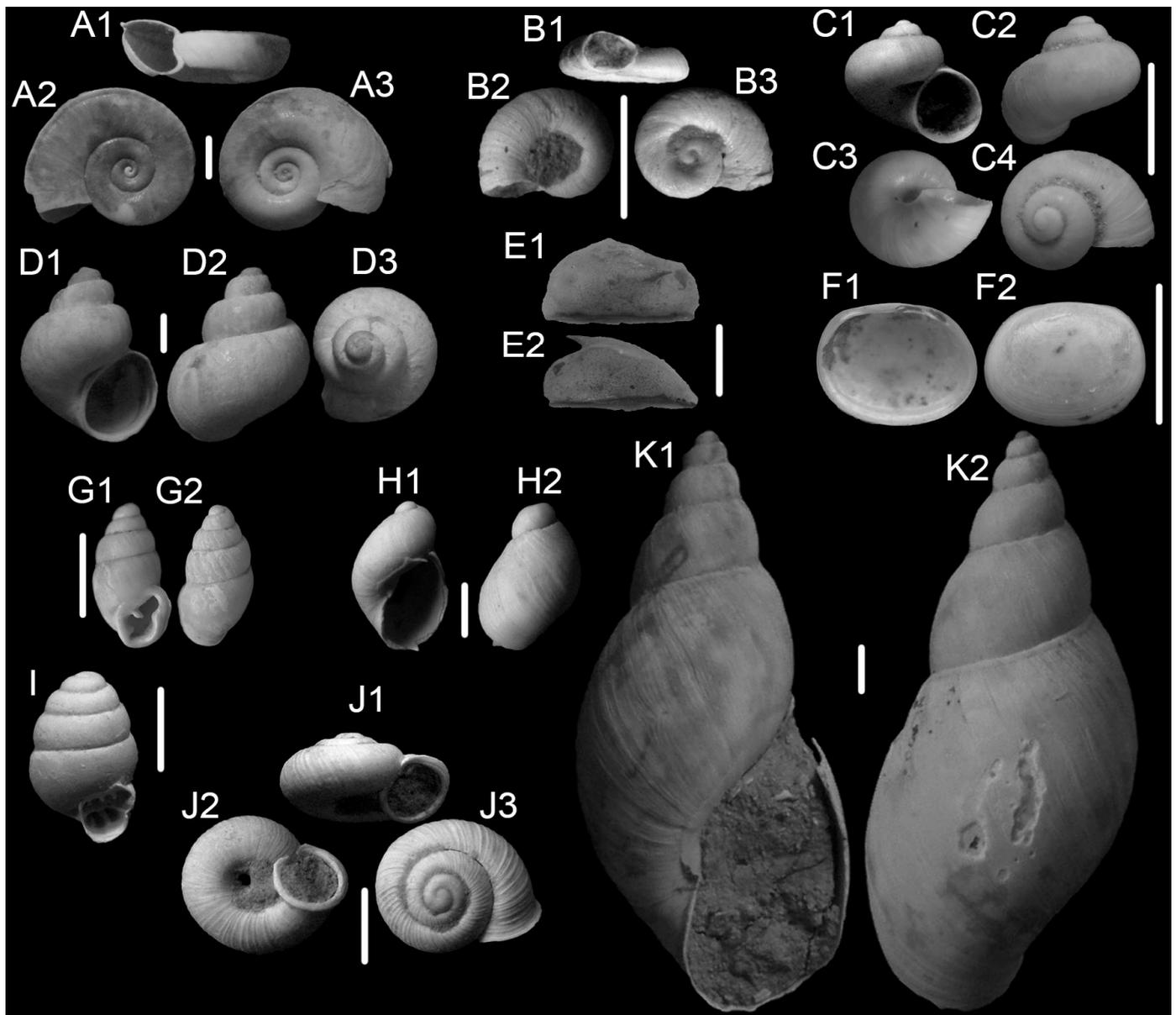


Figure 3. Most abundant molluscs recovered in the ancient Lake Lerna. (A1–A3) *Planorbis* cf. *atticus*, (B1–B3) *Gyraulus crista*, (C1–C4) *Valvata* sp., (D1–D3) *Bithynia* sp., (E1,E2) *Acroloxus* sp., (F1,F2) *Pisidium personatum*, (G1,G2) *Carychium* sp., (H1,H2) *Oxyloma* sp., (I) *Vertigo antiinvertigo*, (J1–J3) *Vallonia* sp., (K1,K2) *Stagnicola* sp. Scale bars: 1 mm.

In samples 3–7 of ALM3 (Figure 4, 78 to 145 cm) and 6–17 of ALM4 (Figure 5, 77 to 197 cm), similar environmental conditions prevailed, characterising MOUC (brown-coloured sediments). The absence of molluscs in ALM3 and ALM4, with a few representative specimens of Planorbidae and Bithyniidae, indicate a transition to a freshwater shallow lake with minimal vegetation, where the typical freshwater ostracod species such as *Candona* cf. *candida* and *Ilyocypris bradyi* of both cores are the only present taxa.

The transition from a freshwater lake to a swampy environment is noted in core ALM4, samples 3–5 (Figure 5, 46 to 57 cm), which corresponds to MOUB, with mollusc and ostracod faunas typical of stagnant to slow-moving waters.

