Diatoms as palaeolimnological indicators: A reconstruction of Late Quaternary environments in two East African salt lakes.

by

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Certificate of originality.

I certify that I am responsible for the work submitted in this thesis, that the original work is my own except as specified in acknowledgements or in references, and that neither the thesis nor the original work contained therein has been submitted to this or any other institution for a higher degree.

Philip Anthony Barker 1990

Abstract.

Lakes Magadi (Kenya) and Manyara (Tanzania) occupy closed basins in the southern Gregory Rift valley. Water in these lakes is presently shallow and saline, testifying to the dominance of evaporation (E) over precipitation (P). Past changes in the P:E ratio, and hence in palaeoclimate, can be reconstructed from evidence of the former extent of these lakes. Lake-level fluctuations engender marked variation in water chemistry, and consequently on the composition of the limnological biota. One approach is to examine the sedimentary record of diatoms (unicellular algae), which are excellent indicators of water chemistry and relative water depth, and whose modern distribution is sufficiently well known to allow the quantitative reconstruction of chemical parameters.

Diatom analysis of 116 samples from a series of radiometrically dated (^{14}C and U/Th) sediment cores has revealed significant changes amongst the diatom assemblages during the Late Quaternary. Conductivity and pH have been estimated from the fossil samples by transfer functions (Gasse unpublished, Gasse 1986b). However, the interpretation of fossil diatom assemblages is often problematical in hypersaline environments. Difficulties arise as a result of the operation of taphonomic and diagenetic processes which can severely alter the composition of the diatom assemblages from the ambient population at the time of deposition. Probably the most important factor responsible for assemblage diagenesis in saline lakes is silica dissolution, and this is explored further by a series of laboratory experiments. Results indicate that silica dissolution acts differentially between species, by removing the smaller, more delicate taxa first, and causing the relative enrichment of large robust forms in the fossil samples. A similar dissolution gradient may be reflected in modern samples studied near hot springs at Magadi. Differential dissolution is potentially an important source of error in palaeoenvironmental reconstructions, but, with the outcome of these experiments, it has been possible to assess the extent to which the dissolution process may have shaped the diatom records from Magadi and Manyara.

The bulk of the palaeolimnological evidence is focussed upon two periods, 30,000-20,000 BP and 12,700-9,500 BP. The earlier period is most clearly dated in the core from Manyara, where the diatom record suggests the development of an intermediate level lake between *c*.27,500 BP and *c*.26,000 BP. This is a more complete representation of the same lake phase found in earlier studies from Manyara by Holdship (1976) based on diatoms, and by Casanova (1986a) on stromatolites 20m above the present lake. This time interval may also be represented by the central portion of the Magadi cores NF1 and NF2 but here dating is more problematical. The period 12,700-9,500 BP was one of major lacustrine transgression across Africa although the fine-structure of this event is less well known. Cores NF1 and NF2 from Magadi provide a detailed register of this phase indicating a major highstand from *c*.12,700-11,000 BP when the lake became deep enough to stratify and deposit laminated couplets. At *c*.11,000 BP the diatoms show that salinity increased greatly from fresh-oligosaline to meso-hypersaline which was probably a consequence of lake-level falling.

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CHAPTER ONE: INTRODUCTION.

Public attention has been drawn to the African rift valleys as a result of spectacular discoveries of hominid fossils, placing them in the forefront of the search for the site of human evolution. Quasi-continuous sedimentation for the 30 million years since their inception provides a unique geological record, not only of human lineage, but also of former environments. Climatic change has left its mark most clearly in the sediments of the rift valley lakes. Sediments of deep ancient lakes such as Tanganyika have been accumulating since the Tertiary, a situation rarely found outside the marine environment. However, palaeoenvironmental potential is not confined to the deep waters of the African great lakes, and many of the smaller lakes preserve high-resolution records documenting the fine structure of the Pleistocene and Holocene. The fact that palaeolimnology can provide evidence of environmental change beyond the written record and for those parts of the world where documentary sources do not exist has given renewed impetus to these investigations, a situation further strengthened by the need to provide analogues for possible anthropogenically induced changes in future climate.

The majority of palaeolimnological studies in Africa have arisen from the northern hemisphere tropics and sub-tropics, particularly from the Ethiopian rifts, whereas the southern hemisphere and equatorial region is comparatively little known. Two equatorial lakes at the southern extreme of the Eastern or Gregory rift valley, Magadi and Manyara, provide the focus for this investigation. Lake Magadi is one of the most studied African lakes by mineralogists and geochemists, but its palaeoenvironmental potential has been little exploited. Lake Manyara, in contrast has one of the longest and most important palaeoenvironmental records from south of the equator (Holdship 1976), although the interpretation of this sequence raises questions which the present study will re-examine.

Rifts, grabens, and lakes.

The East African lakes owe their formation to the Afro-Arabian rift system, which extends 6,500 km, from Turkey to Mozambique. Its course includes the areas now occupied by the Dead Sea, the Red Sea, the Gulf of Aden and the African rift valleys (Baker *et al.* 1972). Gregory (1896, 1921) spoke in the singular of The Great African Rift Valley, but in fact the rifting system comprises three distinct limbs and links to the global network of plate boundaries. The axial region is the Afar triangle

(Ethiopia-Djibouti) from which the Red Sea arm reaches to the north, and the Ethiopian rift extends to the southwest, later to bifurcate into eastern and western branches.

The western branch passes from Ethiopia through Uganda, and via Lake Tanganyika into southern Tanzania where it is re-united with the eastern rift system (figure 1.1). The western rift is typified by a series of long troughs bounded by normal faults, and houses lakes Mobuto Sese Seko, George, Edward, Kivu, Tanganyika and Rukwa. The adjacent eastern arm, or Gregory rift valley, is most clearly defined in Kenya where classical grabens penetrate the regional domal upwarping. A string of lakes follow its course southward through Kenya and into Tanzania, including Turkana, Baringo, Bogoria, Nakuru, Elmenteita, Naivasha, Magadi, Natron, Eyasi and Manyara.

With few exceptions the lakes of the rift valleys owe their inception to the rifting process itself, creating a variety of fault structures that now hold lakes. Half grabens are responsible for the majority of the lakes, with examples including Turkana, Natron, Manyara and Eyasi, whereas Baringo, Bogoria, Elmenteita and Magadi have formed within full grabens (Baker 1986). Naivasha and Nakuru have resulted from a combination of structure and volcanism, the latter creating dams in the early history of these lakes (Baker 1986).

The lakes of the eastern rift excluding Turkana, are generally smaller and shallower than those of the western rift, a consequence of tectonics, volcanism and climate. Of these three Yuretich (1982) identifies volcanism as having the most profound influence. As well as leading to the evolution of distinctive water chemistry and mineralogy, easily erodible volcanic materials contribute to the extremely high rates of sedimentation found in eastern rift lakes, whereas resistant crystalline rocks effectively starve the lakes of the western arm of sediments (Yuretich 1982). Drainage in the eastern branch also owes much to the presence of porous volcanic deposits, reducing surface flows and creating the extensive groundwater systems feeding lakes such as Nakuru and Magadi. However, the contemporary morphology and limnology of these rift valley lakes has emerged from their recent climatic history, and the reconstruction of this offers a rich source of palaeoenvironmental information.

Recent developments in African palaeoclimatology.

Repeated global climatic fluctuations manifested in the glaciations of the middle and high latitudes are the salient feature of the Quaternary period. It is now known that equally dramatic and striking climatic changes occurred within the tropical regions,

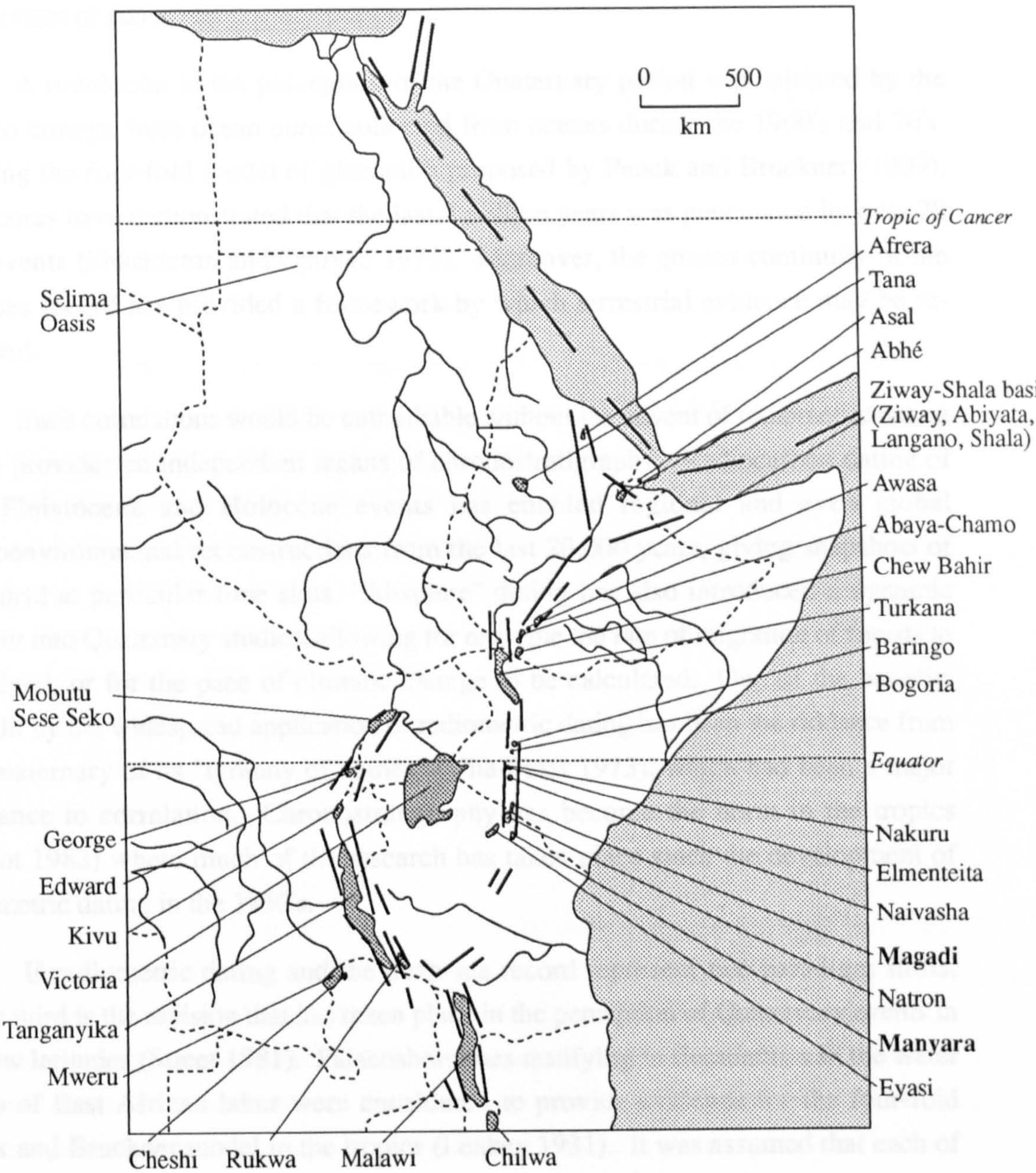


Figure 1.1. East African lakes

resulting in high altitude glaciations, the expansion and contraction of deserts, migrations of the major biomes, and most significantly for this study, massive changes in the extent of lakes.

A revolution in the perception of the Quaternary period was initiated by the story to emerge from ocean cores collected from oceans during the 1960's and 70's. Refuting the four-fold model of glaciation proposed by Penck and Bruckner (1909), these cores have demonstrated that the last 2 million years was punctuated by over 20 such events (Shackleton and Opdyke 1973). Moreover, the greater continuity of the deep sea record has provided a framework by which terrestrial evidence may be re-assessed.

Such correlations would be unthinkable without the advent of radiometric dating which provides an independent means of chronostratigraphy. Radiocarbon dating of Late Pleistocene and Holocene events has enabled regional and even global palaeoenvironmental reconstructions from the last 20,000 years, giving snapshots of the world at particular time slots. "Absolute" dating has also introduced a dynamic element into Quaternary studies, allowing for example the rate of migration of forests to be judged, or for the pace of climatic change to be calculated. One of the benefits brought by the widespread application of radiometric dating has been the riddance from the Quaternary of its "tyranny of names" (Vita-Finzi 1973), which had been a major hindrance to correlation. Chronostratigraphy has become the norm in the tropics (Talbot 1982) where much of the research has taken place since the development of radiometric dating in the 1950's.

If radiometric dating and the deep-sea record represent two paradigm shifts, then a third is the revision that has taken place in the perception of Quaternary events in the low latitudes (Street 1981). Palaeoshorelines testifying to fluctuations in the water levels of East African lakes were considered to provide evidence for the four-fold Penck and Bruckner model in the tropics (Leakey 1931). It was assumed that each of the proposed European glaciations corresponded to a "pluvial" episode in the tropics, as ratified at the 3rd Pan-African Congress on Prehistory (Clark 1957). Moreover, Nilsson (1947) attempting what Goudie (1983) called the "ultimate in transcontinental glacial=pluvial correlation", extended the ill-fated Penck and Bruckner model to deposits from three continents.

These views began to be challenged on both stratigraphical and theoretical palaeoclimatic grounds during the late 1950's and 60's. For example, Tricart writing in 1956 (as quoted in Street 1981);

"Two geographical types of pluvials are therefore to be distinguished: those of middle latitudes which coincide with glaciations and those of low latitudes which on the contrary fall within the interglacial periods"

Rhodes Fairbridge (1963) was also dismissive of the Glacial=Pluvial argument when he wrote;

"The classical pluvial=glacial correlation of the great East African lake deposits has bedevilled African palaeoclimatology for half a century. It rests on palpably false premises"

The glacial=pluvial hypothesis was finally overthrown in Africa by the radiocarbon dating of lake deposits. Faure *et al.* (1963) working in Niger found diatom bearing lake-deposits dating from the early Holocene, and not the time of glacial maximum as the prevailing paradigm would demand. Furthermore, Butzer *et al.* (1972) presented a series of radiocarbon dated lake-level curves indicating broad pan-continental synchroneity in these lake-level phases. Studies from elsewhere in the tropics support this revision, and consequently destroyed the notion of long term environmental stability in the low latitudes (Flenley 1979).

Lake-levels and the African Quaternary.

A convergence of evidence gathered from a diverse range of sources including the former extent of dune fields (Goudie 1983), the distribution of minerals in deltaic sediments (Pastouret *et al.* 1978), peaks of terrestrial sediments in ocean cores (Sarnthein and Koopmann 1980, Gasse *et al.* 1989a), and the migration of vegetation on tropical mountains (Flenley 1979, Bonnefille and Riollet 1988), all point to widespread aridity in the tropics at the time of the last glacial maximum. Oscillation between moist and arid regimes is the dominant palaeoclimatic signal in low latitude regions (Roberts 1990), and the most direct means to reconstruct this is through the fluctuations of closed basin lakes.

Lake-level is a product of the balance of inputs (precipitation, inflowing streams, groundwater inflows) and outputs (evaporation, outflows, groundwater seepage). The relative importance of these factors will govern the responsiveness of particular basins to changes in climate, and these will be examined in the following section.

Water balance changes can be used to model the climatic parameters responsible for maintaining the past equilibria of lakes subject to local hydrological conditions. The equilibrium water balance for any lake is given by the following equation:

$$(P.LA) + R + Gi = (E.LA) + O + Go$$

where P = precipitation on the lake surface, E = evaporation from the lake, R = runoff from the catchment, O = outflow, Gi = groundwater input, Go = groundwater leakage and LA = lake area. In a closed basin O = zero and for the general case (although not for Magadi and Manyara) it may be assumed that Gi = Go. Therefore, the equation simplifies to:

$$P.LA + R = E.LA \text{ (Langbein 1961)}$$

In its simplest form runoff (R) will be the result of precipitation into the catchment minus evapotranspiration for which a value must be found from modern analogues, hence the water balance for a lake of given area is defined by the ratio of P:E. This approach may be used to estimate former P:E ratios if the area of the palaeolake is known. Area is the climatically sensitive parameter (*cf.* Benson and Paillet 1989), whereas lake-level is a function of both the P:E ratio and basin bathymetry. The analysis can be taken a stage further if an estimate of palaeotemperatures is available (*e.g.* Bonnefille *et al.* 1990) from which the evaporation component can be deduced.

An alternative approach was suggested by Kutzbach (1980) who produced a combined water and energy balance model which he applied to Palaeolake Chad. Street-Perrott and Harrison (1985) found that Kutzbach's model generally underestimates palaeoprecipitation compared to water balance models, a discrepancy they assign to a general overestimation of palaeotemperatures and consequently evaporation rates.

The sensitivity of lakes to climate.

Water level curves must be viewed in the context of the different local hydrological characteristics possessed by lakes and their catchments (Street 1980). Present day lakes can be categorized according to their water balance characteristics (Szesztay 1974), which Street (1980) suggests allows the sensitivity to climate of the water balance for a particular lake to be assessed. The inflow and outflow parameters are unlikely to have remained unchanged in the past and hence responsiveness to climatic change will also be variable, an extreme example being when an open lake falls below its outlet.

Reservoir lakes, so termed by Street (1980), may be considered as "little more than wide places in a river" (Langbein 1961). These lakes have water inflow dominated by runoff from their catchments, whilst outflows are largely regulated by discharge through an outlet, rather than from evaporative losses. An example is Lake Mobutu Sese Seko which is fed by Lake Victoria and drains through the White Nile. The use of this type of lake in palaeoclimatic reconstruction is limited, unless they can be shown to have been closed at several times in their history as appears to have been the case for Mobutu Sese Seko (Harvey 1976).

At the opposite end of a continuum of increasing water residence time are the atmosphere controlled lakes. These lakes are extremely large in comparison to their catchments (*i.e.* the lake area:catchment area ratio or z-ratio is small) and as such the runoff component of inflow is small against the contribution from direct precipitation. Similarly, water leaving the lake will be dominated by evaporation due to the large surface area and loss by discharge will be relatively small. Examples of this type of lake include both Victoria and Malawi (Street 1980). These lakes will respond directly to changes in the precipitation/ evaporation ratio, but a low amplitude response in the water level is to be expected. However, a recent study by Owen *et al.* (1990) has shown that lake Malawi has fallen 100m within the last thousand years, suggesting the sensitivity of these atmosphere lakes may have been underestimated.

Street (1980) identifies a second continuum extending from atmosphere controlled lakes to those where runoff becomes increasingly important in comparison to the contribution of direct precipitation. Termed amplifier lakes, these are the most valuable type of lake for palaeoclimatic work. Not only does their level respond directly to changes in climatic parameters, but positive feedbacks within their catchments amplify such changes. These characteristics have been exploited in the palaeohydrological studies of the Ziway-Shala lakes of Ethiopia (Street 1979) and Lake Abhé (Gasse 1977).

Lakes Magadi and Manyara have z-ratios equivalent to those of amplifier lakes. However, their sensitivity to climate is reduced as groundwater is an important contributor to their modern water balance relative to precipitation and runoff. Groundwater fed lakes will experience a damped response to short-lived climatic events, but lagged large amplitude fluctuations may follow longer term climatic shifts. The response time is determined by the individual hydrogeological parameters of the aquifer, such as porosity, structure, relative dimensions, and antecedent conditions. Lakes supplied by deep groundwater are the least responsive and are generally poor climatic indicators, whereas shallow groundwater fed basins can be very sensitive. An

example of the latter are interdune depressions such as those surrounding Lake Chad (Servant and Servant-Vildray 1980, Gasse *et al.* 1990) which record events of only 10^2-10^3 years duration. The spatial extent of the aquifer is also important since deep groundwater systems can cross climatic zones, rendering the fluctuations of lakes supplied by them difficult to interpret if regional climatic conclusions are to be drawn.

A complex interaction of deep and shallow groundwater supplies the Magadi basin today. Magadi is the regional hydrological sump and it is likely that its deep groundwater has an extensive catchment. Shallow groundwater flows through the porous volcanics of the rift floor replenished by inflowing streams such as the Ewaso Ngiro (Eugster 1980). Under favourable conditions it is possible to estimate the recharge rate by ^{14}C dating the groundwater, but this has not proven possible at Magadi due to the presence of a large reservoir of magmatic CO_2 (Hillaire-Marcel and Casanova 1987). The modern water balance of a lake is only an insight into its responsiveness to past climatic changes. Inflows from groundwater are proportionally more important under low lake-level conditions as at present, whereas when the basin was full surface runoff would be dominant over groundwater inputs. Therefore, the sensitivity of Magadi to climate at any particular time is variable depending on the water level.