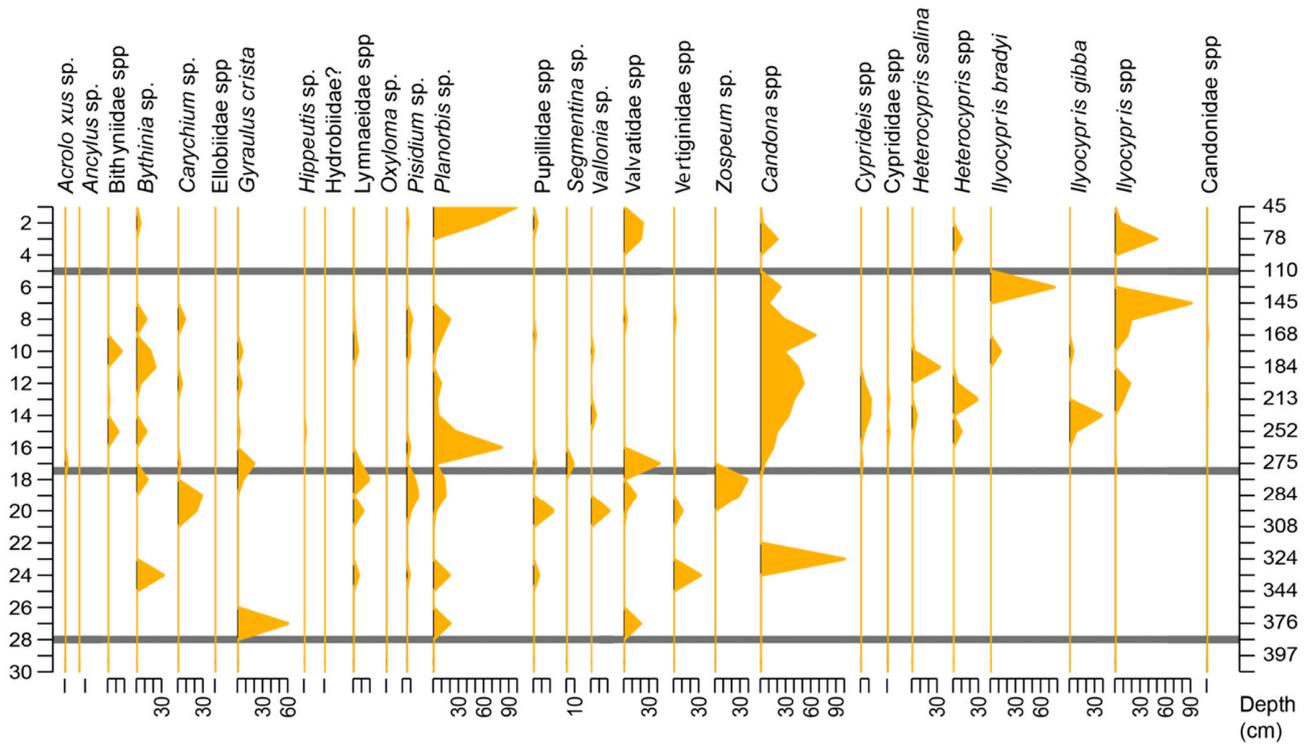


Figure 4. Stratigraphic plot for ALM3, mollusc and ostracod taxa. The horizontal grey lines indicate the limits of molluscan–ostracod units.

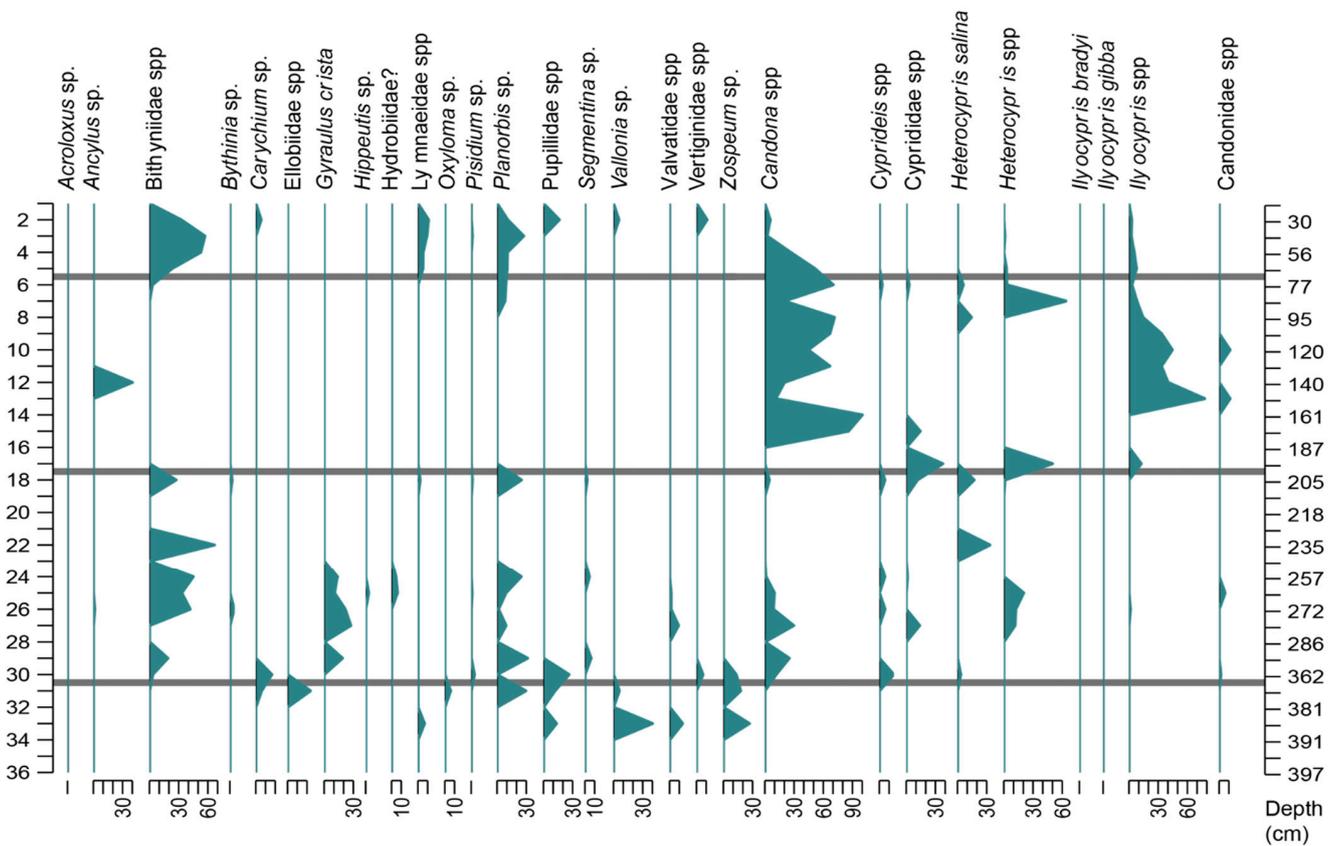


Figure 5. Stratigraphic plot for ALM4, mollusc and ostracod taxa. The horizontal grey lines indicate the limits of molluscan–ostracod units.

Table 2. List of molluscs found in sediments of Lerna and their respective habitats and environments.