The contribution of groundwater to the hydrological inputs to lake Manyara is smaller than at Magadi, and it only becomes important in the dry season when surface contributions decline. Manyara has also a more restricted groundwater catchment, comprised principally from streams disappearing into the western basalt plateau and emerging at the foot of the escarpment. Hence, under the present hydrological situation Manyara is likely to be more responsive to small scale climatic changes than Magadi.

Patterns of Late Quaternary lake-level fluctuation in Africa

The pioneering study of Butzer *et al.* (1972) compared the lake-level records of disparate African lakes and found a surprising degree of synchroneity between these fluctuations. This was greatly extended by Street and Grove (1976 and 1979) who through the compilation of a lake-level database were able to show the geographical spread of lakes of different status for particular time slices. Their classification of lake-level status was three-fold as follows:

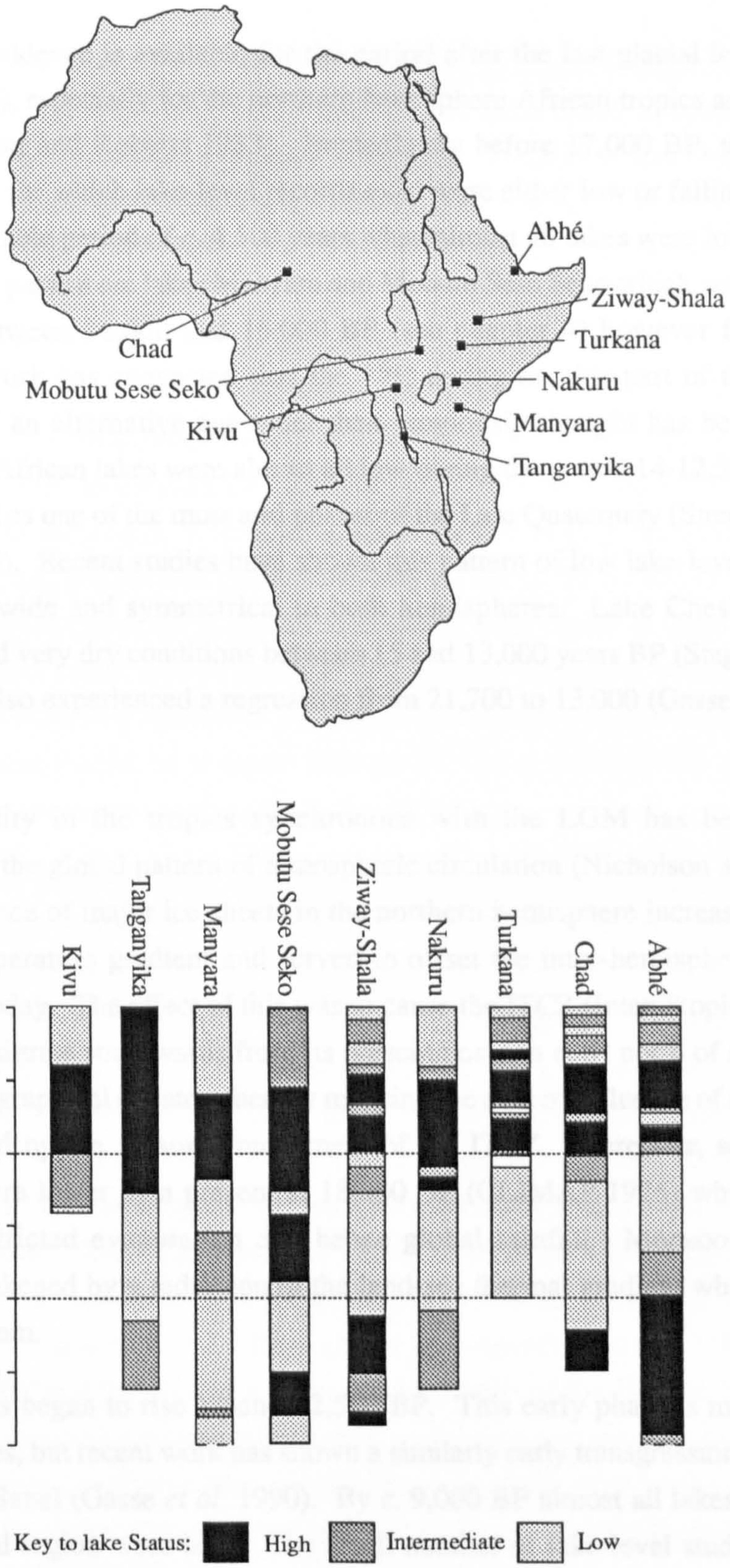
-Low, 0-15% of total vertical range, including dry lakes.

-Intermediate, 15-70% of total vertical range.

-High, 70-100% of total vertical range.

Before *c.* 18,000 BP the lake-level data are sparse and the chronology becomes more uncertain making palaeoclimatic interpretations unclear. The limited amount of evidence from this period is in part a result of desiccation and deflation of sediments during subsequent arid climatic shifts and shoreline evidence is prone to erosion by more recent transgressions. Radiocarbon dating becomes problematic for this early period due to the small amount of ^{14}C remaining in materials of this age and the error margins are accordingly great. Chronological difficulties may in part be overcome by the recent developments in U/Th dating making this method appropriate to this period. Moreover, recent reassessment of ^{14}C dates of 20,000-40,000 BP by U/Th has revealed a considerable discrepancy with a much older date of 90,000-100,000 BP (Causse *et al.* 1990). The authors conclude from this that no major humid period was experienced in the northern Sahara between 90,000 BP and 10,000 BP.

Perrott and Street-Perrott (1981) have synthesized the small amount of data available and have shown that several lakes were intermediate or high between 25,000 and 22,000 BP. One of the best sequences from this period comes from Lake Abhé, Djibouti (Gasse 1977) (figure 1.2). A major lacustrine highstand (Abhé III) is dated at 26,900 ± 700 by ^{14}C from a shell 140m above the present lake. The end of Abhé III is marked by a date from organic matter in the core at 25,600 ± 700. A regression followed this highstand although another recovery occurred at 21,000 prior to the onset of prolonged drying at *c.* 17,000 BP. Perrott and Street-Perrott (1981) also refer to a high level lake filling the Ziway-Shala basin at this time. A minimum age for this is given by a period of soil formation dated to 27,050 ± 1,540, whereas ages from calcite date the culmination of this phase to between 24,000 ± 750 and 22,000 ± 650. However, these latter two dates may be too young owing to recrystallization (Perrott and Street-Perrott 1981). More recent evidence from Lake Tanganyika supports the notion of a lacustrine transgression, as an intermediate lake level is indicated for the period 26,000-21,700 BP (Gasse *et al.* 1989b). Another recent study by Casanova *et al.* (1988), identifies an earlier lacustrine phase between 30,000 and 27,000 BP when a palaeolake 200m deep filled the Suguta valley in northern Kenya suggesting a greater degree of complexity to the lake level record of this period than has previously been envisaged.



Data Sources: Abhe, Gasse (1977); Chad, Servant and Servant-Vildray (1980); Kivu, Degens and Hecky (1974); Manyara, Holdship (1976); Mobutu Sese Seko, Harvey (1976); Naivasha, Nakuru, Richardson and Dussinger (1986); Tanganyika, Gasse *et al.* (1989), Hillaire-Marcel *et al.* (1989); Turkana, Butzer (1980); Ziway-Shala, Perrott (1979).

Figure 1.2. Lake-level status at selected African sites during the Late Pleistocene and Holocene.

More abundant evidence is available for the period after the last glacial ice-volume maximum (LGM), especially for the northern hemisphere African tropics and sub-tropics (Street-Perrott and Roberts 1983). Immediately before 17,000 BP, the majority of African lakes for which lake-level records exist were either low or falling. This was followed by a stable period of *c.* 4,500 years when almost all lakes were low. Exceptions to this general pattern are lakes Manyara and Mobutu Sese Seko which were intermediate or high between 16,000 and 15,000 BP (see chapter 4) however for Manyara recent U/Th work has suggested that the ^{14}C dating for this part of the sequence is in error and an alternative age older than previously thought has been proposed (Goetz 1990). African lakes were almost all low during the period 14-12,500 which has been described as one of the most arid phases of the Late Quaternary (Street-Perrott and Roberts 1983). Recent studies have shown this pattern of low lake-levels to have been continent wide and symmetrical in both hemispheres. Lake Cheshi, Zambia (9°S) experienced very dry conditions between 15 and 13,000 years BP (Stager 1988), and Tanganyika also experienced a regression from 21,700 to 13,000 (Gasse *et al.* 1989b).

Widespread aridity in the tropics synchronous with the LGM has been explained by changes in the global pattern of atmospheric circulation (Nicholson and Flohn 1980). The presence of major ice sheets in the northern hemisphere increased the equator to pole temperature gradient and served to offset the inter-hemispheric thermal contrast found today. The effect of this was to cause the ITCZ (Inter Tropical Convergence Zone) to migrate southwards from its present position *c.* 5° north of the equator, closer to the geographical equator, thereby reducing the area of influence of the summer rainfall initiated by the seasonal movement of the ITCZ. Moreover, sea-surface temperatures were lower than present at 18,000 BP (CLIMAP 1976) which would have greatly restricted evaporation and hence global rainfall. Monsoonal circulation was also weakened by a reduction in the land-sea thermal gradient which presently drives this system.

Lake water-levels began to rise around 12,500 BP. This early phase is most marked in equatorial lakes, but recent work has shown a similarly early transgression in parts of the Sahara and Sahel (Gasse *et al.* 1990). By *c.* 9,000 BP almost all lakes in the northern intertropical region were high. The small number of lake-level studies from the southern hemisphere are broadly in phase with this transgression. Cheshi experienced a lake-level maximum between 8,000 and 4,000 BP, and Rukwa, Tanzania (8°S) rose at 12,000 BP staying high until 4,400 BP (Haberyan 1987). Water-levels in Lake Tanganyika began to rise at 13,000 BP.

The rise in lake levels could be interpreted as either an increase in precipitation or a reduction in evaporation. However, since temperatures were rising alongside precipitation, a positive shift in moisture balance is evident. Nicholson and Flohn (1980) explain this by a rise in sea surface temperatures which in turn created the conditions suitable for enhanced evaporation and global precipitation. The increase in northern hemisphere summer solar radiation up to *c.* 10,000 BP also strengthened the monsoonal circulation increasing the supply of precipitation to sub-tropical Africa north of the equator (COHMAP 1988). Kutzbach and Street-Perrott (1985) have related lake level changes in the northern hemisphere tropics to changes in orbital forcing and in particular to the 21,000 year precessional cycle. At 18,000 BP the earth's orbital configuration was close to that today, whereas boundary conditions (*e.g.* ice sheets, sea-surface temperatures, and greenhouse gases) were very different. However, at 11-10,000 BP ice sheets had retreated and boundary conditions were closer to those of today, but the precessional cycle was in the opposite phase. Therefore, seasonal contrasts were enhanced with July insolation 7% greater and January insolation 7% lower. Kutzbach and Street-Perrott have shown through a GCM simulation how this change in seasonality triggers an enhanced monsoonal circulation.

The period of early Holocene high lake levels was only quasi-stable and many lakes showed a marked regression at 10,800-10,200 BP. High levels persisted until 8-7,500 BP when a second regressional event occurred in several sites. The majority of northern intertropical lakes recovered between 7,300 and 6,800, remaining high to *c.* 5,000 BP after which time they fell to their present relatively low levels. Several climatic mechanisms can be suggested to explain these regressional events, including the clustering of volcanic eruptions, surges of ice sheets or meltwater spikes (Street-Perrott and Roberts 1983). The latter hypothesis has been developed in a recent review by Street-Perrott and Perrott (1990). The release of meltwater from the Laurentide ice-sheet resulted in two events coincident with these regressive lake-level phases. The first was the eastwards diversion of outflow from glacial lake Agassiz into the Gulf of St. Lawrence at 10,800 BP and the second was the disintegration of the Hudson Bay ice cap at *c.* 8,000 BP. Meltwater caused a reduction in sea surface temperatures in the North Atlantic which may in itself have been insufficient to suppress evaporation and therefore precipitation. However, the release of meltwater slows down the formation of North Atlantic Deep Water which in turn provides the driving force for oceanic thermo-haline circulation. Its suppression would initiate a positive feedback mechanism by creating sea surface temperature anomalies. Moreover, cold temperatures in the Northern oceans with relatively warm southern oceanic temperatures have been correlated with recent droughts in the Sahel. Sea surface

temperature anomalies moderate the moisture convergence into the ITCZ and may cause a weakened monsoonal circulation (Street-Perrott and Perrott 1990).

Lake level fluctuation has revealed profound climatic changes throughout Africa since the last global ice volume maximum. Virtually all the lakes studied show a major expansion beginning at *c.* 12,500 (or slightly later) and extending into the early Holocene. Less well known is the fine structure of this episode, such as its exact time of inception in different parts of the tropics, and regressional events occurring within it. Distinguishing abrupt climatic shifts of 10^2 years is critically dependent on the sensitivity of the basin and the resolution of the sedimentary record. Further high resolution studies from responsive basins are required to evaluate these events. Prior to 20,000 BP more data is needed *per se*, but especially from well dated continuous records. This is vital if models such as that proposed by Kutzbach and Street-Perrott (1985) are to be tested against more than a single orbital cycle.

The reconstruction of lake-level.

Lake-level fluctuations can be studied by using a large range of geological, geochemical, and biological techniques. Reconstructions are best undertaken within the context of a multidisciplinary study, with many different analyses performed from the same samples. This overcomes the limitations and biases of individual methods and allows for more holistic conclusions to be reached. Table 1.1 demonstrates the range of investigations that have been used for Late Quaternary palaeolimnological investigations in Africa (overleaf).

TABLE 1.1. Selected examples of methods used in East African lake-level reconstructions.

	Diatoms	Ostracods	Molluscs	Pollen*	Sediment. / Mineral	Shore-lines	Stable Isotopes	Others	References
Abhé	√				√	√	√		1, 2, 3, 4
Asal	√	√	√		√	√	√	Cyano-phytes	3, 5
Baringo	√	√	√	√	√	√		Cyano-phytes	6
Bogoria	√	√	√	√	√	√		Cyano-phytes	6, 7, 8
Cheshi	√				√				9
Elmenteita	√	√			√	√			10
Manyara	√				√	√			11, 12
Mobutu Sese Seko	√				√			Testate amoebae	13, 14
Naivasha	√	√			√	√			10, 15
Nakuru	√	√			√	√		Chloro-phytes	10
Rukwa	√				√		√	Organic petrography	16, 17
Selima Oasis	√			√	√	√		Archaeol.	18
Tanganyika	√			√	√		√		19, 20, 21
Turkana	√		√	√	√	√		Archaeol.	22, 23
Victoria	√		√	√	√		√	Organic petrography	24, 25, 29
Ziway-Shala	√		√	√	√	√			3, 26, 27

[1]Gasse (1975), [2]Gasse (1977), [3]Gasse and Street (1978), [4]Fontes *et al.* (1985), [5]Gasse and Fontes (1989), [6]Tiercelin and Vincens (1987), [7]Young and Renaut (1979), [8]Vincens *et al.* (1986), [9]Stager (1988), [10]Richardson and Dussinger (1986), [11]Holdship (1976), [12]Stoffers and Holdship (1975), [13]Harvey (1976), [14]Stoffers and Singer (1979), [15]Richardson and Richardson (1972), [16]Haberyan (1987), [17]Talbot and Livingstone (1989), [18]Haynes *et al.* (1989) [19]Tiercelin *et al.* (1988), [20]Gasse *et al.* (1989), [21]Hillaire-Marcel *et al.* (1989), [22]Butzer (1980), [23]Owen *et al.* (1982), [24]Kendall (1969), [25]Stager (1982), [26]Perrott (1979), [27]Lezine and Bonnefille (1982).

* Pollen analysis is primarily a means of terrestrial environmental reconstruction rather than a lake-level indicator.

Geomorphological evidence can offer a direct and absolute means by which to reconstruct lake-levels. Shoreline features mark precisely the former extent of lakes, a possibility not afforded by other methods of lake level reconstruction which are able to suggest only relative levels. However, morphological features are only likely to be preserved from the latest lacustrine high-stand, and in order to consider previous events it is often necessary to examine the sedimentary record.

A range of characteristics held by lake sediments can often be used to elucidate relative changes in water depth. These can either directly indicate a particular lake level, or they can be related to lake-level via an intervening parameter. An important consequence of a lake becoming closed is that its salinity will begin to increase due to evaporative concentration (Langbein 1961). Therefore, a relationship exists between water depth and chemical concentration, although this is rarely direct and neither are the processes constant over time (Street-Perrott and Harrison 1985). The reconstruction of salinity offers a useful indirect route to lake level in palaeoenvironmental studies.

The properties of the sediments illustrate these two forms of relationship. Sedimentary structures and particle-size distributions are typical of certain physical environmental parameters which includes water depth, while sediment composition results from changes in the chemical environment and as such is only indirectly related to lake level. Nevertheless sedimentology and mineralogy are probably the most widely utilised techniques in palaeolimnological analysis. Each of the studies listed in table 1.1 employed these methods, although they are often secondary to other lines of analysis used in lake-level reconstructions.

The same direct and indirect relationships are held by biological remains in the sediments. Pollen and other plant remains from aquatic macrophytes found in the sediments can be used to reconstruct lake marginal communities and perhaps changes in the relative distance of these from the coring site (Street-Perrott and Harrison 1985). They can also be indirectly indicative of lake level as may be deduced from the ecological requirements of individual species. Other elements of the limnological biota can be used in this way. For example, ostracods (*e.g.* Löffler 1986), diatoms (see below), molluscs (*e.g.* Owen *et al.* 1982), and even fish (Owen and Renaut 1986) are highly characteristic of certain physical and chemical habitat characteristics, which can be applied to an interpretation of the deposits in which they are found. In addition to their use as palaeoecological indicators, the shell chemistry of ostracods has been employed to estimate palaeosalinity and palaeotemperature, giving a further dimension to their use in lake-level studies (Chivas *et al.* 1986).

The palaeoecological value of a particular organism depends on how well the following conditions are satisfied. Firstly, they should be abundant in the sediments studied in order to produce statistically significant results. This first condition effectively excludes the macro-fauna from lake-level reconstructions except on a presence-absence basis, especially if sediments are sampled from cores when small organism size becomes a virtue. Secondly, they should have well defined modern associations with environmental variables and be present in a wide range of habitat conditions. Finally, they must be readily identifiable from their fossilized remains to high taxonomic level. These conditions are all fulfilled by diatoms which explains their ubiquity in the studies listed in table 1.1.

Diatoms in African lake-level studies.

Diatoms (Bacillariophyceae) are unicellular algae with siliceous frustules. They play an essential role in the global biosphere contributing an estimated 20-25 % of world net primary production (Werner 1977). Much of this is accounted for by marine species but diatoms thrive in a variety of other habitats including soils, bogs, rivers and lakes. Diatoms have strong environmental preferences and tolerances, distinctive morphologies, and frustules which are well preserved in a variety of deposits. They are extremely abundant in particular environments, for example Bradbury (1988) reports concentrations of living diatoms under eutrophic conditions of 1,000-4,000 cells/ml. Their study is therefore a potentially powerful means of palaeoecological reconstruction which has recently been successfully exploited in studies of eutrophication, acidification, changes in sea level, as well as for long term palaeohydrological reconstructions as in this study.

Diatoms have a history of research dating back to at least 1786 when O.F. Müller wrote on the "Diatomaceen" (Werner 1977). Although Taylor (1929) attributes the first observation of diatoms to Leeuwenhoeck, as early as 1703, or to an anonymous contributor to the same edition of the Royal Society's Philosophical Transactions who described what is now known as *Tabellaria flocculosa*. Many subsequent works were to follow during the nineteenth century, for example those by Ehrenberg 1840, Smith 1853-1856, Grunow 1884 and 1889 and Cleve 1884 (cited by Battarbee 1986). Such was the growth of diatom research during the nineteenth century that by 1891 de Toni was able to cite 1500 references in a bibliography of original articles that related to diatoms (Werner 1977). These early studies were principally concerned with diatom taxonomy and systematics, their ecology was little

studied until the end of the nineteenth century with the publication of work by Cleve (1894-95).