Class	Families	Genera	Species	General Habitat	Environment
Gastropoda	Planorbidae	<i>Planorbis</i>	cf. <i>planorbis</i>	Freshwater	Low energy temporary and permanent ponds, streams, rivers, springs, lakes [32]
		<i>Planorbis</i>	cf. <i>atticus</i>		
		<i>Planorbis</i>	sp.		
		<i>Gyraulus</i>	<i>crista</i>		
		<i>Hippeutis</i>	sp.		
		<i>Segmentina</i>	sp.		
	Valvatidae	<i>Valvata</i>	<i>cristata</i>	Freshwater	Cold, clean lakes, rivers, streams [7]
		<i>Valvata</i>	sp.		
	Bithyniidae	<i>Bithynia</i>	sp.	Freshwater	Quiet muddy rivers, lakes, ponds, canals, swamps [7]
	Lymnaeidae	<i>Stagnicola</i>	sp.	Freshwater	Flowing rivers and streams, lakes to stagnant ponds, swamps [7]
		–	sp.		
	Ellobiidae	<i>Carychium</i>	sp.	Permanently wet epigeal environments	Aphotic, permanently wet terrestrial biomes [7]
		<i>Zospeum</i>	sp.	Permanently wet subterranean environments	Cave karstic rock crevice dweller [35]
	Vertiginidae	<i>Vertigo</i>	<i>antivertigo</i>	Terrestrial on water margin vegetation	Wet, unimproved pasture, marshes and tall fen or water margin vegetation [36]
Pupillidae	<i>Pupilla</i>	sp.	Detritus feeder (dead plant remains) [36]		
Valloniidae	<i>Vallonia</i>	sp.	Terrestrial moist environment with plant debris	Humid and wet habitats in lowlands, on humid and uncultivated meadows and in calcareous swamps [36]	
Acroloxidae	<i>Acroloxus</i>	sp.	Fresh water	Lakes [7]	
	<i>Ancylus</i>	sp.			
Hydrobiidae	“ <i>Hydrobia</i> ”	sp.	Freshwater	Springs, streams, rivers, lakes, groundwater systems, estuarine marshes [36]	
Succineidae	<i>Oxyloma</i>	sp.	Terrestrial on water margin vegetation	Feeds on wilting plant parts [36]	
Bivalvia	Sphaerioidea	<i>Pisidium</i> <i>Pisidium</i>	<i>personatum</i> sp.	Freshwater	Bottom dwelling filter feeder [37]

The ordinations of both mollusc and ostracod faunas that were recovered (Figure 6) show a variation in environments throughout the cores. Three main groups were defined, characterising three environments corresponding to three units that were previously defined: stagnant waters, swamps and freshwater (Figure 6).

4.3.2. Palaeoflora

Sixteen pollen and dinoflagellate cyst samples were analysed for the investigation of local floras, particularly covering the upper part sequence of the core sediments (Figure 7). They were separated in three pollen units, PU1 to PU3, that are characterised by differences in abundances of taxa, although some aquatic taxa seem to appear towards the bottom of the core.

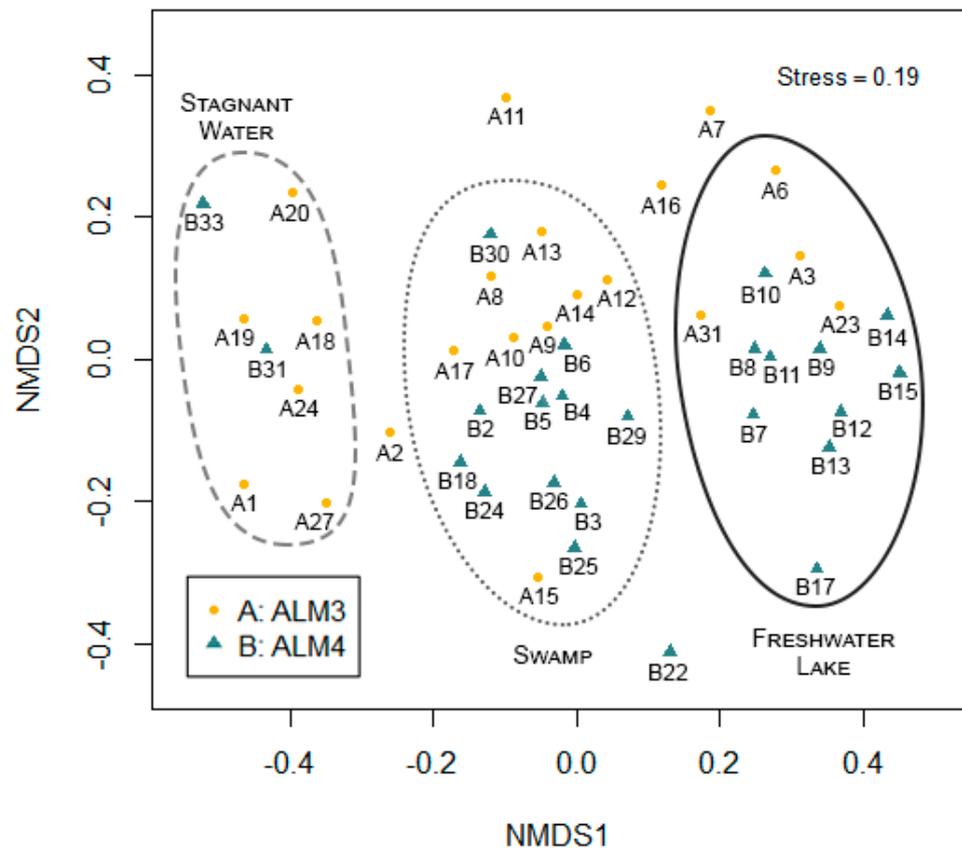


Figure 6. NMDS plot of samples from cores ALM3 and ALM4.