The history of diatom research in Africa mirrors that of the subject generally. It began with taxonomic and systematic studies during the early and mid-twentieth century, for example those by Muller (1903-1910), West (1909), and Hustedt (1922) (as cited by Gasse 1986). Later research by Hustedt (1949), Hecky and Kilham (1973), Richardson *et al.* (1978), Gasse *et al.* (1983) and Gasse (1986a) has attempted to relate the distribution of modern African diatoms to various environmental parameters, thereby providing the modern ecological information vital to palaeoenvironmental studies.

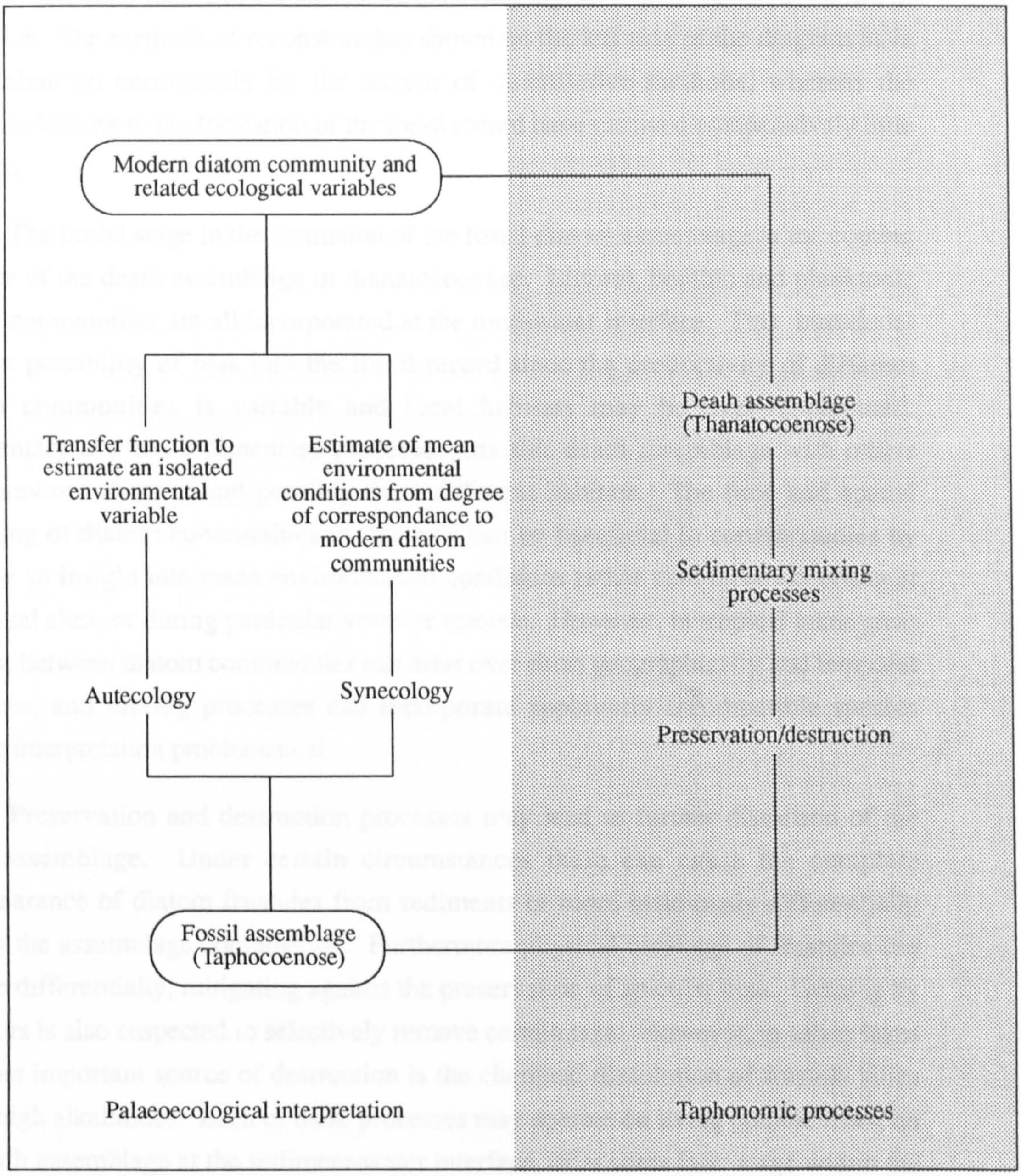
The interpretation of fossil diatom assemblages.

Modern diatom ecology can be used to provide analogues for fossil assemblages if the assumptions of uniformitarianism are fulfilled. Methods of diatom-based palaeoenvironmental reconstruction have become increasingly sophisticated and are discussed below. However, these make considerable assumptions regarding the nature and representivity of the fossil diatom record, and especially of the notion of uniformitarianism. This states that the modern distribution and ecological relationships of organisms can be used to interpret the environment in which the fossils of these organisms were once living (Roberts 1989). Furthermore, the composition of the fossil assemblage is assumed to accurately reflect that of the living community.

The imperfections in fossil assemblages have long been understood, for example Darwin paraphrasing Lyle's literary metaphor for the geological record wrote;

"Of this volume, only here and there a short chapter has been preserved; and of each page only a few lines. Each word of the slowly changing language, more or less different in the succeeding chapters, may represent the forms of life which are entombed in our consecutive formations, and which falsely appear to us to have been abruptly introduced." (Darwin 1859).

Darwin was referring to ancient geological periods, but these issues relate equally to all groups of fossils at any stage of earth history. The study of the imperfections in the fossil record is taphonomy. Its name is derived from the Greek *taphos* meaning burial, and *nomos* meaning law. It was originally proposed as a branch of palaeontology by Ebremov in 1940 (Shipman 1981).



*Palaeoecological interpretation after Gasse (1988).

Figure 1.3. Palaeoecological interpretation of diatom assemblages and intervening taphonomic processes

The taphonomy of fossil diatom assemblages follows the events intervening between the death of living communities and the formation of the fossil assemblage. This is intrinsically linked to the process of palaeoecological reconstruction as shown in figure 1.3. The methods of reconstruction shown on the left side of the diagram have been enhanced enormously by the advent of quantitative methods, whereas the processes leading to the formation of the fossil record have received comparatively little attention.

The initial stage in the formation of the fossil diatom assemblage is the coming together of the death assemblage or thanatocoenose. Littoral, benthic and planktonic diatom communities are all incorporated at the mud-water interface. This introduces the first possibility of bias into the fossil record since the productivity of different diatom communities is variable and local habitats may be over-represented. Sedimentary and bio-sedimentary processes mix this death assemblage with others from previous seasons and possibly from different habitats. The time and spatial averaging of diatom communities in this way can be beneficial to certain studies by offering an insight into mean environmental conditions rather than those occurring at individual sites, or during particular years or seasons. However, in tropical lakes great contrast between diatom communities can arise over short geographically and temporal distances, and mixing processes can incorporate apparently incompatible species making interpretation problematical.

Preservation and destruction processes may lead to further distortion of the fossil assemblage. Under certain circumstances these can cause the complete disappearance of diatom frustules from sediments or more insidiously differentially modify the assemblage composition. Furthermore physical breakage of frustules can operate differentially, mitigating against the preservation of spicular taxa. Grazing by predators is also suspected to selectively remove certain taxa. However, in saline lakes the most important source of destruction is the chemical dissolution of frustule silica under high alkalinities. Each of these processes may operate on living communities, on the death assemblage at the sediment-water interface, or at some later stage within the sediment column.

Despite the importance of these factors and the errors they can introduce into diatom-based palaeoecology, taphonomy has received relatively little attention from diatomists. With the refinement of quantitative techniques of palaeolimnological reconstruction, and their application to saline lakes, these problems require further research if the full potential of these numerical methods is to be realised.

Palaeoenvironmental interpretation of fossil diatom assemblages.

The modern preferences, tolerances and ecological distribution of individual taxa can be applied to fossil assemblages and used to reconstruct certain environmental parameters. Contemporary diatom ecology reflects the interplay of physico-chemical habitat factors and competitive interactions amongst species. Competition for resources amongst diatoms is difficult to quantify and is poorly understood, but the application of eco-physiological work to palaeolimnology will be considered at the end of this chapter. Some of the strongest relationships shown by modern diatoms are those existing with water chemistry, and consequently chemistry is particularly amenable to diatom based reconstruction. Considerable emphasis will be given to the means by which past chemical conditions can be estimated using contemporary diatom syn- and aut- ecology as analogues, but first the utilisation of diatom life-forms for the reconstruction of physical habitats will be discussed.

Reconstruction of physical habitats from diatom life-forms.

The classification of contemporary diatom taxa with respect to their life-form preferences offers a useful palaeolimnological tool by which physical habitat availability can be assessed from fossil diatom assemblages. Various life-form classifications have been proposed in the literature (Round 1984), but the following categories are probably the most widely used.

TABLE 1.2. Life-form terminology used in this study.

	Category	*Definition*
	Aerophilous	sub-aerial, moist habitats
Periphyton:	epilithic	on rock or boulder
	epipelic	on mud or silt
	epipsammic	on sand
	epiphytic	on plants
Plankton:	facultative planktonic	usually planktonic, can be periphytic
	euplanktonic	always planktonic

The life-form distinctions drawn amongst elements of the periphyton often show considerable overlap, and many species are flexible in their precise niche requirements. The adaptability of certain taxa allows them to live beyond their normal life-form. An extreme example is found in shallow, well mixed lakes where opportunistic benthic species are able to enter the plankton through the mixing process. For example in Guidimouni salt pond, Niger, the open water flora contained *Navicula elkab, Nitzschia pusilla,* and *Anomoeoneis sphaerophora*, all of which are usually considered benthic (Gasse 1987).

More problematic to palaeolimnological reconstructions are species commonly found in more than one life-form, including three of the most ubiquitous of the fossil diatoms found in this study. *Cyclotella meneghiniana, Nitzschia* sp. af. *fonticola* and *Nitzschia* "group latens", can all be found frequently in either planktonic or periphytic habitats (Gasse 1986a). Other elements in the assemblage may be of use in suggesting which life-form these fossil taxa occupied.

Aerophilous taxa are found in a wide range of sub-aerial habitats, for example on moist rock surfaces, mosses, or soils (Patrick 1977). Typical aerophilous species include *Pinnularia borealis, Hantzschia amphioxys,* and *Navicula mutica.* Their presence in lake sediments can be highly informative of palaeoenvironmental

conditions. The ratio between planktonic and periphytic forms is often calculated as a useful indicator of lake morphometry, but this should be interpreted with caution as it is equally sensitive to changes in productivity, water transparency, and the development of aquatic vegetation (Battarbee 1986, Gasse 1987).

Diatom ecology and water chemistry.

Diatoms are excellent indicators of water chemistry and can be used to demonstrate changes in the major chemical parameters of salinity, alkalinity and pH as well as variations in ionic ratios by the comparison of fossil samples to modern analogues. Two major approaches are available, the first is to use the autecological relationships found between individual diatom species and particular environmental variables; the second is to consider diatom synecology *i.e.* the relationships existing between diatom communities and environmental variables. Either method can be applied qualitatively to fossil assemblages through a series of classifications, or quantitatively using multivariate statistical techniques. The application of these techniques will be discussed following some definitions of the chemical parameters to be reconstructed.

a) Salinity and alkalinity.

Salinity and alkalinity are often used interchangeably, but they are calculated differently. Salinity may be defined as the concentration of all ionic constituents, which in a practical sense for most lakes can be reduced to the sum of 8 major ions Na, K, Mg, Ca, Cl, SO_4, HCO_3, CO_3, but others may achieve local importance (Hammer 1986). Technically, the alkalinity of water is its capacity to accept protons, and is calculated as the sum of hydroxides (OH^-), carbonates (CO_3) and bicarbonates (HCO_3). In natural waters the contribution of hydroxides to alkalinity is small in comparison to the other constituents and can be excluded from the sum (Lind 1979). A useful surrogate for salinity is electrical conductivity as this is more easily measured especially in the field. Close correlation between the two parameters has been established by studies from different brine types (Hammer 1986). Coefficients in the range 0.5 to 0.9 describe the ratio salinity (‰):conductivity ($mScm^{-1}$) at 25°C (Hammer 1986). The precise value of the coefficient depends on the ionic composition, the temperature, and the salinity of the solution in question. Chemical data presented by Kilham (1971) reveal this coefficient to be close to unity for the brines of Magadi and

Manyara with respective values being 1.18 and 0.94 (for conductivity measured at 20°C).

The relationship between alkalinity, salinity, and pH is a function of anion composition. These may be described empirically as follows:

-lakes of the sodium chloride type; as alkalinity and conductivity increase pH remains close to neutral.

-no relationship is found between pH, alkalinity and salinity for calcium-magnesium carbonate-bicarbonate waters.

-sodium carbonate-bicarbonate lakes; salinity, alkalinity and pH are highly correlated.

A considerable debate has arisen over at what point freshwater becomes saline. Various values have been suggested ranging from 0.2-5‰ (Hammer 1986). The boundary is necessarily arbitrary but an upper limit of 0.5‰ is widely used. A great number of attempts have been made to classify saline waters and have been reviewed by Hammer (1986) and Gasse *et al.* (1987). The present study will use the terminology suggested by Gasse shown below in table 1.3 which is based solely on salinity and does not include biological variables. This is preferable in many ways, and as Hammer comments, biological indices foster confusion as species thresholds and tolerances show considerable overlap. The classification of table 1.3 closely resembles that proposed by the Venice symposium on limnology (cited in Hammer 1986), with the exception of the replacement of the term "haline" with saline, the former term has overtones of chlorinity and is inappropriate to lakes dominated by other anions (Gasse *et al.* 1987). "Brackish" is also avoided as this was originated in an estuarine context and may be taken to suggest "dilute sea water" (Hammer 1986).

TABLE 1.3. Salinity classification used in this study (after Gasse *et al.* 1987).

Salinity (‰)	*Category*
0-0.5	Freshwater
0.5-5	Oligosaline
5-20	Mesosaline
20-30	Polysaline
30-40	Eusaline
40-70	Metasaline
70+	Hypersaline

b) Autecological methods.

The relation of particular diatom taxa to salinity was originally classified by the halobion spectrum (Kolbe 1927, Petersen 1943), which was developed for the freshwater-marine transition in estuarine environments. This has been of use in describing the modern and fossil floras of other coastal (*e.g.* lagoonal) environments where salinity is known to have changed (*e.g.* Ehrlich 1975, Ehrlich and Ortal 1979). Recent work has criticized the general usefulness of this system as it is directly applicable only to waters of the NaCl type (Gasse *et al.* 1987), whereas in saline lakes the dominant ion often has a greater effect on the composition of the diatom assemblages than total salinity (Gasse *et al.* 1983). For example, hypersaline lakes of the chloride-sulphate type are typified by species such as *Amphora coffaeformis, Nitzschia pusilla,* and *Mastogloia braunii,* whilst carbonate-bicarbonate systems of equivalent salinity are characterized by *Anomoeoneis sphaerophora, Navicula elkab*, and *Nitzschia* "group latens" (Gasse 1988).

Hustedt (1949) was one of the first to approach the relationship exhibited between diatom taxa and alkalinity, he produced a classification of indicator species for three different environments (table 1.4).

TABLE 1.4. pH classification after Hustedt (1949).

1. Acid waters -high representation of *Eunotia* spp. and *Pinnularia* spp.
2. More alkaline waters -high representation of *Nitzschia* spp.
2.1 Lakes with alkalinities generally less than 1.5 meq/l -*Aulacoseira* spp. dominate the plankton.
2.2 lakes with alkalinities generally greater than 1.5 meq/l -*Nitzschia* abundant.

Richardson (1968) found this classification to be inadequate when it was applied to lakes outside Hustedt's original data set. He extended this system to include variables in addition to alkalinity (temperature, silica content, and productivity) and produced a more detailed classification of indicator species (table 1.5).

Richardson's classification is not applicable to the most concentrated alkaline lakes such as those under consideration here, and the extension of Richardson's work to include these by Hecky and Kilham (1973) is of more direct interest. They found that four species, *Cyclotella meneghiniana, Thalassiosira rudolfi, Navicula elkab,* and *Nitzschia frustulum,* replace each other in the lakes studied as alkalinity increases (table 1.6).

Table 1. 5. Classification proposed by Richardson (1969)

1. Dilute lakes with low productivity, often acidic.

    1.1 Cool (temperatures <12 °C) mountain lakes dominated by *Fragilaria* (including *F. pinnata, F. bicapitata, F. strangulata* and *F. virescens*.

    1.2 Warmer lakes (12-30 °C). *Aulacoseira ikapoensis* dominant. *A.agassizii, A.nyassensis* and *Fragilaria construens* all abundant.

2. Lakes neutral or alkaline with moderate productivity and elevation.

    2.1 Lakes dominated by cyanophytes, diatoms rare. *Aulacoseira granulata* var. *angustissima* dominant.

    2.2 Lakes not dominated by cyanophytes.

        2.2.1 Lakes are moderately alkaline (0.9-4.5 meq/l)

            2.2.1.1 Silica low (<10mg/l) in surface waters.*Stephanodiscus astraea* dominant, *A.agassizii, A. ambigua, A. granulata, A. granulata* var. *angustissima, A. nyassensis, A. nyassensis* var. *victoriae, Fragilaria construens* (in smaller lakes), *Nitzschia* spp. (in warmer lakes) are all generally abundant.

            2.2.1.2 Silica in surface waters > 10 mg/l. *Fragilaria* spp. dominant with *Aulacoseira ambigua, A. granulata, A. granulata* var. *jonensis, A. agassizii* abundant.

        2.2.2 Lakes more alkaline (2-18 meq/l)

            2.2.2.1 Low silica in the surface waters (<10 mg/l). *Nitzschia* spp. (warm lakes)*Stephanodiscus* spp. dominant. *Aulacoseira goetzeana, Thalassiosira rudolfi, Surirella ngleri, Fragilaria harissonii* abundant.

            2.2.2.2 Silica >10 mg/l in surface waters. *Nitzschia* spp. (warm lakes) and *Thalassiosira* spp. dominant. *Cyclotella meneghiniana, Aulacoseira granulata* var.*angustissima, A. goetzeana* abundant.

TABLE 1.6. Classification proposed by Hecky and Kilham (1973).

1. Lakes with alkalinity less than or equal to 50 meq/l. *Cyclotella meneghiniana* dominates.
2. Lakes with alkalinities between 50 to 80 meq/l. Dominated by *Thalassiosira rudolfi* or *Navicula elkab*.
3. Lakes with alkalinities greater than 80 meq/l. Diatom flora dominated by *Nitzschia frustulum*.

The position of *Nitzschia frustulum* in this spectra is contradicted by more recent work (Gasse 1986a), and it would seem that this species is more eurytopic than Hecky and Kilham's work suggests. It should be noted that the taxonomy of *Nitzschia frustulum* is difficult and this may account for some of the apparent breadth of its distribution.

The close relationship shared by diatoms and pH is well known, and has been expressed quantitatively since Hustedt's pioneering work on the diatoms of Sumatra, Java and Bali (Hustedt 1937-39) placed modern diatoms into five pH categories, alkalibiontic, alkaliphilous, indifferent, acidophilous, acidobiontic (Battarbee *et al.* 1986). Nygaard (1956) modified Hustedt's classification by acknowledging the importance of the relative abundance of species, and by introducing weightings to the alkalibiontic and acidobiontic categories as taxa from these groups have greater predictive value. Three indices resulted which were developed further by Meriläinen (1967) and have since been widely applied. However, possibly Nygaard's most important contribution was to apply his method to the diatom record contained within a sediment core from Store Gribsø, Denmark, and thereby establishing the principle of quantitative reconstruction of chemical parameters from fossil diatoms (Battarbee *et al.* 1986). This principle has subsequently been exploited in palaeolimnological research world-wide, but perhaps most rigourously in the studies of acidification in NW Europe and North America (Battarbee *et al.* 1990, Charles *et al.* 1990). These have employed equations or transfer functions to relate modern diatom species with pH. Transfer functions for pH (Gasse and Tekaia 1983, Gasse 1986b) and conductivity (Gasse unpublished) have also been calculated for East African diatoms. These methods have been adopted in this study and are described in the following chapter.

Theoretically, it should be possible to construct transfer functions for environmental variables other than pH and conductivity if a sufficiently strong relationship to contemporary diatom communities can be established. Indeed several authors have tried to use diatoms as indicators of palaeotemperatures which would be extremely valuable in palaeoclimatic reconstructions (*e.g* Servant and Servant-Vildray 1980). Unfortunately these studies have generally proved inconclusive (*e.g.* Haworth 1976) with most diatoms appearing to be eurythermic beyond a macro scale division of polar and tropical types. Within Africa diurnal temperature differences are often much greater than temperature gradients between sites (Gasse *et al.* 1983). It would seem that palaeotemperatures can be better represented by studies of other organisms, for example from ostracod shell chemistry (Chivas *et al.* 1986) or from pollen analysis (Bonnefille *et al.* 1990).

c) Synecological methods.

A second approach available to the interpretation of fossil diatom assemblage is to compare the whole assemblage, either qualitatively or statistically, to its nearest living community, under the assumption that the environmental situation associated with contemporary diatom population is analogous to that which supported the fossil community. Since the ecological niche is not defined by isolated variables but by a whole series of parameters the more holistic palaeoecological approach offered by this method has much merit. However, in practical terms this is difficult to achieve as the range of potential diatom communities is enormous and far exceeds the number of analogues yet available.

Gasse *et al.* (1983) undertook an extensive survey of the synecology of East African diatoms. Statistical techniques were used to classify the diatom community data and to identify the relationships present with a large range of environmental variables, including the concentrations and ratios of major ions, temperature, water balance, climate, silica concentration, turbidity, water depth and geology. This survey included 210 samples from 98 localities with 579 taxa, which were classified into 5 major groups and 17 assemblages using Factor Analysis of Correspondence (table 1.7).

TABLE 1.7. Major habitat types and diagnostic taxa. After Gasse *et al.* (1983).

Group 1. Highland peat bogs and lakes, tropical acid swamps. *Eunotia* and *Pinnularia* - uncommon to abundant.
Group 2. Freshwater lake periphyton, swamps, rivers. *Achnanthes, Amphora, Cocconeis, Cymbella, Navicula, Nitzschia* - abundant.
Group 3. Freshwater lake plankton.*Aulacoseira* spp. and/or *Fragilaria acus* abundant.
Group 4. Alkaline rift lakes and crater lakes, hot springs, plankton and periphyton. *Nitzschia* spp., *Thalassiosira rudolfi*, *Anomoeoneis sphaerophora, Rhopalodia gibberula* - common to abundant.
Group 5. Closed tectonic or volcanic lakes, hot springs, plankton and periphyton. *Amphora coffaeformis, A. tenerrima, Campylodiscus clypeus, Mastogloia* spp., *Nitzschia punctata* - common to abundant.

It was found that the variables relating to water chemistry, and in particular, ionic concentration (pH, alkalinity) were the most statistically influential factors describing diatom groups 1, 3 and 4. Group 5 is best related to habitats of high salinity and sodium chloride concentration. Microhabitat (swamps, rivers or life-form in the lake) is the strongest factor influencing the diatom assemblages of group 2. Group 3 includes assemblages found in the plankton of many relatively dilute East African lakes and is characterized by *Aulacoseira* and *Fragilaria* species. This group includes lakes of low to moderate alkalinity (0.8 - 12 meq/l), neutral to high pH and carbonate-bicarbonate waters. Particular assemblages within this group seem related to lake hydrology, assemblage 3a is found in lakes whose hydrological input is largely a result of runoff, whilst 3c occurs in "atmosphere- controlled" lakes (Street 1980). In contrast to the relatively dilute lakes occupied by the diatoms of group 3, the lakes of group 4 are generally silica rich and more chemically concentrated. These lakes were found to have alkalinities of 14 - 965 meq/l and pH's between 9.1 and 10.6.

This study found only weak correlations between diatom assemblages and temperature, and diatom assemblages and silica content, the latter being particularly surprising given the importance of silica for frustule development. Statistical studies such as this do not allow causal variables to be isolated; for example, it is difficult to determine the respective influences of specific ions against ionic ratios. However, they

do allow the major environmental parameters explaining the composition of particular diatom communities to be determined.

Eco-physiological approach.

While most modern analogue studies approach diatom analysis from an empirical ecological perspective, an alternative viewpoint is provided by laboratory based physiological experiments. These have examined the role of limiting nutrients and resource relationships for individual temperate diatom species grown in culture (Kilham and Tilman 1975, Kilham and Kilham 1980, Tilman *et al.* 1982). Little physiological work has been undertaken on African diatoms, although many of the temperate species analysed are also found in Africa.

These studies are especially valuable in understanding processes such as resource competition which are difficult to measure outside the controlled laboratory environment. Physiological work has demonstrated resource competition amongst different diatom genera, and particularly clear relationships are found for silica and phosphorous (Kilham *et al.* 1986). Genera are replaced as the Si:P ratio is changed, leading Kilham *et al.* to propose that planktonic *Fragilaria* require high Si:P ratios, but when this is reduced *Nitzschia* and then *Stephanodiscus* are able to become abundant. Nitrogen appeared to be a less important limiting nutrient than either Si or P except for certain species that are obligate nitrogen heterotrophs such as *Nitzschia fonticola*. This original eco-physiological observation made by Cholnocky is supported by field observations in which *Nitzschia fonticola* has been found living heterotrophically on colonies of the cyanophyte *Microcystis* (Kilham *et al.* 1986).

The difficulty of all laboratory based studies is knowing how well the hypotheses generated are transferable to the real world situation (*cf.* the dissolution experiments of chapter 5). Experimental work is able to identify causal relationships only when individual variables can be isolated, and results may become unpredictable when a melange of environmental variables and other organisms are introduced. However, they provide a useful starting point, producing hypotheses which are falsifiable from carefully collected modern ecological data. Eco-physiological studies can also be used to explain palaeoecological problems (*e.g* Kilham and Kilham 1990), but at present their utility is limited by the relatively few species that have been studied.

Aims and objectives.

This work forms part of a wider research project, EQUARIFT, coordinated by Maurice Taieb at the CNRS Laboratoire de Géologie du Quaternaire (LGQ), Marseille. The EQUARIFT programme has collected a series of cores from lakes Magadi, Natron, and Manyara, and used them in a palaeoenvironmental reconstruction of the region during the Late Quaternary (*e.g.* Taieb *et al.* 1989). Foremost in palaeoenvironmental work is the need for dating control, which for the EQUARIFT programme has been provided by ^{14}C, U/Th, and palaeomagnetic secular variations. A palynological investigation has suggested changes in the terrestrial vegetation, whereas other analyses, sedimentology, mineralogy, and organic matter determinations have contributed to the study of lake-level history. A list of the major participants in the EQUARIFT project is tabulated in Appendix 4.

The aims of this thesis are two-fold. Primarily it is a contribution to the central palaeoenvironmental theme of the EQUARIFT programme. Diatom analysis of the cores from Magadi and Manyara offers a unique insight into the former chemistry and water balance of these lakes. With support from the other analyses these changes in lake level may be related to regional environmental and climatic fluctuations through time. The equatorial location of Magadi and Manyara makes the study of their lake-level fluctuations particularly interesting because of the limited amount of palaeoclimatic data from this region especially for the period prior to 20,000 BP. Previous shoreline investigations at Manyara have suggested a relatively humid episode from 25-26,000 BP (Casanova 1986a) but the sedimentary record of this is poor (*cf.* Holdship 1976). Re-examination of the Manyara record and the addition of the new data from Magadi will help to evaluate this event. High lake-levels were found throughout Africa in the Early Holocene and were centred on 9,000 BP. However, the high lacustrine phase in the equatorial lakes generally occurred earlier and Magadi may have even begun to decline by this period (*cf.* Hillaire-Marcel and Casanova 1987). Therefore, the investigation of the sedimentary record spanning the Pleistocene-Holocene transition should offer a useful insight into the palaeohydrology of the region at this time.

Realising this first objective requires the assumption that the diatom assemblages found within the cores are representative of those communities once living within the lake. Unfortunately, saline lakes are not always conducive to the preservation of diatom frustules, as outlined above. Moreover, the earlier work of Holdship (1976) from Manyara has revealed several gaps in the diatom record which he suggests arises from the destruction of frustules under episodes of high chemical concentration. The process of chemical destruction, or dissolution, is to be examined

experimentally with particular emphasis given to the testing of the hypothesis of differential dissolution as this can potentially lead to considerable error in palaeoenvironmental interpretation. A second taphonomic factor which can distort the fossil diatom record in tropical lakes is the extreme contrast in environments, which can arise over short distances spatially and temporally. Mixing processes can incorporate apparently incompatible species into the same fossil assemblage, making environmental interpretation problematic. Therefore, the second aim of this thesis is to examine the role of taphonomy in tropical diatom palaeoecology in order to provide a more secure basis for palaeoenvironmental interpretation from the Magadi and Manyara cores.

The methods used in this study and the techniques employed for palaeoenvironmental reconstruction from fossil diatom assemblages are evaluated in chapter 2. Chapters 3 and 4 introduce the geographical and geological situation of lakes Magadi and Manyara respectively. The results of diatom analysis from the various cores and modern samples (Magadi only) are presented and the Manyara core is correlated with the earlier work of Holdship (1976). A series of laboratory experiments concerning the dissolution of diatom frustules has been performed and these are described in chapter 5. Taphonomy and palaeoenvironmental reconstruction are the twin themes of chapter 6 which discusses the interpretation of the cores from Magadi and Manyara and proposes models of water level fluctuation for each lake. In the concluding chapter the methodological significance of this work is summarised and the implication for regional palaeoclimatology of the lake level changes is assessed.

CHAPTER TWO: METHODOLOGY

Diatom analysis results from a series of sampling decisions, beginning with the collection of material in the field, leading through preparation techniques, and ending in the counting of slides and the presentation of data. Therefore, each stage can potentially introduce biases or errors into the analysis, and the limitations of these methods must form a part of the results discussed. This chapter presents the methods used in this study, the rationale behind them, and the problems anticipated from the decisions made. Recent advances in the application of multivariate statistics to diatom analysis have made possible the quantitative estimation of pH and conductivity (*e.g.* Gasse *et al.* 1983). Numerical techniques will be applied wherever possible in this study and the methods by which this may be achieved and the assumptions involved are to be given further consideration here.

Coring and sub-sampling.

Lake sediments may be sampled from either cores or exposed sections. In general, sections are desirable as they allow an unlimited amount of material to be collected and additional stratigraphical information to be gained. However, to obtain the greatest temporal continuity requires the collection of sediments from the lake bed, usually by the taking of a core.

The type and number of cores recovered depends upon the purpose for which they are to be applied. With few exceptions palaeolimnological research programmes in Africa have tended to address broad temporal issues (*e.g.* Pleistocene-scale climatic change) rather than detailed spatial questions such as sediment budget studies. Therefore, the collection of the longest core possible has almost invariably been the primary aim, and the lake-wide areal representivity of single cores has had to be assumed. Multiplication of long cores (>6m) has only recently been attempted (*e.g.* at Lake Turkana, Barton and Torgersen 1988) largely because of the expense of such operations. The EQUARIFT project falls within this general analytical framework, its aim being to obtain long cores from climatically sensitive equatorial lakes. Thus, analysis has been concentrated on a few relatively deep cores rather than a large number of short cores. Multiple cores were collected from Magadi, but the poor preservation of environmental indicators (*e.g.* pollen and diatoms) and the different time periods covered by the cores removed the possibility for lake-wide replication of results (see following chapter).

Piston cores using a modified Wright corer (Wright *et al.* 1984), and numerous short box cores were taken by EQUARIFT members during fieldwork in 1987 and 1988. This resulted in five piston cores from Magadi and one from Manyara (another core has already been studied from this lake by the Duke University team, (Holdship 1976)). The cores were taken at the end of the dry season (*i.e.* October-November), from exposed mudflats at Manyara (core MANE-87) and from the marginal springs at Magadi (cores NF1, NF2, NL1, BR1).

The use of littoral cores is discouraged by Dearing and Foster (1986) as these are often prone to disturbance by sedimentation processes, although this may be less of a problem in flat-bottomed lakes such as Manyara and Magadi than it would be in more steeply sloping basins. Choice of coring sites at Magadi is severely restricted by an impenetrable soda crust covering much of the lake's surface (see chapter 3), and the marginal springs are the only sites from which cores can be recovered without the use of drilling techniques. Marginal cores are conventionally assumed to contain a more incomplete sediment record than those from the lake centre. Whilst this assumption may have validity for lakes that perennially contain water (and possibly for deepwater phases at Magadi), at present the marginal springs supply the only permanent water to Magadi and in consequence probably contain the most continuous sediment sequences deposited under the present climatic regime. At Manyara, permanent water is still to be found, and it is here that the most continuous sedimentation is to be expected. The core studied here from Manyara (MANE-87) was taken from a site that is seasonally exposed, and hiatuses are inevitable, although during periods when the lake was more extensive a peripheral core might be palaeolimnologically more responsive than a central core by recording minor changes in the position of the lake margins. However interpretation of these cores may be more complex.

Diatom analysis of the Magadi cores has focussed primarily upon NF1 collected in 1987 and NL1 taken in 1988. NF2 was also taken in 1988 primarily to cover sections absent from NF1 and has only been studied in selected sections for diatoms. A preliminary investigation of BR1 scanned at 10cm intervals revealed no diatoms and this has not been subjected to further study. The cores were collected in approximately 1m sections and were stored in a cold room at LGQ, Marseille until required. Upon extraction from their tubes, the cores were bisected length-wise by a piano wire into two, one half being immediately re-sealed in polythene and returned to the cold room, the second half was logged, and sampled for the various analyses. The palaeomagnetic work required the insertion of 2cm cubes into the undisturbed core, this effectively cut the core into 2cm slices from which material was collected for the other studies.

The sampling interval used should be as fine as possible given the constraint of time available. Its adequacy is determined by the sediment accumulation rate which for the cores studied was highly variable. Therefore, no rigid sampling interval was employed and each core was examined to determine the most appropriate spacing. Firstly, raw sediment from the cores was examined at 10cm intervals to verify the presence or absence of diatoms. Samples were then collected and prepared from the 2cm slices at 20cm intervals for the diatom bearing sections of MANE-87 and NL1, and at 20-30cm intervals from the longer NF1. Analysis of these revealed the parts of each core that warranted further study. Intermediate samples from MANE-87 were prepared, reducing the spacing of levels to 10cm. Additional samples were also collected from the upper and lower sections of NF1, with emphasis placed on those areas where inter-sample variation was greatest. A second core from close to NF1 was used to examine the nature of the diatom zone boundaries. These were sampled directly from the intact half of the core in much greater detail (*i.e.* at 1cm intervals, see chapter 3).

The collection of recent diatom samples.

To facilitate the interpretation of the core material surface diatom samples were collected from several of the springs and lagoons of Magadi during fieldwork in November 1988. No visit to Manyara was made by the author and therefore a comparable study was not possible.

Bottom mud samples from the uppermost few millimetres of sediment were collected in preference to rock scrapings or water samples. These are expected to show a closer relationship to the core samples as they will have been subjected to sedimentary, taphonomic, and diagenetic processes, and are expected to represent the diatom population of the last hydrological year. This overcomes the problem of seasonal representivity encountered when only living diatoms are collected (Hecky and Kilham 1973, Metcalfe 1988). This "time averaging" is particularly important in strongly fluctuating climatic regimes, where widely differing diatom communities are to be found during contrasting seasons of the year as reported by Gasse (1987). Even bottom mud samples are not free from bias and are likely to over-represent the standing crop of diatoms relative to the core samples which will show a greater degree of mixing. The samples were fixed in alcohol and stored in the dark to prevent subsequent diatom growth, and were prepared for counting using the techniques applied to the core samples described in the following section.

Preparation of diatom samples.

The laboratory procedures used to prepare the diatom samples as outlined in figure 2.1 follows closely those given by Battarbee (1986) and Gasse (1975). Either 0.2g or 0.5g of oven-dried sediment was used, depending on diatom concentration. Carbonate material was dissolved in 10% HCl and organic materials were oxidised in 30% H_2O_2. A large amount of mineral matter remained on many of the slides after this preparation, this largely comprised volcanic glasses and various silicate minerals, which cannot be removed chemically without also destroying the diatoms. This often made counting difficult and time consuming as slides had to be greatly diluted, thereby increasing the number of traverses necessary to achieve the requisite count size. Various flotation techniques are available to separate diatoms from such minerogenic material (Battarbee 1986) but these risk the selective loss of diatoms of particular densities. It was therefore considered that the errors which might result from flotation techniques outweighed the problems of counting and identifying diatoms amongst the mass of mineral material.

Samples were washed three times after each treatment, and allowed to settle for 24 hours in between washes. This method was preferred to centrifuging the samples as diatoms could be lost when transferring between vessels, and furthermore, it avoids any risk of breaking valves during centrifugation. Whilst this method extends the preparation period considerably, the total amount of time taken is not increased greatly as a large number of samples can be processed at the same time, and other tasks accomplished during the settling periods. Occasional checks for diatoms in the water being decanted were made to verify the settling time was adequate.

After washing, the samples were diluted in their beakers to a level determined by trial and error, which resulted in a suitable concentration of valves being evaporated onto the coverslips. After homogenizing, the samples were introduced into an ultrasonic bath for a few seconds, this dispersed any agglomerations of small particles and helped to separate valves. An aliquot of sample was then allowed to evaporate on a coverslip at room temperature (for approximately 24 hours) before being mounted onto a slide in Naphrax high resolution diatom mountant.

Taxonomy.

Identification of diatoms was made at x1250 magnification on a Zeiss "Universal R" microscope, with the scanning electron microscope (SEM) used for difficult taxonomy. The major taxonomic references used included Gasse (1986a),

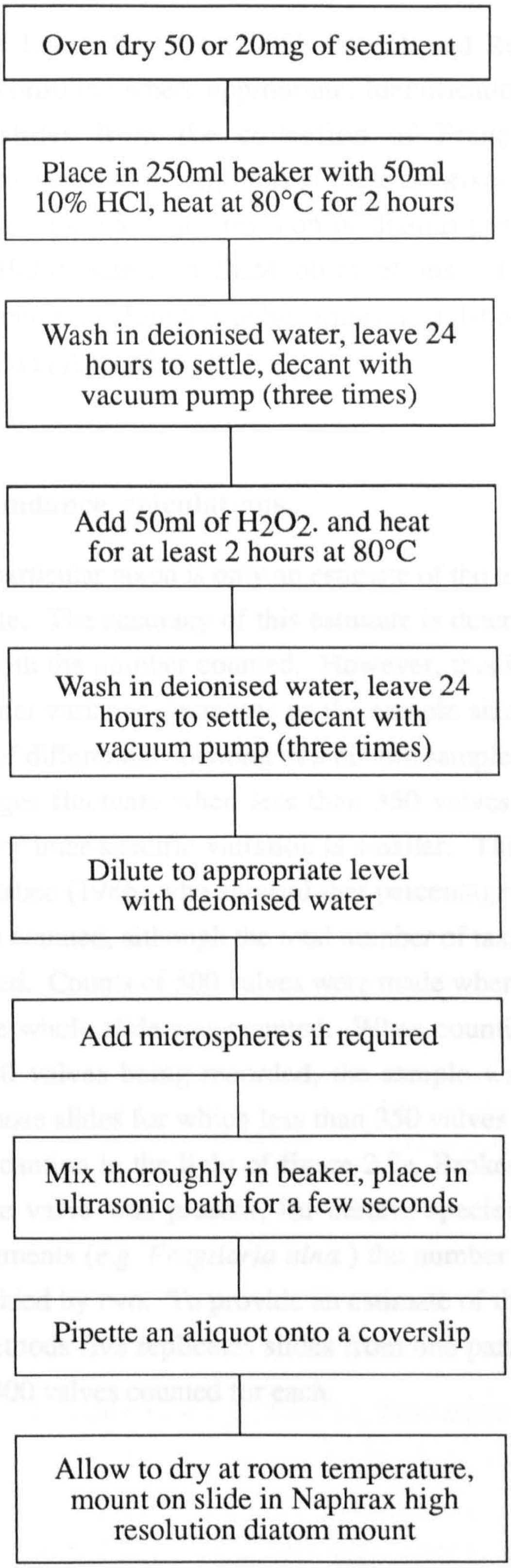
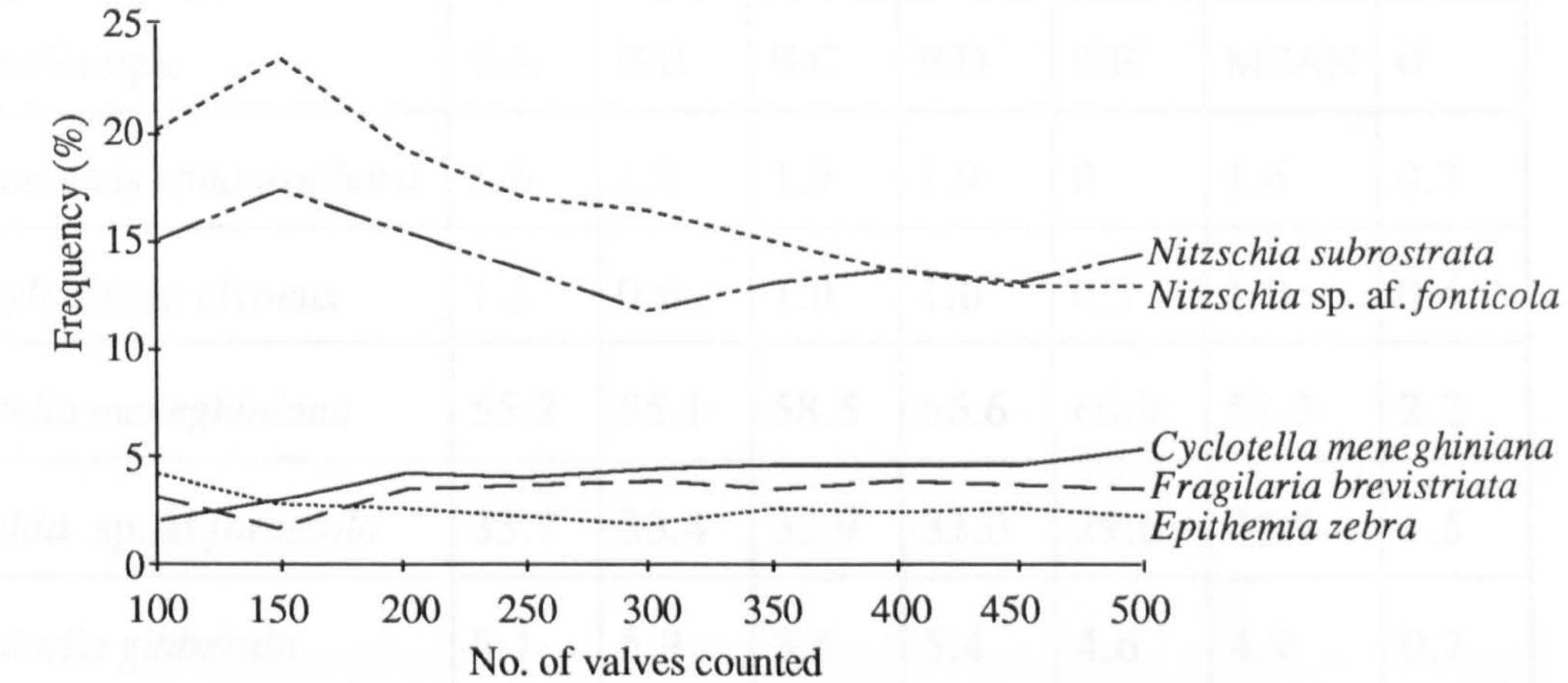


Figure 2.1. Preparation used for diatom analysis.