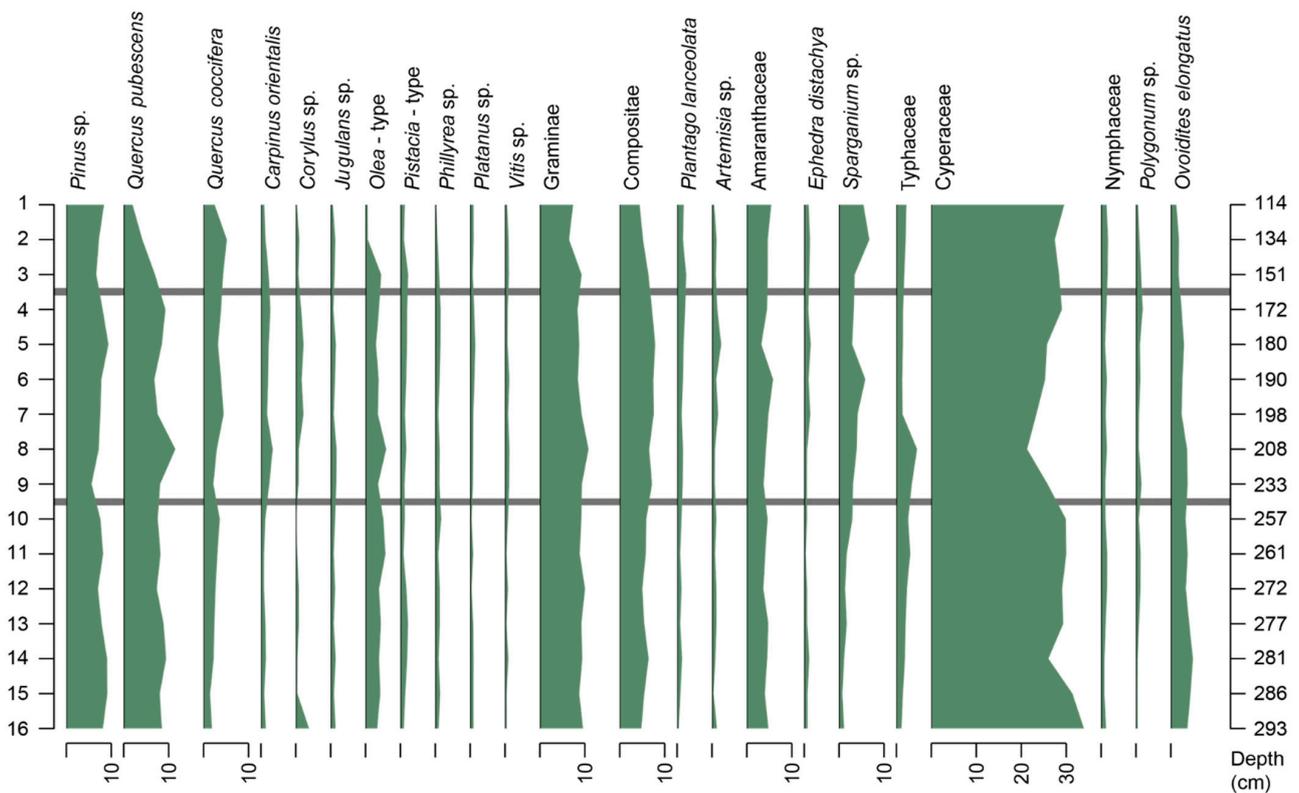


Figure 7. Stratigraphic plot for ALM3 pollen taxa (taxa with abundances higher than 10% are present). The horizontal lines separate the three pollen units.

Pollen Unit 1 (PU1) (Figure 7, 257 to 293 cm) is dominated by angiosperms while presenting a high taxonomic diversity. Woodland vegetation is characterised by mixed vegetation comprising species such as *Juglans*, *Ulmus*, *Ostrya*, *Platanus*, *Acer*, *Castanea*, *Quercus coccifera/ilex* and *Cistus*. Grasses are represented by Gramineae, Asteraceae, Amaranthaceae/Chenopodiaceae, Ericaceae, Caryophyllaceae, Polygonaceae, *Artemisia* and *Ephedra*. They are equally distributed in PU1. What is exceptional in this unit is the presence of aquatic plants such as members of the families Nymphaeaceae, Typhaceae, Sparganiaceae, Nupharaceae and Cyperaceae. The presence of freshwater phytoplankton genera (*Botryococcus*, *Ascomyces*, *Ovoidites*) is notable and suggests a freshwater character of the samples.

In PU2 (Figure 7, 172 to 233 cm) there is a progressive increase in coniferous pollen and a more noted presence of xerophytic taxa such as *Quercus coccifera/ilex*. Grasses are present and relatively diverse, dominated by Gramineae and Asteraceae, with *Artemisia* having a stable presence throughout the unit. Aquatic plants are still present, represented by members of Cyperaceae, Nymphaeaceae and Typhaceae.

Lake deposits of Unit PU3 are defined by three samples, representing a swamp environment that is found in the stratigraphic sequence (lighter-coloured grey sediments) that includes samples 1 to 3 (Figure 7, 114 to 151 cm) of ALM3. They are characterised by the presence of deciduous trees such as *Quercus pubescens* and a stronger presence of aquatic vegetation, mainly represented by the Cyperaceae.

In general, a decrease in non-arboreal pollen (NAP) is observed throughout the core, reaching a maximum in the uppermost sample. Charophyte oogonia are present in samples ALM3, further characterising freshwater settings within PU2.

In total, three units were determined by the aforementioned assemblages. The sub-units reflect the variation in the environmental conditions within a greater sedimentary setting. Faunal units coincide significantly with pollen units, with the exception of MUC1, which corresponds to the lower part of PU2.

5. Discussion

All the elements that were analysed in the present work point to a dynamic environment of a coastal wetland. The units defined by the sedimentological and palaeobiological analyses reflect significant changes in the depositional environments of the studied area.

5.1. Sedimentology

The sedimentological analysis revealed four units (SUA to D), separated based on grain size and colouration. The bases of both studied cores are composed of dark-coloured sediments, rich in organic material, leaning towards lighter and brown-coloured sediments in the top part of the cores. Sub-units defined for SUB and SUC indicate smaller-scale changes in the sedimentation, whereas layers of peat mark other events tied to precipitation and oxygen levels in the lake. Deep grey-black sediments indicate anoxic conditions, which show a stagnant lake.

Katrantsiotis and colleagues [12] retrieved a core in the area of Lerna (GreekGrid, EGSA '87: x: 387,952.268, y: 4,159,981.561, 1 m.a.s.l) in order to study environmental changes during the Holocene. The analytical methods included a combination of n-alkane distributions and their hydrogen isotopic composition (δD), as well as sediment optical lithological characterisation, in comparison with the total organic content (TOC). Our results are in agreement with those of [12] (Figure 8). The units with dark-coloured sediment (Table 1) are present in [12] as layers of high organic concentrations, while brown-grey to brown layers correspond to less organic material [12] (Figure 8). However, in [12], all sediments were characterised as gyttja, which in this study is observed only in specific layers rich in organic material.