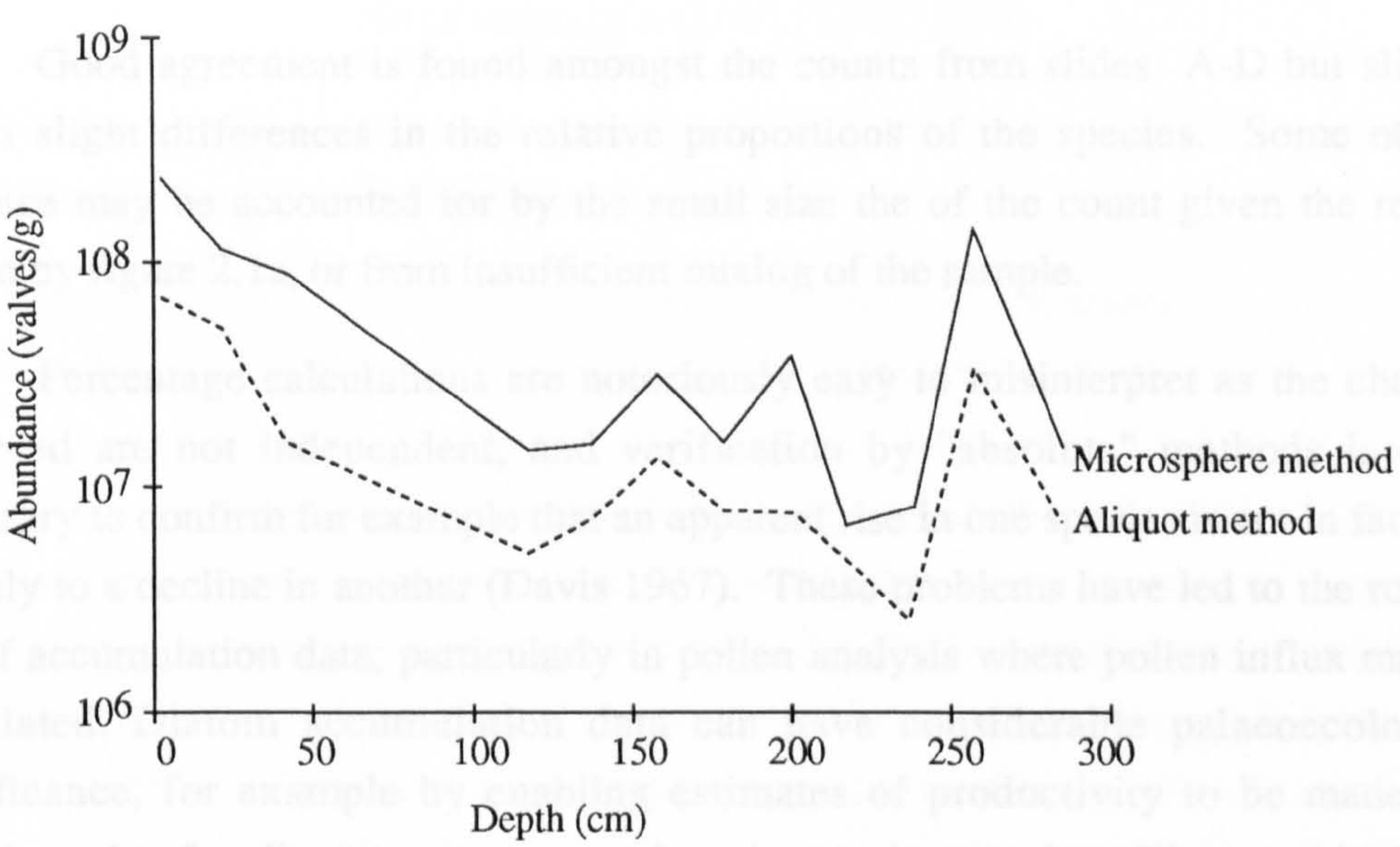
Hustedt (1930), Krammer and Lange-Bertalot (1988), Patrick and Reimer (1966, 1975) with additional sources consulted where appropriate. Identifications were also verified against reference slides from the collection of Françoise Gasse. Photomicrographs of problematic taxa and descriptions of these are given in Appendix 3. Since the completion of this study a major revision of diatom genera has been proposed by Round *et al.* (1990) based on SEM observations. Therefore the definitions used here are those current before this publication and a list of the changes relevant to this study are included in Appendix 1.

Counting strategy and abundance calculations.

The percentage of any particular taxon is only an estimate of the true proportion of that taxon in the total sample. The accuracy of this estimate is determined by the sample size which increases with the number counted. However, this is not a linear relationship and the proportional variance decreases as the sample size is extended. Figure 2.2a depicts the results of differential counting of a diatom sample from Magadi (NF1, 540cm). The percentages fluctuate when less than 350 valves are counted, while above this the amount of inter-specific variation is smaller. This agrees well with results obtained by Battarbee (1986) who showed that percentages are unstable until 300-400 valves have been counted, although the total number of taxa continues to rise as the count size is increased. Counts of 500 valves were made wherever possible, and if diatoms were scarce the whole slide was counted. When counting the entire slide resulted in less than 150 valves being recorded, the sample was rejected as unrepresentative. However, those slides for which less than 350 valves were counted must also be interpreted with caution in the light of figure 2.2a. Broken valves were counted if more than half the valve was present, for certain species which were invariably encountered as fragments (*e.g Fragilaria ulna*) the number of valve ends were counted and the total divided by two. To provide an estimate of the accuracy of the sampling and counting methods five replicates slides from one particular sample were counted (table 2.1) with 300 valves counted for each.



a) The effect of count size on percentage counts (Core NF1, 540cm).



b) A comparison of methods used to calculate diatom abundance (Core NL1).

Figure 2.2. An assessment of counting methods.

TABLE 2.1. A comparison of replicate slides.

Species/Sample	%A	%B	%C	%D	%E	MEAN	σ
Anomoeoneis sphaerophora	1.6	1.2	1.9	1.9	0	1.6	0.7
Campylodiscus clypeus	1.3	0.6	1.0	1.6	0.3	1.0	0.4
Cyclotella meneghiniana	55.2	55.1	58.5	56.6	60.9	57.3	2.2
Nitzschia sp. af.*fonticola*	33.7	33.4	32.9	33.0	29.6	32.5	1.5
Rhopalodia gibberula	5.1	5.9	3.5	5.4	4.6	4.9	0.7
Others	3.2	3.7	2.2	1.6	4.6	3.1	1.1
ABUNDANCE ($x10^6$)	34.9	45.6	35.1	35.7	40.3	40.0	4.14

Good agreement is found amongst the counts from slides A-D but slide E shows slight differences in the relative proportions of the species. Some of this variance may be accounted for by the small size the of the count given the results shown by figure 2.1a, or from insufficient mixing of the sample.

Percentage calculations are notoriously easy to misinterpret as the changes observed are not independent, and verification by "absolute" methods is often necessary to confirm for example that an apparent rise in one species is not in fact due entirely to a decline in another (Davis 1967). These problems have led to the routine use of accumulation data, particularly in pollen analysis where pollen influx may be calculated. Diatom accumulation data can have considerable palaeoecological significance, for example by enabling estimates of productivity to be made, but abundance/g of sediment can also produce interesting results. Three methods are available for estimating diatom abundance, the evaporation tray method, the microsphere method and the aliquot method, as reviewed by Battarbee (1986). The latter two techniques have been used in this study, the aliquot method was used on the earliest samples studied from the cores NF1, and MANE87, whilst microspheres were introduced to core NL1 and the samples used in the dissolution experiments.

The aliquot method is probably the most widely used abundance estimate, and is measured according to the following formula:

$$\text{No of valves/g} = V.D/A.W$$

Where V is the total number of valves on the coverslip, D is the dilution, A is the volume of the aliquot deposited on the slide, and W is the weight of dry sample. The variable most difficult to calculate is V, since it is extremely time consuming to count the whole coverslip and a partial area of the coverslip has to be assumed to be representative of the entire area. This assumption has been criticized by Battarbee (1973) who found the distribution of valves on the coverslip to be non-random. Further error might be introduced when trying to measure the size of the aliquot being evaporated which is typically less than one millilitre and an adjustable micro-pipette is essential for this purpose.

The microsphere method described by Battarbee and Kneen (1982) is developed from the exotic marker grain technique commonly used in palynology (Benninghoff 1962). A known quantity of suitable markers are introduced into the sample, in this case polystyrene spheres of 6μm diameter, and thoroughly homogenized. Diatom abundance is calculated as:

$$\text{No of valves/g} = (1/W).(TM.D/SM)$$

With TM being the total microspheres introduced into the sample and SM the number of microspheres counted on the slide.

A comparison of the two approaches has been made on samples from core NL1 from lake Magadi, as shown in figure 2.2b. The agreement between the two counts is good and a correlation coefficient of 0.902 has been calculated, although the microsphere method produced values systematically greater than the totals obtained by aliquots. This could be caused by an underestimation of the number of spheres as locating the spheres amongst the analcime spherules of the same size range abundant in these samples proved difficult, or also from errors in calculating the stock suspension of microspheres. Alternatively, the discrepancy may result from the aliquot method underestimating the number of valves, for example due to the non-random distribution of diatoms on the slide or an error in estimating the size of the aliquot introduced. However, the results are within an order of magnitude which allows some confidence in broadly comparing values derived from the different methods.

The calculation of diatom accumulation data requires a knowledge of both diatom abundance and sedimentation rates. Therefore, it has not been possible to translate these abundance values into diatom accumulation rates as the sedimentation rate is difficult to estimate from the dating available for the cores studied.

Diagram zonation.

The results of diatom analysis from the four cores studied have been presented diagrammatically as frequency histograms for selected taxa, with full counts given in Appendix 2. Zonation of the diatom diagram was undertaken to simplify the interpretation of the diatom sequence. Establishing zones is necessarily an artificial exercise as up-core changes in the frequency of species often takes place along a gradient making it difficult to place zone boundaries. The definition of diatom zones used here follows that for pollen zones expressed by Cushing (1964 in Birks 1986):

"a body of sediment distinguished from adjacent sediment bodies by differences in kind and amount of its contained fossil pollen grains and spores which are derived from plants existing at the time of deposition of the sediment."

A range of numerical methods are available to facilitate zonation, which help to remove bias and simplify the vast amount of data generated. Ideally, numerical zonation could form the basis of quantitative core correlation, following the manner suggested by Birks (1986) for regional pollen spectra. However, assemblage taphonomy and spatial differences in diatom communities make direct correlation difficult (see chapter 5). Principle component analysis was used to zone the diagram from Manyara, although several other multivariate statistical methods could have been used to calculate sample scores. The cores from Magadi were zoned qualitatively since the major changes in the diatom assemblages were particularly distinct and did not warrant the use of statistical methods.

Species diversity and palaeolimnology.

Although little used by palaeoecologists, species diversity provides a useful stand-point from which to investigate the fossil record, as this can be a useful indicator of habitat availability and the nature of the palaeoenvironment. A measure of diversity has been constructed for each of the cores in this study. Several indices are available for this purpose, but that developed convergently by both Shannon and Weiner is probably the most widely used (Magurran 1988), and has the advantage of combining the number of species encountered with a measure of their abundance. The Shannon-Weiner index (H) is constructed from the following formula:

$$H = -\sum p_i.\ln(p_i)$$

where p_i is the proportion of individuals found. The base of the logarithm for this index is often given as 2, but natural logs are increasingly becoming the standard measure and are used here (Magurran 1988). The use of proportions assumes that all species in the total population are included in the sample population. In practice this is rarely fulfilled as some sampling strategy is employed, for example diatom counting methods give only an approximation of the true fossil assemblage.

In saline lakes diversity is dependent on numerous factors including physical habitat heterogeneity, the extremity of the chemical environment, and especially when fossil assemblages are being considered- taphonomic and diagenetic processes. Relatively few species have been able to adapt to the extreme habitats provided by saline lakes resulting in species diversity being inferior to comparable freshwater bodies (Beadle 1974, Williams 1981). Therefore, an increase in species diversity might be interpreted in a crude sense as indicative of a freshening of the lake. However, diversity is also a function of niche availability, and is greater in the more varied littoral margins of lakes than the relatively homogeneous planktonic zone. Hence a change to more diverse assemblages could also result from a greater representation of littoral taxa at the coring site, perhaps caused by a change in sedimentation patterns or by a fluctuation in lake water-level.

Assemblage taphonomy can bring together species of several different environments causing an apparent increase in diversity which has no ecological basis; conversely disparities in preservation potential could artificially reduce the diversity of a fossil assemblage. Therefore, assessments of diversity have considerable utility, but the interpretation of this concept is rather enigmatic and assemblage diagenesis could create considerable distortion.

Reconstruction of water chemistry.

Chapter 1 reviewed some of the methods available for diatom-based palaeolimnological reconstruction. Former chemical conditions may be estimated using the modern aut- and synecological relationships of contemporary diatoms supplemented by ecophysiological information. The present study employs the autecological route to produce quantitative estimates for pH and conductivity. Both parameters were reconstructed for the fossil data from Magadi and Manyara using transfer functions derived from the East African diatom database (EADD) made available by Françoise Gasse. The transfer functions were derived using the following methodology and assumptions.

Chemical and diatom data were treated statistically using multiple regression analysis (Gasse 1986b). Those species which did not occur in at least three samples and did not achieve at least 2% in any one sample were excluded from the data. This produced a regression coefficient for each species against pH and conductivity. The parameter to be reconstructed *e.g.* pH for sample j is then estimated from the following equation:

$$pH_j = \sum(a_i.P_{ij}/100) + pH_t \pm e_j$$

Where a_i is the species coefficient calculated by regression; P_{ij} is the percentage of species $_i$ in sample $_j$; pH_t is the mean pH of all samples (7.93) and ej is the difference between the estimated and actual which was ± 1.0 for 96 % of cases. A correlation coefficient of 0.86 was obtained between the diatom estimated pH and its actual value. This transfer function has been applied to fossil assemblages from Mt. Badda, Ethiopia and compares favourably with the results obtained using Nygaard's indices (Gasse 1986b).

An identical approach to that described for pH has been used to establish a transfer function for conductivity (Gasse, unpublished data). The strength of the correlation derived between the estimate for conductivity and measured values is only 0.69, less than that for pH.

The values resulting from these analyses are estimates of average environmental values (Gasse 1987), and only hold if the following assumptions are satisfied.

-the transfer functions are strongest for estimates lying close to the mean of the original data (pH 7.93, conductivity 7,000μScm^{-1}), extreme values are represented by fewer samples and are therefore less secure.

-it is assumed that the diatom assemblage adequately reflects the chemical properties of the water at the time of sampling. However, pronounced seasonal and spatial variability in both diatom communities and water chemistry may be a considerable source of error. Other taphonomic and diagenetic processes can distort the relationship between the ambient chemistry and diatom flora.

-a problem arises with eurytopic species, which have broad chemical tolerances and can therefore not be relied upon to give an accurate reflection of chemical environments. A mean value is given to these species and this receives the same weight to values obtained by stenotopic species.

-transfer functions cannot be applied to samples containing a substantial number of species lying outside the database *i.e.* those that either have no modern analogue or are rare in modern samples and have been rejected on the grounds of statistical significance.

These assumptions prohibit the construction of standard errors for the diatom derived estimates of pH and conductivity calculated in this study. The problem of "quality control" in quantitative diatom reconstructions of pH has been discussed by Birks *et al.* (1990).

Conclusion.

Despite the problems considered in this chapter, many of which can be overcome within the context of a multidisciplinary study, diatom analysis remains one of the most appropriate means of reconstructing aquatic palaeoenvironments. Sampling strategies as described above can be designed so as to reduce inherent bias in the methods used and their reliability can be tested. Notwithstanding the problems of interpreting the fossil record, present day diatom communities provide useful analogues, and can by a range of analytical methods be used to interpret palaeoecological data. If it can be shown that a single environmental variable, for example pH or salinity, largely explains the distribution of modern diatom assemblages, then a transfer function approach will not result in significant amounts of information being lost. The more holistic interpretations which can arise from the use of synecological data have to be judged in the light of the difficulties involved in finding a direct analogue for the fossil assemblage. Contemporary ecological data can be effectively supplemented for a limited number of taxa by the information provided by ecophysiological studies. These approaches are consequently considered appropriate for the reconstruction of palaeoenvironments from the fossil diatom records of lakes Magadi and Manyara.

CHAPTER THREE: LAKE MAGADI, KENYA

The Gregory Rift has as its symmetrical centre the Nakuru district of Kenya. The rift system spreads laterally to both Turkana in the north and Magadi-Natron in the south, losing the elevated flanks and deep grabens of the axial region. Lake Magadi (1° 54', 36° 16') occupies a series of interconnected basins at an altitude of *c*. 600m, the lowest point in the southern Gregory rift valley. Magadi cannot be viewed in isolation without consideration of its larger, southern near-neighbour Lake Natron, with which it shares a large drainage basin of 23,207km^2. There is presently no surface connection between the two lakes, a situation known not to have been the case in the recent geological past, and in contemporary times connections may be maintained through groundwater reservoirs (Eugster 1980).

Magadi, meaning soda in Swahili, offers an appropriate description of the present lake as open water covers only 40% of the depression, the remainder giving way to a thick salt crust. This deposit of sodium carbonate or trona has been commercially exploited since 1917 by the Magadi Soda Company which is the world's second largest producer of this mineral. A combination of the economic opportunities afforded by this deposit, the almost unique hyper-saline ecosystems, and archaeological finds have made Magadi one of East Africa's most intensely studied lakes, stimulating interest amongst scientists since European explorers first visited the region in the late 19th century.

The geological background.

Volcanism in the Magadi area began 15myr ago, much later than in the northern extension of the rift valley, and it produced lavas that filled a shallow downwarp marking the site of the incipient rift (Baker 1986). In the Magadi region widespread volcanic activity ceased at about 0.8myr but it is prolonged south of Lake Natron by the presently active Oldoinyo Lengai. Development of the half-graben that eventually came to hold the Magadi-Natron basin commenced with the formation of the Nguruman fault to the west of Magadi 7myr ago. Structural evolution has continued to the present day crafting the myriad of small faults that have served to progressively deepen the Magadi-Natron trough.

The Magadi-Natron catchment spreads 150km north of Magadi to the Mau escarpment reaching an altitude of 3000m, a height equalled at the catchment's

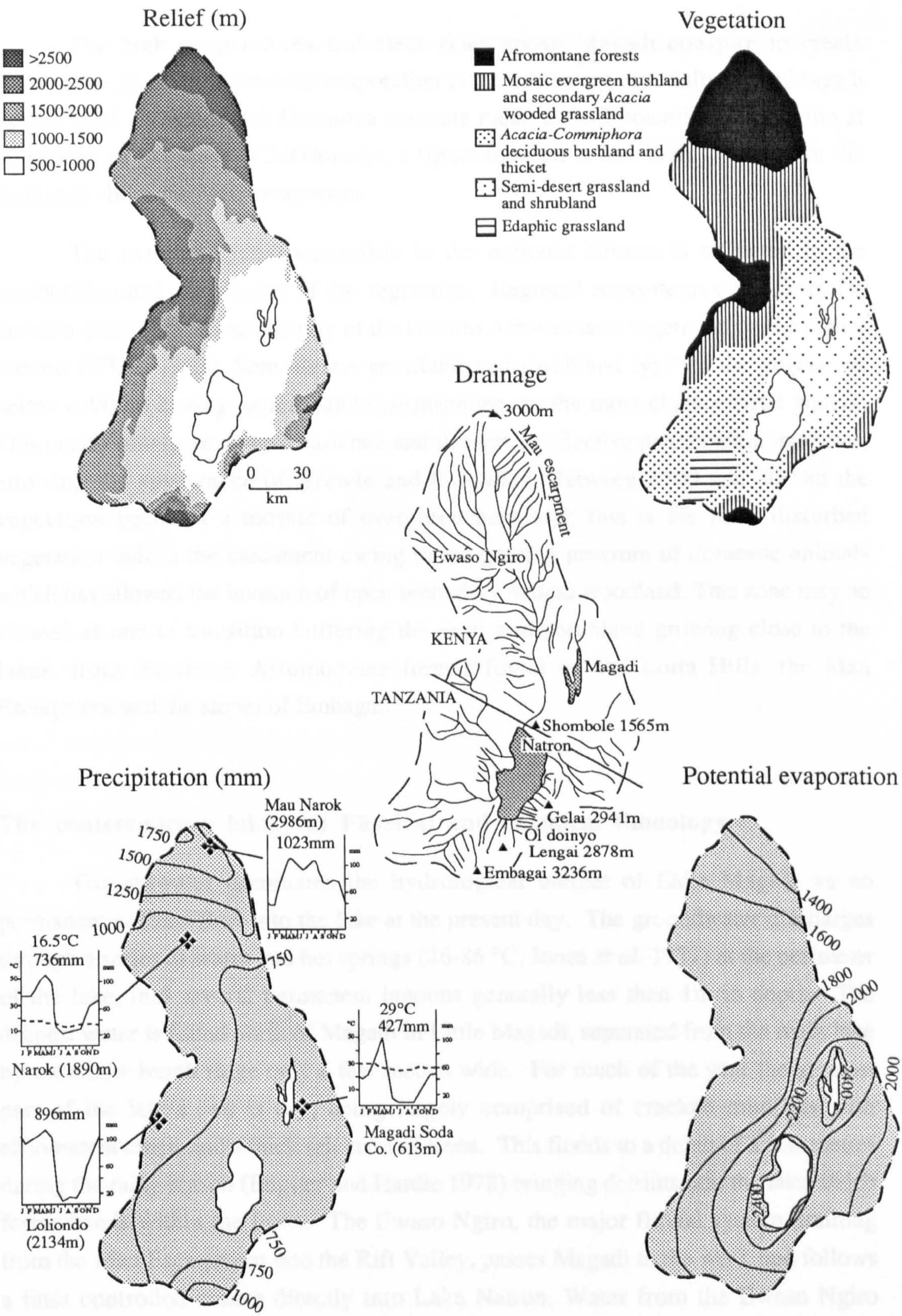
southern boundary marked by the Embagai volcano (3048m) south of lake Natron. The east-west axis of the catchment is much shorter, and is confined by the walls of the rift system, represented by the Nguruman escarpment to the west, and a more complex series of minor faults east of Magadi. The well preserved cones of Plio-Pleistocene volcanoes litter the catchment, and include Sambu (2045m), Shombole (1565m), Gelai (2942m), Embagai (3048m) and Oldoinyo Lengai (2878m).

Climate and Vegetation.

Vincens and Casanova (1987) have studied the contemporary climatology and vegetation patterns in the Magadi-Natron catchment. Only limited meteorological data have been collected in the catchment, with four monitoring stations now providing monthly records of rainfall and temperature. One of these at Loliondo, west of Magadi, has only recently been established and gives data for 5 years. Elsewhere longer records are to be found; that from Mau Narok extends 30 years, a station maintained by the Magadi Soda Company has a 52 year record, and climate statistics spanning 58 years exist from Narok. Although the records given by these stations are geographically and temporally limited, they clearly depict the semi-arid climate experienced by much of the Magadi-Natron catchment, only yielding to more humid conditions in the surrounding highlands (figure 3.1)

Rainfall in the catchment is strongly related to altitude, declining sharply from the well-watered Mau escarpment which receives *c.* 1000mm/year, to the arid lands around Magadi at the base of the rift that can expect a mean annual rainfall of only 400-500mm. Seasonally, rainfall shows a double maximum, having a long rainy season that persists from March through until May, with shorter less predictable rains falling in November. In extreme years the two rainy seasons may merge to give what is essentially a single period of precipitation between November and May. The long rains result from the northwards movement of the ITCZ bringing wet southeasterly winds from the Indian ocean to the Magadi region, whereas, the short rains are a product of the relatively dry northeasterly winds.

Temperatures also show a pronounced altitudinal gradient, maximum values are found at Magadi where mean monthly temperature seldom falls below 30 °C, this decreases rapidly with elevation, giving Narok at 1890m typical monthly average temperatures of just 17 °C. Seasonal variation in temperature is slight in comparison to spatial variations with average monthly temperatures at Magadi having a range of only 3-4 °C throughout the year.



*Data from Vincens and Casanova (1987)

Figure 3.1. Contemporary geography of the Magadi-Natron catchment.

The high temperatures and clear skies above Magadi conspire to create extremely high rates of potential evaporation in the catchment especially in the Magadi trough itself. Vincens and Casanova estimate mean annual potential evaporation at Magadi to be in excess of 2400mm/yr, a figure reduced to less than 1400mm for the highlands above the Mau escarpment.

The extreme spatial variability in the regional climate is reflected in the composition and distribution of the vegetation. Regional ecosystems range from the Somalia-Masai type in the vicinity of the lakes to Afromontane vegetation on the higher ground (White 1983). Semi-desert grassland and shrubland typifies the vegetation below *c*. 900m having *Acacia* and *Commiphora* as the most characteristic genera. This grades into more diverse bushland and thickets as effective precipitation increases, allowing the appearance of *Grewia* and *Balanites*. Between 1500 and 2000m the vegetation becomes a mosaic of evergreen bushland; this is the most disturbed vegetation unit in the catchment owing to the grazing pressure of domestic animals which has allowed the invasion of open secondary *Acacia* woodland. This zone may be viewed as one of transition buffering the semi-arid shrubland growing close to the lakes, from the dense Afromontane forests found on the Loita Hills, the Mau Escarpment and the slopes of Embagai.

The contemporary lake. a) Physical and chemical limnology.

Groundwater dominates the hydrological budget of Lake Magadi as no permanent streams flow into the lake at the present day. The groundwater discharges through a series of warm and hot springs (26-86 °C, Jones *et al.* 1977) at the perimeter of the lake, into several permanent lagoons generally less than 1m in depth. The deepest water is found north of Magadi in Little Magadi, separated from the main lake by a shallow basalt ridge only a few metres wide. For much of the year the greatest part of the lake's bed is dry, being largely comprised of cracked mudflats with efflorescent crusts and a thick salt crust of trona. This floods to a depth of a few metres during the rainy season (Eugster and Hardie 1978) bringing detritus into the lake which forms bands within the trona. The Ewaso Ngiro, the major fluvial system draining from the Mau Escarpment into the Rift Valley, passes Magadi to the west, and follows a fault controlled course directly into Lake Natron. Water from the Ewaso Ngiro probably contributes to the groundwater reservoir as do rim streams such as the Endosapia and Oloibortoto that flow perennially but disappear beneath alluvial fans before reaching the lake (Eugster 1986). Eugster and Hardie (1978) propose seepage

from Lake Naivasha as another important contributor to the deep groundwater reservoir.

The evolution of the concentrated brines of Magadi and the establishment of the trona crust has been studied in detail by Hans Eugster and his co-workers for over 20 years (Eugster 1967, Eugster 1970, Jones *et al.* 1977, Eugster and Hardie 1979, Eugster and Jones 1979, Eugster 1980, and Eugster 1986). A model has been proposed to explain the development of the trona deposit at Magadi and the chemically concentrated springs which enter the lake. Dilute runoff in the catchment is initially of the Na-Ca-HCO_3 type, gradually becoming enriched in Na relative to Cl by evaporative concentration as shown by successive hydrochemical measurements taken along the course of the Ewaso Ngiro (Jones *et al.* 1977). Bicarbonate has a four-fold dominance over the alkaline earths (Ca and Mg) in the influent streams which encourages their early loss during evaporative concentration by calcite precipitation. HCO_3 and CO_3 are more conservative and are lost slowly to the processes of CO_2 degassing and ultimately by the precipitation of trona. Both result in a rise in pH in the residual brines (Eugster 1986). Chloride inputs to Magadi are only moderate (>8ppm) and sufficient concentrations for halite precipitation are not normally reached. The suggestion has been made that carbonates are supplemented in Magadi by the natrocarbonatite ash which emanates from Oldoinyo Lengai (Baker 1986). This is disputed by Eugster who considers enough HCO_3 and CO_3 is present in the solutes entering Magadi to account for the large amounts of precipitated sodium carbonate.

The behaviour of other elements have also been traced through the Magadi system by Jones *et al.* (1977). Silica declines dramatically from the relatively high total concentrations carried by streams entering the groundwater to the much lower levels found in the emergent springs, relative to a conservative ion such as chloride. Moreover, Jones *et al.* calculate that 99% of the dissolved silica is lost to mineral precipitation during the passage through the groundwater reservoir. Phosphorous levels follow the opposite trend to that of silica becoming proportionately enhanced in the springs relative to chloride. Typical ionic concentrations found in the streams, springs and final brines of the Magadi catchment by Jones *et al.* (1977) are shown overleaf in table 3.1.

TABLE 3.1. Water chemistry of selected sites in the Magadi catchment, from Jones *et al*. 1977.

	Temp (°C)	pH	Si	Ca	Mg	Na	K	HCO_3	CO_3	SO_4	Cl	F	Br	B	PO_4	TDS	Specific Density
River																	
A	16.5	7.7	57	5.9	1.2	15	7.1	55	-	6.2	4.5	1.3	-	-	-	152	-
Springs																	
B	-	9.8	17	-	-	15,500	175	8,480	9,850	246	7,770	155	-	-	-	37,700	1.031
C	42	8.9	104	-	-	8,060	104	11,200	1,810	227	3,930	69	15	6.3	3.1	20,000	1.018
D	44	9.6	79	-	-	13,200	190	8,640	7,120	231	6,390	141	33	2.5	-	30,700	1.025
Brine																	
E	-	10.5	1,240	-	-	117,000	2,210	0	70,700	2,450	95,800	1,860	-	121	87	291,000	1.266

Key to sites with sample numbers or description given by Jones *et al*. 1977 shown in parenthesis: A Ewaso Ngiro (at Steel Bridge); B Bird Rocks, (M80); C Flamingo Nursery (M1009); D Southwestern lagoon, (M588); E Final Brine (M710). Values in mg/l, except for pH, temperature, and specific density.

b) Ecology and modern diatom communities.

Magadi's extreme environment restricts species diversity to a few specialised taxa adapted to withstand these unusual habitats. However, biological productivity in the Magadi springs is high, with large concentrations of bacteria, algae (including cyanophytes and diatoms), and an endemic fish population of *Oreochromis alcalicus grahami* [1] (Coe 1966). The fish can survive in waters with temperatures of up to 44°C and pH values of 10.5. Even these conditions exclude them from the hottest Magadi springs and also from particular locations within the more moderate springs where temperatures exceed their tolerance (Coe 1966). The springs and lagoons also support a large community of wading birds notably the Greater and Lesser Flamingos (*Phoeniconaias roseus* and *P. minor*), of which over a million pairs were counted in 1961 (Brown and Root 1971). However, 1961 was exceptional and the number at Magadi depends on the relative water levels in Natron and Nakuru. The most numerous is the Lesser Flamingo which feeds on algae, especially cyanophytes and the larger diatoms that are able to be filtered (Burgis 1987). Cyanophyte blooms at Magadi and Natron in the early 1960's followed extreme flood events and may have been responsible for a widespread fish kill (Coe 1966).

Recent diatom assemblages were collected from four peripheral lagoons and springs, Flamingo Nursery, Northern Lagoon, Bird Rocks, and the Southwestern spring during fieldwork in November 1988 (figure 3.2, plates 3.1-3.3). Samples were taken as described in chapter 2 from scraping the uppermost few millimetres of sediment.

Samples from Flamingo Nursery were collected from beneath 10-20cm of water, along a *c.* 100m transect, beginning close to the spring seepage (NFa) and ending in the shallow lagoon (NFe). NFa-d are dominated by *Navicula jakhalsensis* (48-73%) with *Nitzschia* "group latens", *Rhopalodia gibberula* and *Anomoeoneis sphaerophora*. *Navicula jakhalsensis* is described as an aerophilous form by Gasse (1986a), who encountered it frequently (19%) in a mud sample collected from a geyser at Lake Bogoria (temperature 50°C, pH 9.8, conductivity 24,000μScm^{-1}). More common are *Anomoeoneis sphaerophora*, *Nitzschia* "group latens", and *Rhopalodia gibberula* which together form an assemblage highly characteristic of shallow saline-alkaline water bodies in East Africa, that have conductivity >10,000μScm^{-1}, and pH >9.4 (Gasse 1986a, Hecky and Kilham 1973).

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[1] Formerly *Tilapia grahami* and *Sarotherodon alcalicus grahami*.

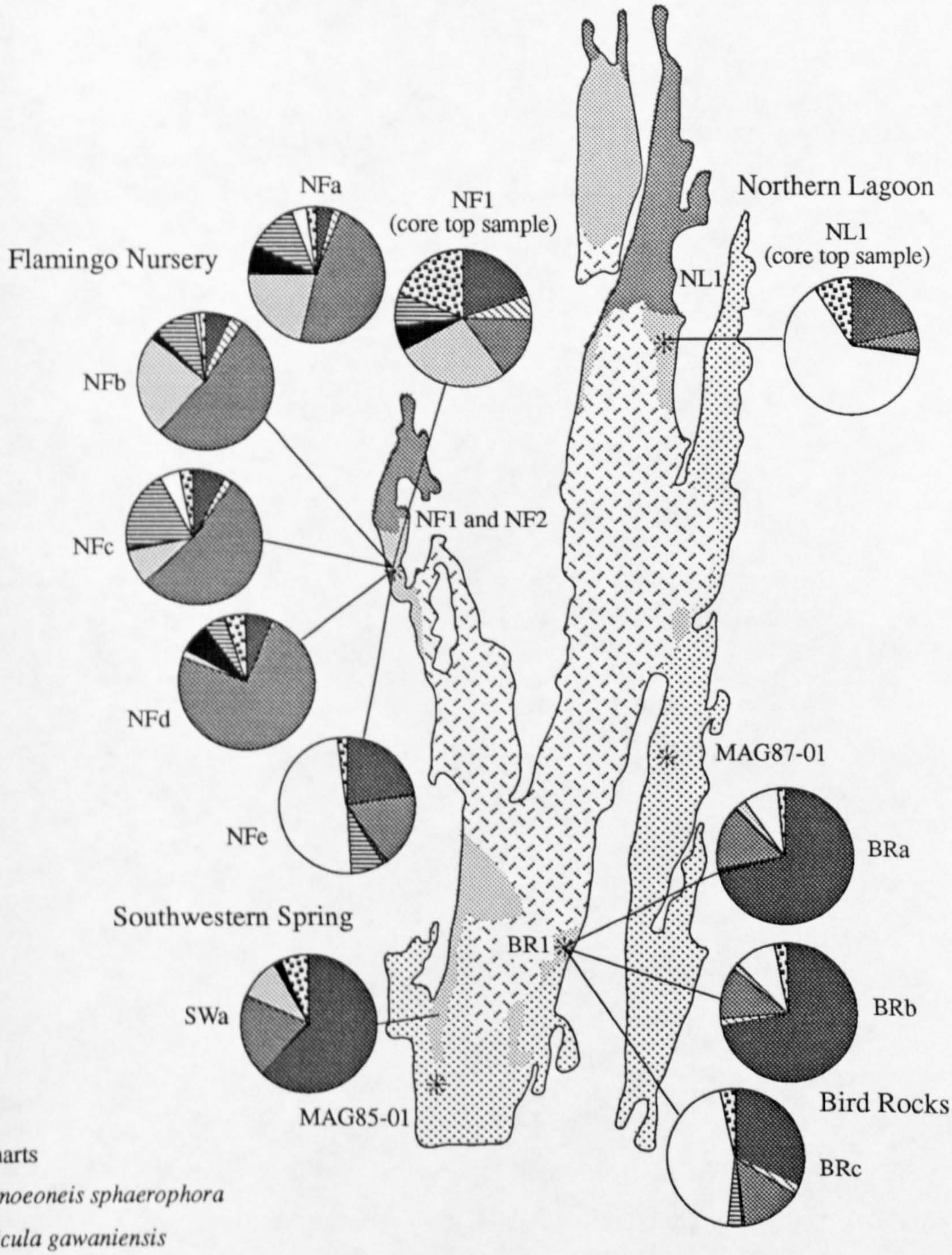


Figure 3.2. Modern diatom samples from Magadi

Captions for plates overleaf.

3.1. Flamingo Nursery.

3.2. Bird Rocks.

3.3. Northern Lagoon.

Plate 3.1

Plate 3.2

Plate 3.3

The sample collected furthest from the Flamingo Nursery spring, NFe, was also taken from the deepest water (20cm). Its diatom flora differs markedly from the others of Flamingo Nursery, in being dominated by *Stauroneis* sp. af. *wislouchii* (see Appendix 3 for taxonomic details) which accounted for 49% of the assemblage. Other species also found in NFa-d include *Anomoeoneis sphaerophora*, *Navicula jakhalsensis* and *Rhopalodia gibberula*. The dominant taxon is little reported in the literature, but was found as a rare element in the periphyton of hypersaline-alkaline lakes Nakuru and Elmenteita and hot springs in the Afar triangle of Ethiopia and Djibouti (Gasse 1986a).

The samples from Bird Rocks (BRa and BRb) and the Southwestern spring (SWa) have *Anomoeoneis sphaerophora* (62-72%) as their most abundant species, with *Navicula jakhalsensis* and *Stauroneis* sp. af. *wislouchii* present in smaller amounts. However, BRc has a closer resemblance to NFe than either of the other samples collected from Bird Rocks. *Stauroneis* sp. af. *wislouchii* (40%) is its dominant taxon, with *Anomoeoneis sphaerophora* (32%) and *Navicula jakhalsensis* (14%) also significantly represented. The close correspondence existing between the diatom communities in BRc and NFe can in part be explained by similarities in their physical habitat conditions. Both were collected considerably further from the spring outlet than the other samples and from under slightly deeper water (*c.* 20cm).

Three characteristic diatom assemblages can be distinguished from this survey of the Magadi springs (table 3.2). The classification was made with the aid of Detrended Correspondence Analysis (DCA) (CANOCO ter Braak 1987) which was used to ordinate the samples according to their species composition (figure 3.3).