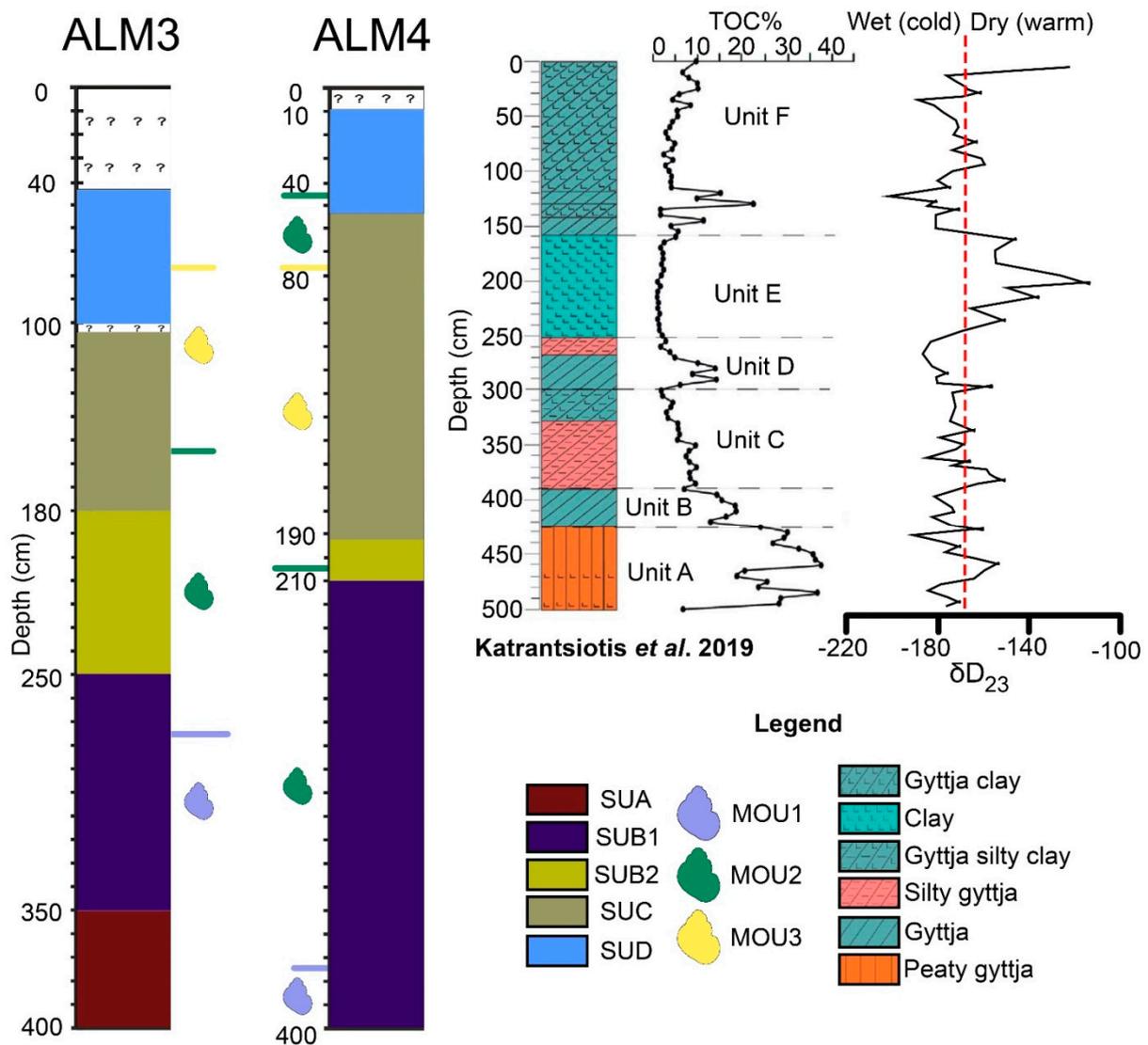


Figure 8. Combination of lithostratigraphic and palaeontological units for the cores ALM3 and ALM4. The question marks (?) are indicative of disturbed material during coring. Comparison with [12] (including TOC and δD_{23} data).

Comparing the present results with [12] yields the following findings.

- Unit B (390–425 cm) of [12], characterised as gyttja with high TOC values, is equivalent to SUB1 of ALM3 (250–350 cm) and ALM4 (350–400 cm) (Figure 8), as these are the levels with the highest concentrations of organic material. The peat deposits seen here between gyttja are rather thin. In [12], Unit B was estimated to have been deposited around 4000 BP.
- The deepest part of Unit C from [12]’s core could be related to the lower SUB2 of ALM3 (208–250 cm) and the middle SUB1 of ALM4 (270–350 cm) (Figure 8). These units have similar silty sediment, as they are characterised by medium to low concentrations in TOC. In [12], the Unit C was dated around 3700 BP.
- The upper Unit C and Unit D of [12] correspond to the upper part of SUB2 (208–180 cm) of ALM3 and the upper part of SUB1 (270–210 cm) and SUB2 of ALM4 (Figure 8). The latter units have similarities in sediment composition as well as in organic material concentration (gyttja silty clay). In [12], these units were dated around 2500 BP.
- Unit E of [12] is characterised by clay and low TOC, matching with SUC of ALM3 and mid-SUC of ALM4 (100–190 cm) (Figure 8).

- The lower part of Unit F (120–155 cm) of [12] can be compared with lower SUD of ALM3 (75–100 cm) and upper SUC of ALM4 (55–100 cm) (Figure 8). These units are all characterised by clayey sediment with similar concentrations of organic material. The age given for lower Unit F of [12] is approximately 1500 BP.

The most accurate dates of the present study are the ones originating from gyttja, such as the LTL19748A (5640 ± 45 BP) from ALM3, and LTL20302 (4610 ± 45 BP) from ALM4. The two samples are very near the ash layer, present in both cores, as were those of [12]; thus, we expected the dates to be similar, yet they differ by nearly a thousand years. A similar dating result of a seed sample from [12] near the ash layer is around 3970 ± 30 BP, while the “charred” layer itself had a result of 4370 ± 30 BP [12]. The rest of our dating results have considerable uncertainty, as most of them contain mollusc parts. Due to these differences in ages, we are reluctant to discuss age estimations for our samples, and therefore, we mainly compared the cores using sedimentological similarities. We are also concerned about the validity of results of [12] at the upper part of their core (upper 0.5–1 m), since the Argive Plain has been deeply ploughed in recent years, meaning that the upper sedimentary layers are mostly disturbed.

5.2. Palaeofauna and Flora

The recovered mollusc and ostracod faunas also correlate with significant environmental changes, mainly by a variation in abundances, which can be useful indicators of the lake’s condition at that time. Freshwater taxa are dominant in all samples for both molluscs and ostracods. Nevertheless, some gastropod species, such as the Bithyniidae and Planorbidae, as well as some ostracod species, such as *Cyprideis torosa* and *Heterocypris salina*, can withstand higher salinities [38]. Ordination through NMDS shows groupings of samples coming from different parts of the cores; this reflects the dynamic environments that were successively established in the area of the former lake. The presence of gastropod *Zospeum* sp. in the basal part of both cores suggests that the shells could have been transported through a nearby karstic system and deposited in the lake area.

Pollen data, spaced in the length of core ALM3, depict a trend that agrees with previous findings in the area of the ancient Lake Lerna [39]. Anthropogenic disturbance, from PU2 onwards, is indicated by the increased presence of *Plantago lanceolata* [39]. Since the present work is centred on the freshwater character of the ancient lake, aquatic taxa are mentioned here additionally in PU1 and 2. An element that differs from previous studies, namely [39], is the representation of *Olea*, which is present here in relatively low abundances.

5.3. Palaeobiological Evolution of the Lake

Previous studies [4] suggest that the lake formed around 8330 ± 100 BP is a stagnant body of water, accumulating peaty gyttja [12]. The lake was first colonised by Planorbidae, such as *Gyraulus crista*. Moving upwards in the cores, we find gastropod species living in close proximity to lake environments (e.g., Succineidae). This correlates with the wet climate, as suggested by [12] (see also Figure 8, δD_{23} graph), which helped in the accumulation of plants near or inside the lake area, and a subsequent accumulation of detritus and herbivorous gastropods on the lake bottom. The excess organic material caused anoxic events. The absence of an ostracod fauna in the base of the cores further indicates nearly anoxic conditions [34] of the lake (Figures 4 and 5, MOU1). However, the presence of the fully aquatic gastropods Valvatidae is evidence that the water had enough oxygen for these organisms to survive. Furthermore, the transported cave-dwelling gastropod *Zospeum* sp. confirms that the karstic system of the wider area was more active during that wet period [12], and provided water to the lake.