Assemblage 1 incorporates samples NFa-d from Flamingo Nursery and is distinguished by having *Navicula jakhalsensis* as its most abundant element, but it also has significant amounts of *Nitzschia* "group latens". This assemblage is sub-divided into 1.1 which has both of the nominate taxa (samples NFa-c), and sample NFd which is placed separately within assemblage 1.2, since here *Nitzschia* "group latens" is proportionally replaced by *Navicula jakhalsensis*. However, the samples of these two groups are aligned along a gradient of decreasing *Nitzschia* "group latens" matched by the proportional increase of *Navicula jakhalsensis*, and the distinction drawn between them is somewhat arbitrary.

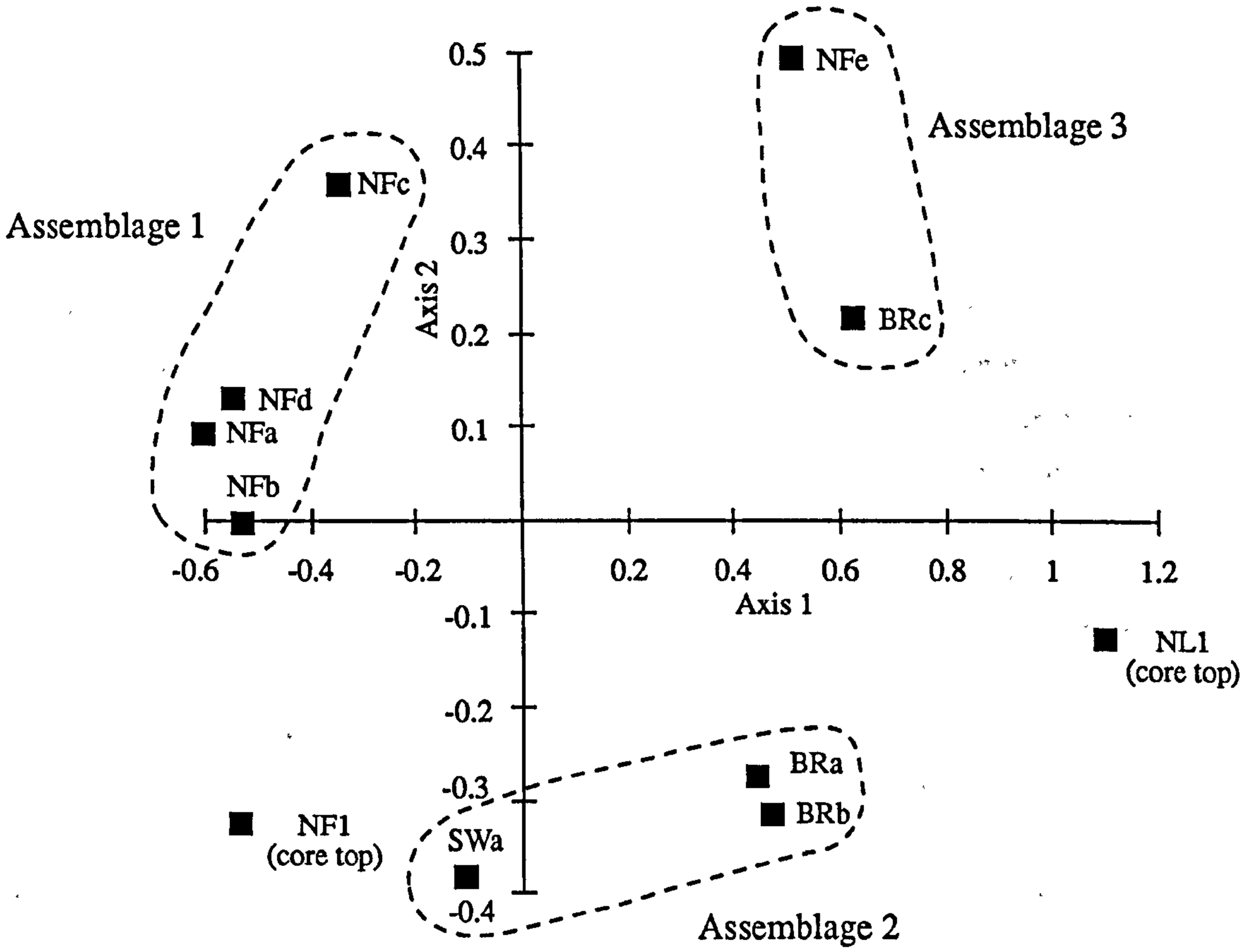


Figure 3.3. DCA ordination (axes 1 and 2) of surface samples and core tops.

TABLE 3.2. Modern diatom assemblages at Magadi.

Assemblage	Samples	Definitive species
1.1 and 1.2	NFa-d	*Navicula jakhalsensis, Nitzschia* "group latens"
2	BRa, BRb, SWa	*Anomoeoneis sphaerophora, Navicula jakhalsensis*
3	NFe, BRc	*Stauroneis* sp. af. *wislouchii*

Core-top samples from Flamingo Nursery and Northern Lagoon (see below) can also be considered to approximate modern samples. However, they are not directly comparable as they will represent conditions persisting over a longer period of deposition, and they are more prone to taphonomic and diagenetic processes than true surface muds. The uppermost sample from the Northern Lagoon (3.5cm) has an assemblage abundant in *Stauroneis* sp. af. *wislouchii* (58%) with *Anomoeoneis sphaerophora* as the second most important taxon (20%), placing it close in composition to NFe and BRc of assemblage 2. The core top sample from Flamingo Nursery (mean depth 1cm), has 33% *Nitzschia* "group latens", which is a higher percentage than found in the other surface samples. This value could be erroneous as a result of contamination from older material rich in this taxon lying immediately below this sample. *Anomoeoneis sphaerophora, Navicula jakhalsensis,* and *Rhopalodia gibberula* are also important in this sample, and occur here in similar proportions to their levels in the other modern samples. Surprisingly, the samples comprising the closest diatom assemblages to this are from Bird Rocks and the Southwestern springs and not Flamingo Nursery.

Compositional disparities found amongst the modern diatom assemblages may result from both physical (*e.g.* depth, spring discharge, temperature) and chemical variations existing between the springs. Chemical concentrations of the springs at Bird Rocks, Flamingo Nursery, and the Southwestern Springs as measured by Jones *et al.* (1977) are shown by table 3.1. No data are available for the Northern Lagoon. However, the comparison of these chemical data with those of the diatom assemblages cannot be made directly, given that the samples of Jones *et al.* were collected almost 20 years previously and at different times of the hydrological year. Furthermore, the location of the chemical samples may not equate precisely to the position from which the diatoms were collected, as the former can only be estimated from the map given by

Jones *et al.* (1977). Although problems exist, these data might still be relevant to the present study, especially since the broad chemistry of the springs is known not to have changed greatly in the period between the first chemical analysis performed by Stevens 1932 in Baker 1958), and the later work of Eugster and his co-workers (Eugster and Hardie 1978).

On the assumption that the data of Jones *et al.* do adequately describe the environments that the diatom assemblages found here were living in, some empirical relationships linking diatom composition to the chemical properties of the various springs might be suggested. Assemblages 1.1 and 1.2 (*Nitzschia* "group latens" and *Navicula jakhalsensis* dominant) are associated with the most dilute of the springs, Flamingo Nursery. TDS is 20,000 mg/l with a pH of 8.9, and the carbonate/chloride ratio is high. Assemblage 2 (rich in *Anomoeoneis sphaerophora*) is found in the more concentrated Bird Rocks and Southwestern springs. Here, pH is in the range 9.6-9.8, and TDS is 31-38,000 mg/l, but the carbonate/chloride ratio is smaller. The third diatom assemblage dominated by *Stauroneis* sp. af. *wislouchii* is difficult to categorize chemically as it contains samples from both Flamingo Nursery (NFe) and Bird Rocks (BRc), together with a third from the Northern Lagoon core top. Interestingly, this assemblage combines BRc and NFe which were both collected further than other samples from their spring outlets, suggesting that localized differences in physical habitat or water chemistry may help to explain the variation in diatom assemblages. Support for the latter is given by the Eugster-Hardie model of brine evolution, which proposes that spring waters will become increasingly concentrated by evaporation as they enter the lagoons. Hence, assemblage 3 may represent the most salt tolerant diatom community. However, more detailed chemical measurements are needed to verify these relationships between diatoms and their environments, and therefore they must remain as hypotheses.

The modern distribution of diatoms at Magadi is a product of the interplay between habitat conditions and preservation processes. Chemical conditions are undoubtedly paramount amongst the factors responsible for frustule destruction. Differences in the preservation of diatoms was observed between the various spring sites. Samples from Flamingo Nursery contained the best preserved diatoms, whilst those from Bird Rocks and the Southwestern springs showed considerable evidence of silica dissolution. Even within individual sites preservation is highly variable, with the samples collected furthest from the spring outlets (*i.e.* NFe and BRc) holding the highest proportion of partially dissolved diatom frustules. This could arise from the brines becoming increasingly concentrated with distance from the spring as proposed above to explain the differences in assemblage composition. Furthermore dissolution is

thought to selectively remove delicate taxa (see chapter 5), and preferentially enrich the assemblage in more robust species, a selection procedure which will artificially increase the similarity of two partially dissolved assemblages. Dissolution could also account for the differences found between the core top sample from Flamingo Nursery and the modern mud scrapings from this site, as the former will have had more exposure to such taphonomic processes.

The higher pH values and lower silica levels of the Bird Rocks (9.8 and 17 mg/l) and Southwestern springs (9.6 and 79 mg/l) in relation to those of Flamingo Nursery (8.9 and 104mg/l), could be important in explaining the state of preservation of the diatom frustules, since as pH rises above 9.5 the solubility of silica increases exponentially (Iler 1979) and diatom frustules will become more liable to dissolution. Therefore, the Flamingo Nursery springs and those of Bird Rocks and the Southwestern springs may fall on opposite sides of this solubility threshold for amorphous silica and consequently provide disparate environments for diatom frustule preservation, as well as different habitats for diatoms.

Therefore, these modern data provide a useful reference with which to interpret the fossil assemblages found in the cores. However, it highlights the difficulty in distinguishing the role of taphonomic and ecological factors which can both influence the composition of diatom assemblages.

Palaeolakes in the Magadi trough.

More extensive lakes than that of today have occupied the Magadi basin on several occasions since the Early-Middle Pleistocene. Evidence for these has arisen from stratigraphical studies of exposed lake beds, shoreline deposits, and latterly from sediment cores. The oldest exposures of lacustrine sediments are the Oloronga beds, resting on the 1.7myr old plateau volcanics that cover the base of the rift valley (Baker 1958, 1986). A minimum age for these deposits is 780,000yrs BP as established by the K-Ar method on a trachyte flow overriding the Oloronga beds (Fairhead *et al.* 1972). This series comprises olive-green silty-clays and cherts rich in erionite, chabazite and analcime, capped by a caliche crust (Eugster 1980). Abundant zeolites and cherts present in the Oloronga sediments led Eugster to infer that for at least part of its duration Lake Oloronga was alkaline, although freshwater gastropod shells and the localised occurrence of phillipsite are indicative of more dilute episodes (Surdam and Eugster 1976). Fluctuations in lake-level known to have occurred frequently in the Late Pleistocene suggest that the Oloronga sediments are unlikely to represent a single

lacustrine phase, instead a succession of lakes may have become established, each in turn contributing to the formation of these sediments. The lake, (or lakes) was expansive, probably filling both the Magadi and Natron basins on occasions as suggested by the broadly temporally comparable Humbu and Moinik formations of Lake Natron (Thouveny and Taieb 1984). However, the uncertainty of dating sediments of this age prohibits their firm assignment to a particular lacustrine event. The caliche crust is thought to signify a long period of desiccation following the deposition of the Oloronga lake beds prior to the development of the next major lake in the Magadi trough (Eugster 1980).

During the Late Pleistocene, lakes developed in the Magadi-Natron catchment on at least three occasions as marked by the formation of three generations of stromatolites 47-80m above the present lakes (Casanova 1986a, 1987, Hillaire-Marcel *et al.* 1986, Hillaire-Marcel and Casanova 1987). Stromatolites provide a useful indication of minimum water depth at the time of formation, and indicate the presence of a relatively stable, calcium carbonate rich water body. Stromatolites can form at great depths in certain lakes (*e.g.* Tanganyika, Casanova pers. comm.) but in the case of Magadi-Natron their biogenic component suggests an ecological zonation between 0 and 14m below the water surface (Casanova 1986b). As with other shoreline deposits stromatolites are liable to erosion by subsequent lacustrine events and short lived events are unlikely to be preserved. Stromatolites, being made essentially of calcium carbonate, can be dated directly radiometrically. This represents a great advantage over other shoreline deposits where dating is reliant on finding datable material (*e.g.* shells, organic material) "*in situ* ".

The oldest group of stromatolites are found undisturbed at just one location 80m above Lake Natron, elsewhere they are preserved merely as detrital fragments among the later stromatolitic deposits (Hillaire-Marcel and Casanova 1987). This generation is estimated by Uranium series dating to have formed *c.* 240,000 years ago (with large error margins of +34,000 and -52,000 years, Hillaire-Marcel *et al.* 1986). The second generation of stromatolites is much younger than the first, yeilding average U/Th ages of 142,000±25,000. These are well preserved on shallow slopes and are found at several locations around both lakes at an altitude of 656m.

The third and youngest generation is the most complete, it encircles both Magadi and Natron at approximately the same altitude as the second generation. Radiocarbon dating of these stromatolites places their period of formation to within the range *c.* 12,450±100 and 9,650±200 (uncorrected dates). The thirty radiocarbon dates have three modal clusters of 11,500, 10,300, and 9,000 (corrected ages after consideration of stable isotope ratios) which Hillaire-Marcel and Casanova (1987)

suggest represents three distinct phases of high and relatively stable lake levels. The single strand stromatolite girdle is interrupted by a section west of Magadi where two vertically separate bands of stromatolites 20m apart, are dated to 11,300-11,500 and at *c* 9,800. Two other dates from the earlier period were made west of Natron are found at the lower altitude, and the discrepancy is interpreted by Casanova as localized vertical tectonic displacement caused by rejuvenation of the Nguruman fault between 11,800 and 10,300 BP.

In addition to the shoreline deposits, deeper-water lacustrine deposits of Late Quaternary age are found in the Magadi basin, notably as the so-called High Magadi beds (Temperley 1951 cited in Baker 1958). The High Magadi beds are widespread at the periphery of the Magadi trough and may equate with a similar sequence from Lake Natron (Baker 1958, 1986). The beds are green and brown tuffs and clays, containing detrital silicates, reworked volcanic minerals, and authigenic zeolites. In many places the High Magadi beds contain horizons of chert and the white sodium silicate mineral magadiite first reported from Magadi by Eugster in 1967 and which has since been discovered at several other locations (plate 6.5). The same suite of minerals is found in drilled cores from beneath the trona evaporite series indicating that the High Magadi beds have lake-wide significance.

Palaeoecological interpretation of these deposits rests largely upon the carbonized fish remains identified as *Tilapia nilotica*, now named *Oreochromis niloticus* (Baker 1958, Coe 1966) which are abundant in this series either as isolated fragments or occasionally as complete skeletons forming distinctive beds. One of these skeletons has been radiocarbon dated, producing an age of 9,120±170 years BP (Butzer *et al.* 1972). This age possibly corresponds to that of the third generation of stromatolites. Therefore, we may infer that the early Holocene lake was much deeper than the maximum 13m envisaged previously (*e.g.* Eugster 1986, Baker 1986) on the grounds of a palaeoshoreline to the east of Magadi. Instead, this may refer to a regressional phase or perhaps even to a mid-Holocene lake as discussed below.

The formation of beds of fossil fish as at Magadi, implies the almost instantaneous death of a large fish population. Contemporary studies show that fish kills can result from various phenomena, and several hypotheses have been proposed to explain similar deposits elsewhere in Africa, for example at Lake Abiyata, Ethiopia (Perrott 1979). The applicability of these to the Magadi fish beds will be examined here. Algal blooms were probably responsible for recent fish kills at Magadi, as the algae can deoxygenate the water or clog the fish's gills causing asphyxiation (Coe 1966). Asphyxiation can also occur following the breakdown of stratification when anoxic bottom water is brought to the surface (Beadle 1974), either by increased

Captions for plates overleaf.

3.4 Ewaso Ngiro swamps close to Lake Natron.

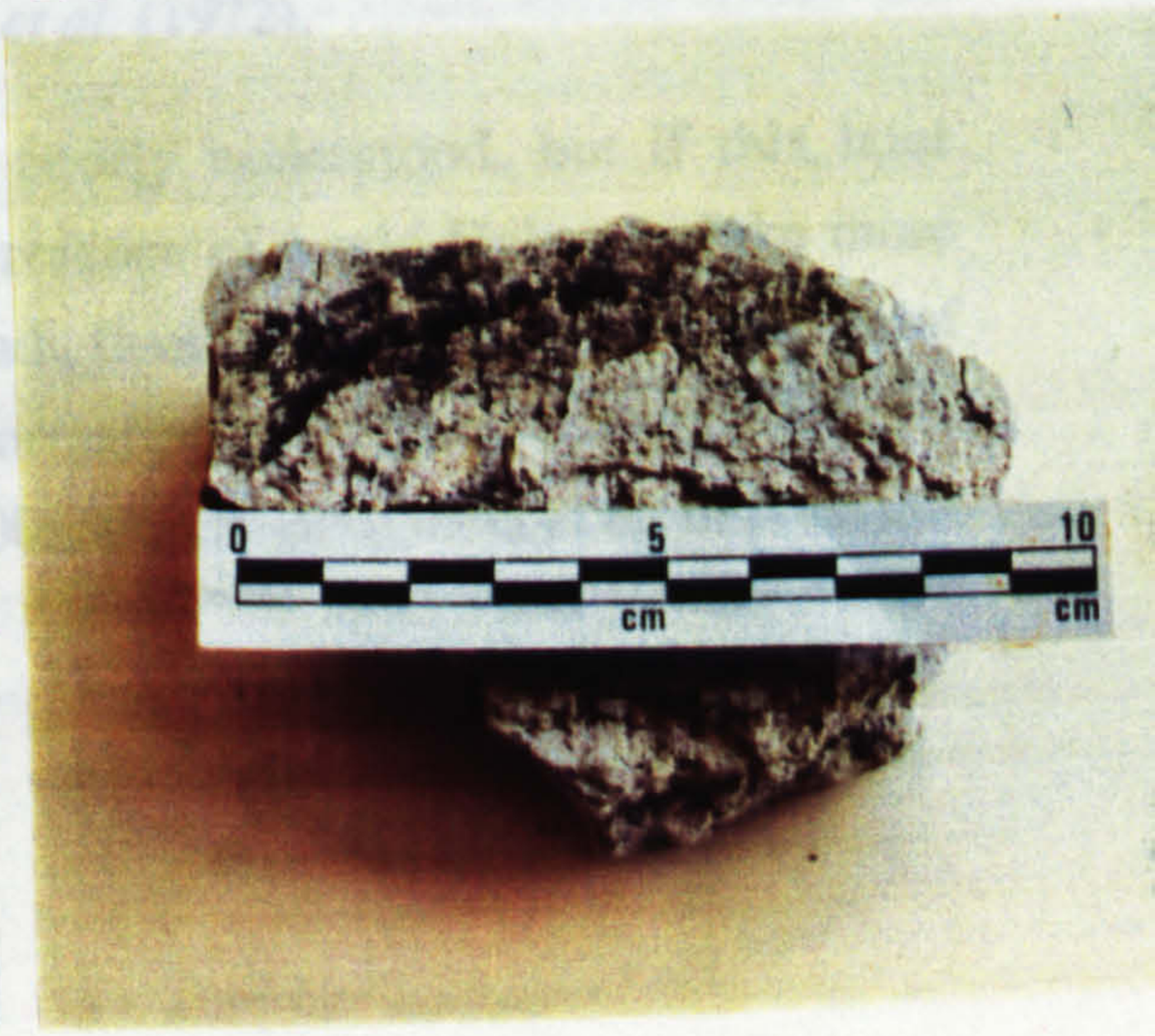
3.5. Section through High Magadi beds. The white laminae are comprised of magadiite. The Upper Tuff caps the section.

3.6. Fish fossil from the Karami section.

Plate 3.4

Plate 3.5

Plate 3.6



windiness or perhaps as a result of seismic activity at Magadi during this period. The tuffs of the High Magadi beds point to strong volcanic activity in the region at this time, and ash falling directly into the lake could have proven toxic to the fish, as hypothesized by Hillaire-Marcel *et al.* (1986). Finally, the death of the fish could be triggered by a rapid fall in lake level, leading to chemical concentration beyond the species tolerance, support for this is provided by the radiocarbon date of *c.* 9,100 yrs BP from the fish beds which places them at the end of the high lake-level phase marked by the stromatolites.