In both cores, we found an ash layer (ALM3 2.95 m, ALM4 3.93 m). This layer might indicate a fire, something that is likely since other low-temperature forest fires were recorded in the Peloponnese around that time [40]. Moreover, this ash layer has been reported as charred material by [12], almost 1 km away to the north east from our sampling sites, highlighting that the fire was widespread in the area.

Sedimentological changes in SUB1 had a drastic effect on the fauna of the lake, with several ostracod species appearing, an indication that the water was no longer anoxic [34]. Furthermore, the gastropod fauna displayed an increase in species diversity and abundance (Figures 4 and 5). The sudden increase in populations, displaying peaks in species of ostracods (Figures 4 and 5) such as *Cyprideis* and *Heterocypris*, indicate swift sea-water influxes into the lake. The simultaneous peaks of gastropods of the families Planorbidae and Bithyniidae can also be explained, as these organisms can tolerate salinity levels up to 16 ppt [38]. The intensity and position of those events is not similar in both cores (Figure 8), suggesting that these influxes were local and sporadic, as the quantity of sea-water was not enough to affect large portions of the lake. The peaks being caused by dry events, which would have resulted in an increase in the salinity, is improbable, since both cores display dissimilar peaks and because this MOU2 corresponds to a wet and cold climate (Figure 8) [12].

After SUB, shifts in sedimentology and aquatic faunas suggest that the marsh transitioned into a clear-water lake environment. This would correspond to the brown-coloured sediment of [12], containing low TOC levels (Figure 8). This period is characterised by a dry and hot climate [9,10,12,41,42] (see also Figure 8, δD_{23} graph), which halted the growth of marginal plants around the lake, thus reducing the deposition of organic material. The absence of molluscs can be a result of various factors, such as the absence of sufficient plants for the molluscs to thrive on. We could argue that the lake was ephemeral at that period of time, but we and [12] did not observe any sedimentological indications of such events, nor did [12] display any abrupt changes in their age model. Therefore, we disregard such a scenario.

Finally, the fauna present in the upper layers of ALM4 (SUC and D) suggests that the lake had sufficient water to sustain both plants and the associated gastropod and ostracod faunas (corresponding to an abrupt increase in TOC [12] seen in Figure 8). This re-establishment of the lake as a permanent body of water with rich fauna and flora partly coincides with the results of [4,18]. It also agrees with the archaeological finds of porotic hyperostosis [43] during the Late Hellenistic Period, as according to the dating results of [12], this wet period started somewhere around 1850 BP. Nevertheless, the reappearance of a swamp would have affected the nearby populations' health.

5.4. What Is Causing These Environmental Fluctuations?

Concerning the environmental changes recorded in localities of the Peloponnese [10,12,41,44], there have been alterations of dry and wet conditions throughout the past 6000 years, with human settlements existing in the area from 8500 BP on [42,45]. The results of [12] on the climate fluctuations are interesting as they illustrate that climate can drastically alternate the sedimentology of the lake (Figure 8), thus highlighting the dynamic character of this coastal wetland.

During the Late Bronze age, the population in the Argive Plain was devastated by successive changes in precipitation levels that potentially led to decreased agricultural output around 3200 BP [42,46–48]. In the Late Bronze age (3550–3200 BP), according to [49], the climate was dry, with considerable erosion due to land overuse and deforestation [50], but later studies in the Peloponnese demonstrate a brief wet period between 3300 and 3100 BP [9,10,41]. A prolonged dry period between the wet periods in the Argive Plain [12] (not observable in our samples) might have destabilised the Peloponnesian populations during the end of the Late Bronze Age [41]. After that, the climate was wet, while deforestation and land use, in general, were more intense after the Middle Geometric period (~2750 BP) [51]. Prehistoric degradation of ecosystems has been investigated in the past through vertebrate remains in the area of Lerna during archaeological investigations [11]. It is possible that these changes in the surrounding land were the reason for the lake's prolonged low TOC levels [12] and brown colour seen in our cores. As such, we found clues of indirect human intervention in the lake due to deforestation and land use [51]. For most of the lake's lifetime, however, despite humans potentially interacting with the

lake, environmental factors were the key drivers for the water conditions, as well as the fauna and flora living in and around the lake. The evidence for human interaction with the surrounding fauna (e.g., deer, sea shell ornaments) [52,53] as well as the environmental destruction have been investigated through the remains of larger vertebrates in nearby archaeological sites (including birds thriving in lakes and wetlands) [11].

6. Conclusions

Through the study of two cores from the area of ancient Lake Lerna, sedimentological and palaeobiological analyses were carried out to investigate environmental changes, with molluscs being studied and used as palaeoenvironmental indicators for the first time in the region.

Three major units were determined, confirmed by the sedimentological and palaeobiological analyses. They reflect changes in the environments of the area in the following sequence. Fluvial deposits are followed by stagnant waters, then a swamp is formed favouring periodical peat formation; after this, a freshwater lake is characterised by the development of large molluscan and ostracod populations. Occasional storm events could overcome the barrier and contaminate the lake with salt water, evidenced by the molluscan and ostracod faunas, but these events are ephemeral.

The studied material covers a period of the Holocene starting at about 8630 years before the present, during the early to middle Neolithic. This means that all recovered faunas and floras have been potentially affected by the human presence in the area, and no undisturbed conditions were found. Despite that fact, all of our results suggest that the changes happening in the lake were caused mostly by climate fluctuations rather than human intervention.

Concluding, most of the changes happening in the lake are correlated with climatic fluctuations. Parameters such as the vegetation, dead organic material in the water, oxygenation of the water and rainfall in the region can affect the lake's fauna and flora. By investigating these changes, we were able to coordinate our results with other environmental works in the region. Although humans were present, their impact on the lake was minimal in comparison to climatic changes.

The case of Lerna can be used as an example for the evolution of coastal aquatic ecosystems in the Holocene.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/quat5020022/s1>, Table S1: Dataset used for NMDS analysis and stratigraphic plots, presenting the species and their abundances in the samples of cores ALM3 and ALM4. Table S2: Pollen species recovered in the examined samples of core ALM3. Figures S1–S8: Triangular diagrams of sedimentological texture for both cores (ALM-3 and ALM-4) and their corresponding cumulative particle mass curves created using GRADISTAT statistical package; these include sediment particle size (φ) retained during sieving.

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References

1. Economidou, E. The Ecological Value of Coastal Ecosystems. *Ekistics* **1982**, *49*, 98–101.
2. Paine, L. *The Sea and Civilization: A Maritime History of the World*; Knopf Doubleday Publishing Group: New York, NY, USA, 2013.
3. Mariolakos, I.D. Ancient Greece and Water: Climatic Changes, Extreme Events, Water Management, and Rivers in Ancient Greece. *Handb. Environ. Chem.* **2017**, *59*, 3–30. [[CrossRef](#)]
4. Zangger, E. Prehistoric Coastal Environments in Greece: The Vanished Landscapes of Dimini Bay and Lake Lema. *J. Field Archaeol.* **1991**, *18*, 1–15. [[CrossRef](#)]
5. Oertel, G.F. Coastal Lakes and Lagoons. *Encycl. Earth Sci. Ser.* **2005**, *14*, 263–266. [[CrossRef](#)]
6. Barbieri, R.; Zogaris, S.; Kalogianni, E.; Stoumboudi, M.T.; Chatzinikolaou, Y.; Giakoumi, S.; Kapakos, Y.; Kommatas, D.; Koutsikos, N.; Tachos, V.; et al. *Freshwater Fishes and Lampreys of Greece: An Annotated Checklist*; Monographs on Marine Sciences No. 8; Hellenic Centre for Marine Research: Athens, Greece, 2015; p. 130.
7. Strong, E.E.; Gargominy, O.; Ponder, W.F.; Bouchet, P. Global Diversity of Gastropods (Gastropoda; Mollusca) in Freshwater. *Hydrobiologia* **2008**, *595*, 149–166. [[CrossRef](#)]
8. Caskey, J.L.; Blackburn, E.T. *Lerna in the Argolid*; American School of Classical Studies at Athens: Athens, Greece, 1997.
9. Weiberg, E.; Unkel, I.; Kouli, K.; Holmgren, K.; Avramidis, P.; Bonnier, A.; Dibble, F.; Finné, M.; Izdebski, A.; Katrantsiotis, C.; et al. The Socio-Environmental History of the Peloponnese during the Holocene: Towards an Integrated Understanding of the Past. *Quat. Sci. Rev.* **2016**, *136*, 40–65. [[CrossRef](#)]
10. Norström, E.; Katrantsiotis, C.; Finné, M.; Risberg, J.; Smittenberg, R.H.; Bjursäter, S. Biomarker Hydrogen Isotope Composition (ΔD) as Proxy for Holocene Hydroclimatic Change and Seismic Activity in SW Peloponnese, Greece. *J. Quat. Sci.* **2018**, *33*, 563–574. [[CrossRef](#)]
11. Gejvall, N.-G. Prehistoric Environmental Destruction, Lerna (Greece). *Museum Int.* **1973**, *25*, 93–96. [[CrossRef](#)]
12. Katrantsiotis, C.; Norström, E.; Smittenberg, R.H.; Finne, M.; Weiberg, E.; Hättestrand, M.; Avramidis, P.; Wastegård, S. Climate Changes in the Eastern Mediterranean over the Last 5000 years and Their Links to the High-Latitude Atmospheric Patterns and Asian Monsoons. *Glob. Planet. Chang.* **2019**, *175*, 36–51. [[CrossRef](#)]
13. Janssen, J.; Rodwell, J.; Criado, M.G.; Gubbay, S.; Haynes, T.; Nieto, A.; Sanders, N.; Landucci, F.; Loidi, J.; Ssymank, A.; et al. *European Red List of Habitats Part 2. Terrestrial and Freshwater Habitats*; Publications Office of the European Union: Luxembourg, 2016. [[CrossRef](#)]
14. Cuttelod, A.; Seddon, M.; Neubert, E. *European Red List of Non-Marine Molluscs*; Publications Office of the European Union: Luxembourg, 2011. [[CrossRef](#)]
15. Kelletat, D.; Kowalczyk, G.; Schröder, B.; Winter, K.-P. A Synoptic View on the Neotectonic Development of the Peloponnesian Coastal Regions. *Z. Dtsch. Geol. Ges.* **1976**, *127*, 447–465. [[CrossRef](#)]
16. van Andel, T.H.; Zangger, E.; Demitrac, A. Land Use and Soil Erosion in Prehistoric and Historical Greece. *J. Field Archaeol.* **1990**, *17*, 379. [[CrossRef](#)]
17. Finke, E.A. *Landscape Evolution of the Argive Plain, Greece: Paleoecology, Holocene Depositional History, and Coastline Changes*; Stanford University: Stanford, CA, USA, 1988.
18. Zangger, E. The Geoarchaeology of the Argolid. *Am. J. Archaeol.* **1993**, *100*, 636. [[CrossRef](#)]
19. Koutsouveli-Nomikou, A. *Contribution a l'Etude Quaternaire de la Région d'Argos (Nord-Est du Péloponnèse, Grèce)*; Université d'Aix: Marseille, France, 1980.
20. Gaki-Papanastassiou, K. *The Geomorphological Evolution in and around the Argive Plain since the Quaternary*; National and Kapodistrian University of Athens: Athens, Greece, 1991. [[CrossRef](#)]
21. Seni, A.; Gaki-Papanastassiou, K.; Karymbalis, E.; Zouva, C. Anticipated Sea-Level Rise Vulnerability Assessment Along Part of the Eastern Argolic Gulf and the Argive Plain With the Use of G.I.S. In Proceedings of the 8th Pan-Hellenic Geographical Conference, Athens, Greece, 4–7 October 2007; pp. 146–155.
22. Gaki-Papanastassiou, K.; Maroukian, H. Late Quaternary controls on river behaviour in the eastern part of the Argive plain, eastern Peloponnesus, Greece. In Proceedings of the International Symposium on Mediterranean Quaternary River Environments, Cambridge, UK, 28–29 September 1992; Balkema: Rotterdam, The Netherlands, 1995; pp. 89–95.
23. Liritzis, I.; Raftopoulou, M. Argolid: Connection of Prehistoric Legends with Geoenvironmental and Archaeological Evidence. *Tubaar* **1999**, *2*, 87–99. [[CrossRef](#)]
24. De Wever, P. *Etude Géologique des Series Apparaissant en Fenêtre sous l' Allochtone Pindique (Série de Tripolitza et Série Épimetamorphique de Zarouchla), Péloponnèse Septentrional, Grèce*; Université de Lille: Lille, Greece, 1975.
25. Tataris, A.; Kounis, G.; Maragoudakis, N. *Geological Map of Greece on a Scale 1:50,000, "Vagia" Sheet*; IGME: Madrid, Spain, 1970.

26. Exidavelonis, P.; Taktikos, S. *Geological Map of Greece on a Scale 1:50,000, "Tripolis" Sheet*; IGME: Madrid, Spain, 1988.
27. *Geological Map of Greece on a Scale 1:50,000, "Argos" Sheet*; IGME: Madrid, Spain, 1960.
28. Theodoropoulos, D.; Papapetrou-Zamani, A. Geological and Geomorphological Investigations of the Argos Plain. *Ann. Géologiques Pays Helléniques* **1970**, *22*, 269–294.
29. Folk, R.L.; Ward, W.C. Brazos River Bar [Texas]; a Study in the Significance of Grain Size Parameters. *J. Sediment. Res.* **1957**, *27*, 3–26. [[CrossRef](#)]
30. Blott, S.J.; Pye, K. Gradistat: A Grain Size Distribution and Statistics Package for the Analysis of Unconsolidated Sediments. *Earth Surf. Process. Landf.* **2001**, *26*, 1237–1248. [[CrossRef](#)]
31. Psilovikos, A.A. Sediment Analysis at Gibraltar Point, Lincolnshire. *East Midl. Geogr.* **1979**, *7*, 128–133.
32. Rossetti, G.; Bartoli, M.; Martens, K. Limnological Characteristics and Recent Ostracods (Crustacea, Ostracoda) of Freshwater Wetlands in the Parco Oglia Sud (Northern Italy). *Ann. Limnol. Int. J. Limnol.* **2004**, *40*, 329–341. [[CrossRef](#)]
33. Aneta, S. Woodland Ponds as an Important Habitat of *Hippeutis Complanatus* (Linnaeus 1758) Occurrence—Effect of Environmental Factors and Habitat Preferences. *Ekológia* **2014**, *33*, 101–115. [[CrossRef](#)]
34. Ruiz, F.; Abad, M.; Bodergat, A.M.; Carbonel, P.; Rodríguez-Lázaro, J.; González-Regalado, M.L.; Toscano, A.; García, E.X.; Prenda, J. Freshwater Ostracods as Environmental Tracers. *Int. J. Environ. Sci. Technol.* **2013**, *10*, 1115–1128. [[CrossRef](#)]
35. Weigand, A.M.; Jochum, A.; Slapnik, R.; Schnitzler, J.; Zarza, E.; Klussmann-Kolb, A. Evolution of Microgastropods (Ellobioidea, Carychiidae): Integrating Taxonomic, Phylogenetic and Evolutionary Hypotheses. *BMC Evol. Biol.* **2013**, *13*, 18. [[CrossRef](#)]
36. Welter-Schultes, F.W. *European Non-Marine Molluscs, a Guide for Species Identification/Bestimmungsbuch für Europäische Land- und Süßwassermollusken*; Planet Poster Editions: Goettingen, Germany, 2012.
37. McMahon, R.F.; Bogan, A.E. 11—MOLLUSCA: BIVALVIA. In *Ecology and Classification of North American Freshwater Invertebrates*; Thorp, J.H., Covich, A.P., Eds.; Academic Press: Cambridge, MA, USA, 2001; pp. 331–429. [[CrossRef](#)]
38. Abdelhady, A.A.; Khalil, M.M.; Ismail, E.; Fan, J.; Zhang, S.; Xiao, J. Water Chemistry and Substrate Type as Major Determinants of Molluscan Feeding Habit and Life-Mode in Lagoon Sediments. *Estuar. Coast. Shelf Sci.* **2019**, *220*, 120–130. [[CrossRef](#)]
39. Jahns, S. On the Holocene Vegetation History of the Argive Plain (Peloponnese, Southern Greece). *Veg. Hist. Archaeobot.* **1993**, *2*, 187–203. [[CrossRef](#)]
40. Norström, E.; West, J.; Kouli, K.; Katrantsiotis, C.; Hättstrand, M.; Smittenberg, R.H. Evaluation of Anhydrosugars as a Molecular Proxy for Paleofire Activity: A Case Study on a Holocene Sediment Core from Agios Floros, Peloponnese, Greece. *Org. Geochem.* **2021**, *153*, 104193. [[CrossRef](#)]
41. Finné, M.; Holmgren, K.; Shen, C.C.; Hu, H.M.; Boyd, M.; Stocker, S. Late Bronze Age Climate Change and the Destruction of the Mycenaean Palace of Nestor at Pylos. *PLoS ONE* **2017**, *12*, e0189447. [[CrossRef](#)]
42. Weiberg, E.; Hughes, R.E.; Finné, M.; Bonnier, A.; Kaplan, J.O. Mediterranean Land Use Systems from Prehistory to Antiquity: A Case Study from Peloponnese (Greece). *J. Land Use Sci.* **2019**, *14*, 1–20. [[CrossRef](#)]
43. Angel, J.L. Ecology and Population in the Eastern Mediterranean. *World Archaeol.* **1972**, *4*, 88–105. [[CrossRef](#)]
44. Boyd, M. *Speleothems from Warm Climates: Holocene Records from the Caribbean and Mediterranean Regions*; Department of Physical Geography, Stockholm University: Stockholm, Sweden, 2015.
45. Weiberg, E.; Bevan, A.; Kouli, K.; Katsianis, M.; Woodbridge, J.; Bonnier, A.; Engel, M.; Finné, M.; Fyfe, R.; Maniatis, Y.; et al. Long-Term Trends of Land Use and Demography in Greece: A Comparative Study. *Holocene* **2019**, *29*, 742–760. [[CrossRef](#)]
46. Knapp, A.B.; Manning, S.W. Crisis in Context: The End of the Late Bronze Age in the Eastern Mediterranean. *Am. J. Archaeol.* **2016**, *120*, 99–149. [[CrossRef](#)]
47. Middleton, G.D. *The Collapse of Palatial Society in LBA Greece and the Postpalatial Period*; University of Michigan Press: Ann Arbor, MI, USA, 2010. [[CrossRef](#)]
48. Weiberg, E.; Finné, M. Mind or Matter? People-Environment Interactions and the Demise of Early Helladic II Society in the Northeastern Peloponnese. *Am. J. Archaeol.* **2013**, *117*, 1–31. [[CrossRef](#)]
49. Angel, J.L. *The People of Lerna: Analysis of a Prehistoric Aegean Population*; American School of Classical Studies at Athens: Princeton, NJ, USA, 1971; Volume 2.
50. Fuchs, M. An Assessment of Human versus Climatic Impacts on Holocene Soil Erosion in NE Peloponnese, Greece. *Quat. Res.* **2007**, *67*, 349–356. [[CrossRef](#)]
51. Weiberg, E.; Bonnier, A.; Finné, M. Land Use, Climate Change and 'Boom-Bust' Sequences in Agricultural Landscapes: Interdisciplinary Perspectives from the Peloponnese (Greece). *J. Anthropol. Archaeol.* **2021**, *63*, 101319. [[CrossRef](#)]
52. Reese, D.S. Faunal Remains from Late Helladic Lerna (Argolid, Greece). *Mediterr. Archaeol. Archaeom.* **2008**, *8*, 5–25.
53. Reese, D.S. Faunal Remains from Early Helladic II Lerna (Argolid Greece). *Mediterr. Archaeol. Archaeom.* **2013**, *13*, 289–320.