Diatoms are rare within the High Magadi Beds but in a sample from a fish bed a few diatoms (2,420 per g) were found by Eugster and Chou (1973), with the fossil assemblage dominated by *Nitzschia latens, Nitzschia fonticola, Nitzschia frustulum,* and *Nitzschia amphibia* with single valves of *Cyclotella meneghiniana, Rhopalodia gibberula, Stephanodiscus rotula* and *Cocconeis placentula.* Fieldwork at Magadi in 1988 confirmed the general absence of diatoms in the High Magadi Beds as almost all of the samples collected proved to be sterile with the exception of a single sample from the tuff above the fish beds in the Dry Lagoon south of Magadi. The Upper tuff is a homogeneous brown erionite-rich deposit found above the fish beds dated at *c.* 9,100 yrs BP. Diatoms are sparse within this unit, but a diverse assemblage was found including, *Nitzschia* sp. af. *fonticola, Nitzschia subrostrata, Cyclotella meneghiniana, Aulacoseira granulata, Rhopalodia gibba* and *Rhopalodia gibberula.*

More abundant diatoms were present in the matrix housing a fish fossil collected by Maurice Taieb from an exposure at Karami between Magadi and Little Magadi (plate 6.6). The fossil diatom assemblage was similar to that described by Eugster and Chou, being dominated by *Nitzschia* spp. (*Nitzschia* "group latens 48%, *Nitzschia frustulum* 27%, *Nitzschia* sp. af. *fonticola* 22%). The exposure contained sediments typical of the High Magadi Beds with green clays, magadiite, cherts and abundant fish bones. A radiocarbon date of 4,650±350 yrs BP was obtained from a sample of fish bones (Taieb pers. comm.), a much later age than the earlier one obtained from the High Magadi Beds by Butzer *et al.* (1972).

The Holocene history of Magadi is poorly understood, but if this later radiocarbon date is reliable, it points to the presence of a mid-Holocene lake more extensive than that of contemporary Lake Magadi, flooding the basin. The existence of a lake at this time is also indicated by the formation of diagenetic calcite in core MAG87-01, with a suggested U/Th age of 5,200±500 yrs BP (Goetz *et al.* in press).

The EQUARIFT coring programme.

A coring programme initiated by the Laboratoire de Géologie du Quaternaire, Marseille has resulted in six piston cores and several box cores being collected from Magadi between 1985 and 1988. The two longest *c.* 9m cores (NF1 and NF2) are from Flamingo Nursery in the northwestern arm of Magadi, and a 7m core was taken from Bird Rocks (BR1). Shorter cores of 2.8m were made from the Northern Lagoon (NL1), 2.2m from the dry eastern arm (MAG87-01), and 1.2m from the southwestern mudflats (MAG85-01). The present study is concerned with diatom analysis of the two cores taken from Flamingo Nursery and the shorter core from the Northern Lagoon. The latter has so far been studied only for diatoms and the sequence of assemblages in this core will be discussed after a more exhaustive analysis of the Flamingo Nursery cores. The Bird Rocks core was also examined for diatoms without success; this is rather surprising given the relative abundance of diatoms in the surface samples taken from this site.

NF1 and NF2 are parallel cores, situated just 10m apart, the second core was taken primarily in order to overlap missing sections found in the first. The Flamingo Nursery cores have been the object of a multidisciplinary study (Taieb *et al.* 1989), incorporating sedimentology (Damnati 1989), mineralogy (Quash pers. comm.), palynology (Vincens *et al.* in press), and palaeomagnetics (Williamson *et al.* 1989), in addition to diatom analysis which provides the subject of this thesis.

A tripartite division of the core is suggested by many of the analyses studied, and not least the sediment stratigraphy. The lithology of the lowest section of the core below 730cm changes from fine homogeneous clay at the base to laminated clay sediments, and incorporating horizons rich in magadiite. In contrast the central section (730-280cm) is notable for its homogeneity, comprising a uniform silt-clay except for a small section at 335cm which displays faint lamination. The major mineral present in this central section is anorthoclase with some calcite and pyrite. The lithology changes abruptly at 280cm to fine laminated clay extending to *c.* 130cm, above which the lamination disappears. Organic matter values follow this three-fold distribution, being relatively abundant in the upper and lower sections and greatly reduced in the central portion.

The chronology of the Flamingo Nursery cores is problematical, and contrasting chronologies are given by different radiometric methods. Five radiocarbon dates (three using accelerator mass spectrometry, two from conventional methods) have been obtained from total organic matter the upper and lower organic rich sections of the

core placing the sequences in the Late Pleistocene period (table 3.3). Organic matter in the central section of the core was too low to allow radiocarbon dates to be made.

TABLE 3.3. Radiocarbon dates from Magadi.

Mean depth (cm)	Radiocarbon age	Type
115	10,800±120	AMS
175	12,100±357	Classical
225	12,080±120	AMS
800	17,203±493	Classical
840	17,710±220	AMS

These ages have recently been disputed by U/Th datation, which suggests that the dates from the lower section of the core are too young, but supports those from the upper part (*viz* 10-12.5 kyr). The residence time of U/Th measured from diagenetic minerals within the central section of the core produced an age of *c.* 24,000±2000, whereas the lowest section was estimated to date in the range 30,000-50,000 years BP (Goetz 1990). Magnetic secular variation shows a marked oscillation in the central section of the core. Unfortunately this could support either time scale as similar events have been dated from both *c.* 16,000 and *c.* 24,000 elsewhere in Africa (Williamson pers. comm.).

Results of diatom analysis, a) Flamingo Nursery (NF1).

Following an initial investigation of raw sediment at 10cm intervals from the core which noted the presence of diatoms, ostracods and pollen, 55 samples were selected for detailed diatom analysis. Wherever possible counts of 500 valves were made (as discussed in chapter 2), although this had to be reduced at certain levels due to low diatom abundance. The total was increased to over 1000 valves when the assemblage was found to be dominated by a single taxon in order to count statistically significant numbers of rare diatom taxa. The three-fold division of the core suggested by many of the analyses undertaken on NF1, is valid also for the diatom analysis (figure 3.4). Three principal diatom zones are proposed, zone 3 from 869-791cm, zone 2 from 750-280cm, and zone 1 from 280-0cm.

Magadiite was noted in varying amounts on the diatom slides from zone 3 and was found to entirely comprise the samples where diatoms were absent (760cm, 809cm, 829cm, 841cm). Abundance (valves/g of dry sediment) is low throughout zone 3, and diatoms were also scarce in three other samples enabling counts of only 150 valves to be made (820cm, 850cm, 861cm). This lowest section of the core is characterized by the dominance of *Anomoeoneis sphaerophora*, with *Rhopalodia gibberula, Hantzschia amphioxys, Nitzschia* "group latens", *Nitzschia frustulum* and various *Navicula* spp. (including *Navicula mutica, Navicula tenella* and *Navicula jakhalsensis*) as commonly occurring secondary taxa (figure 3.4). However, the sample analysed at the very base of the core (869cm) differs from the rest of zone 3 and is labelled as sub-zone 3B. In addition to the species characteristic of this zone, (*e.g.* *Anomoeoneis sphaerophora* 11%, *Nitzschia* "group latens" 7%) significant amounts of *Nitzschia* sp. af. *fonticola* (13%), *Nitzschia subrostrata* (12%), *Cyclotella meneghiniana* (7%), *Navicula elkab* (5%), and *Aulacoseira granulata* (4%) were recorded. The uniqueness of this sample is demonstrated by the fact that none of the taxa mentioned above is found at levels greater than 1% in other parts of this zone.

Aerophilous taxa are very important at 861cm with *Hantzschia amphioxys* (23%) and *Navicula mutica* (9%) being particularly abundant. *Rhopalodia gibberula* becomes the dominant taxon at 850cm comprising 32% of the assemblage but high proportions of aerophilous taxa (>20%) are also found in this sample. The fossil assemblage at 842cm is notable for a return to prominence of *Anomoeoneis sphaerophora* (65%), with *Rhopalodia gibberula* and *Nitzschia frustulum* as secondary elements. The most abundant species in the samples at 820cm and 800cm are again *Anomoeoneis sphaerophora* (25% and 45%) and *Rhopalodia gibberula* (23% and 9%), however a significant share of these samples is occupied by *Nitzschia* "group latens" (17% and 15% respectively). The sample at 800cm is distinct from the others of zone 3, in that although *Anomoeoneis sphaerophora* (37%) still dominates the next most important taxon is *Navicula jakhalsensis* (25%). Other than in the assemblage from the core top this species does not occur above 2% in NF1. The zone seems to end abruptly, but a critical section of NF1 between 790cm and 767cm is missing and this boundary will be considered below with reference to the second core from Flamingo Nursery (NF2).

The most pronounced feature of zone 2 is its remarkably low temporal variability, with diatom assemblages changing little in composition throughout over 3.5m of sediment despite displaying wide species diversity. This characteristic is reflected not only in the diatom flora but also by the sedimentology, the mineralogy, the organic carbon curve and the magnetic signature. The diatom flora is dominated by

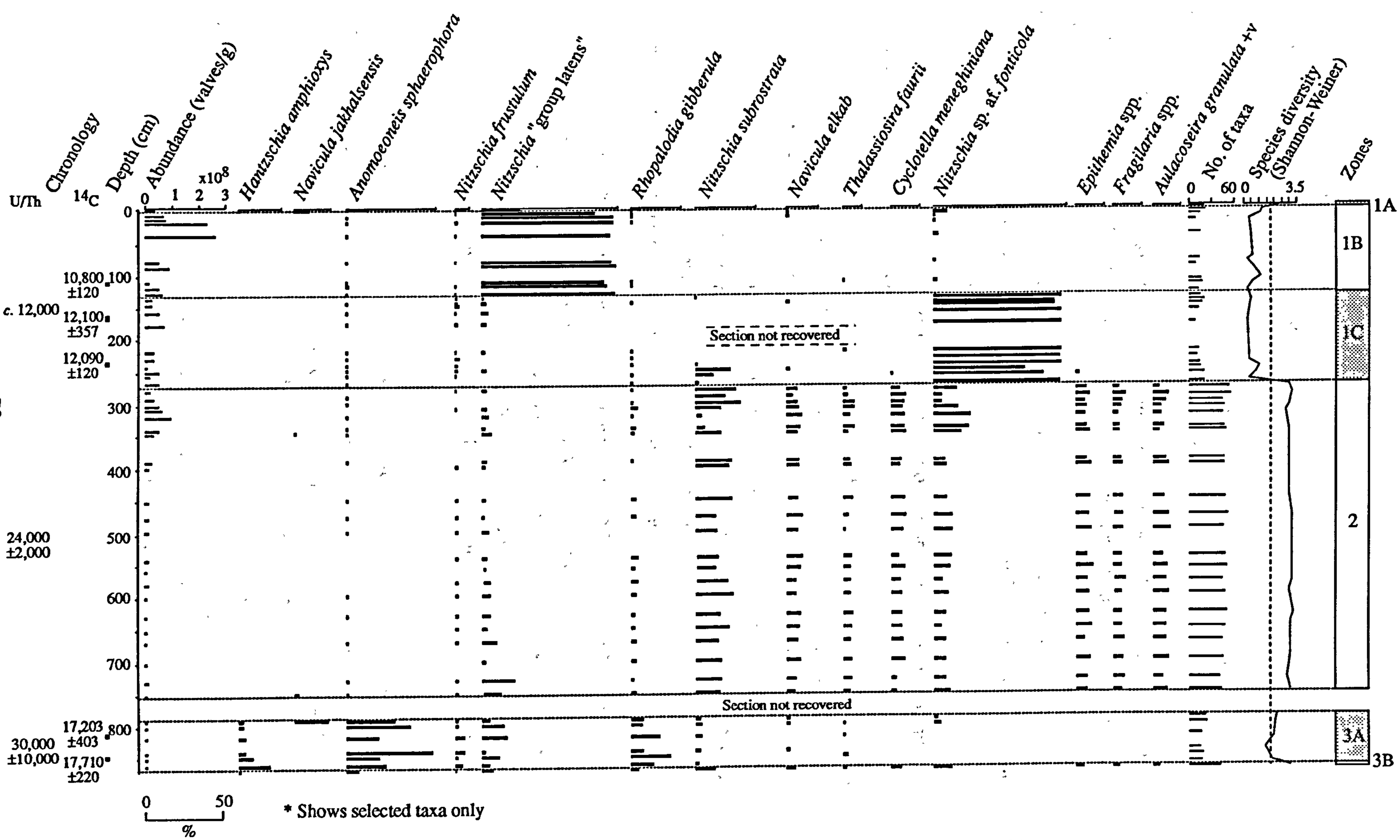


Figure 3.4. Diatom analysis of core NF1

members of the genus *Nitzschia*, including *Nitzschia* sp. af. *fonticola*, *Nitzschia subrostrata*, *Nitzschia* "group latens" and *Nitzschia frustulum*. *Navicula elkab*, *Thalassiosira faurii*, *Rhopalodia gibberula*, *Cyclotella meneghiniana*, *Cyclotella ocellata*, *Aulacoseira granulata*, *Epithemia sorex*, *Epithemia zebra*, several *Fragilaria* spp. and *Stephanodiscus minutus* are also well represented in this zone.

The lowest two samples in this zone at 750cm and 731cm are enriched in *Nitzschia* "group latens" (14% and 23%) in relation to the rest of zone 2, where this taxon is found at levels below 7% (with the exception of 13% in a sample at 671cm). Other small differences are apparent concerning the diatom assemblages of these two samples, *Cyclotella meneghiniana* is present at levels less than 3%, whereas elsewhere in this zone values between 5 and 11% are found.

Between 700cm and 350cm up/down variations in species ratios are so small as to be within the statistical tolerance limits of counting procedures, although overall abundance does increase up-core (figure 3.4). At 341cm and 320cm *Nitzschia subrostrata* declines from the 13-24% typical of this zone to less than 5%, being replaced by *Nitzschia* sp. af. *fonticola* which becomes the dominant taxon. Also found at 320cm are the maximum percentages achieved by *Cyclotella meneghiniana* and *Navicula elkab*. *Nitzschia* sp. af. *fonticola* and *Nitzschia subrostrata* are the co-dominant species in the sample at 309cm, whereas in the remainder of zone 2 *Nitzschia subrostrata* rises in proportion to dominate the assemblage.

Zone 2 finishes as suddenly as it begins in core NF1 with a striking change in the fossil diatom assemblage taking place, only *Nitzschia subrostrata* and *Nitzschia* sp. af. *fonticola* continuing to be present in zone 1. Other parameters such as mineralogy, sedimentology and magnetics also change at or close to this point, perhaps indicating an hiatus in deposition. This transition is studied in more detail from core NF2.

Zone 1 may be divided into three sub-zones, 1C from 270cm-139cm, 1B from 130cm-6cm, and 1A a single sample at the surface. Sub-zone 1C comprises almost entirely *Nitzschia* sp. af. *fonticola* which accounts for over 69% of the diatom assemblage, and more than 90% in eight of the ten samples. The other significant element in this sub-zone is *Nitzschia subrostrata* which accounts for 13% and 23% of the samples at 259cm and 250cm respectively. No species other than those of the genus *Nitzschia* occupy more than 2% of any sample, *Nitzschia* "group latens" reaches 4% at 250cm and 3% at 160cm, whilst *Nitzschia frustulum* is found in small percentages up to 4% at 230cm.

Sub-zone 1B begins at 130cm, the point where the stratigraphy reverts from fine laminated clay to homogeneous clay. The diatom flora becomes almost entirely dominated by *Nitzschia* "group latens" (>83%) This taxon contains within it considerable morphological variation, and in sub-zone 1B different forms were found to be abundant at different levels. The samples at 130cm and 120cm are dominated by a more elongate, slightly rhombic form that compares favourably to *Nitzschia* sp. af. *pura;* this morphotype is also important at 110cm and at 11cm. The shorter and well rounded *Nitzschia elliptica* is found at 11cm and 6cm, but elsewhere in this sub-zone the dominant valve shape is lanceolate, the shape typical of *Nitzschia latens sensu stricto*. The distinction of these different morphotypes is difficult and a range of intermediate forms are to be found, therefore supporting the combination of these forms into a single taxon.

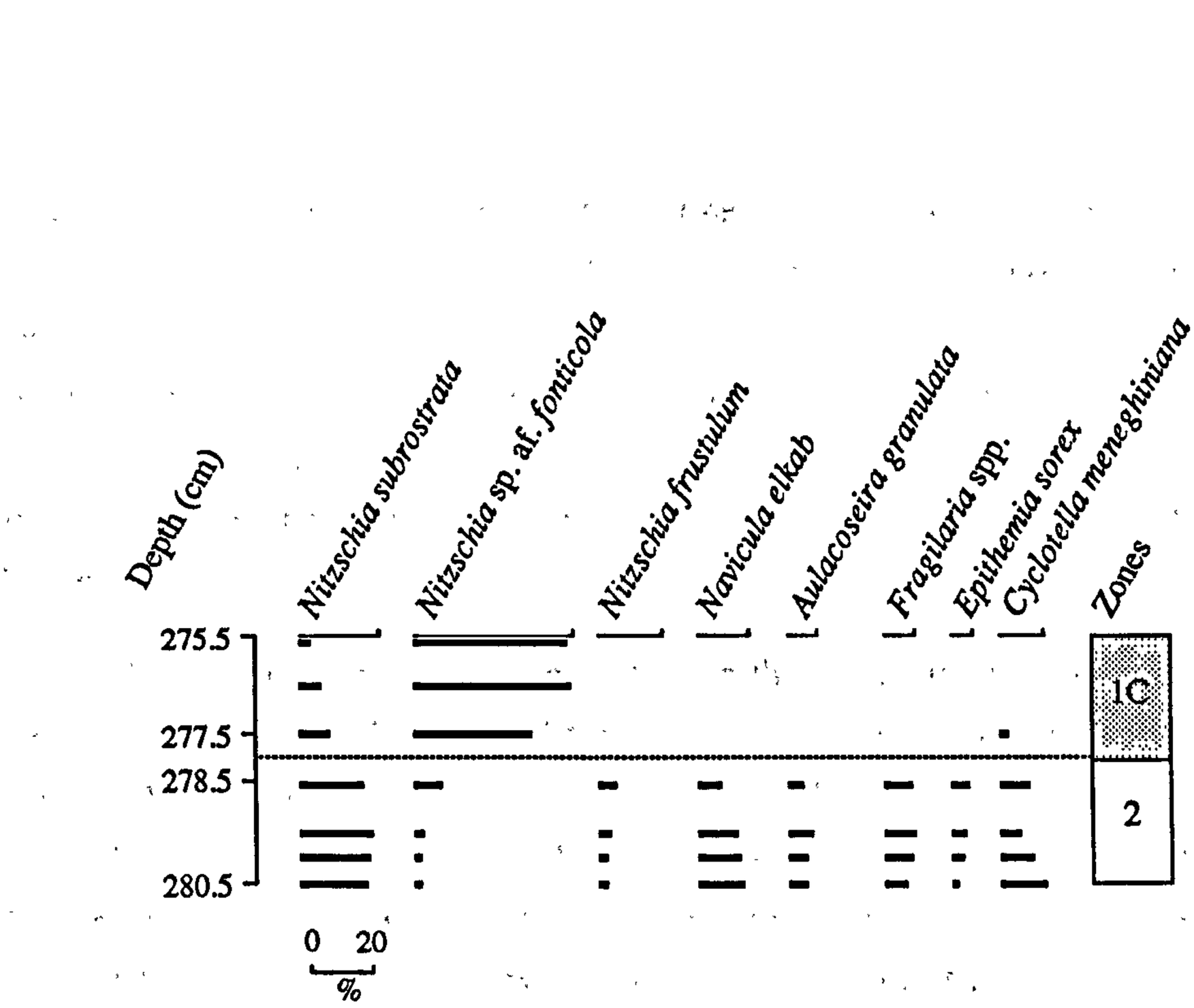
Nitzschia sp. af. *fonticola* is present in small amounts throughout sub-zone 1B, and reaches 10% of the assemblage at 6cm. *Rhopalodia gibberula* is also found at levels less than 3% in each sample of this sub-zone. The diatom assemblage changes abruptly again in the uppermost 6cm of NF1, with *Nitzschia* "group latens" reduced from 83% to 28%, *Anomoeoneis sphaerophora, Navicula jakhalsensis*, and *Rhopalodia gibberula* also become important. This single sample at the surface of the core corresponds well to the modern samples collected from around the Magadi area described above.

b) Core NF2, an examination of the zone boundaries.

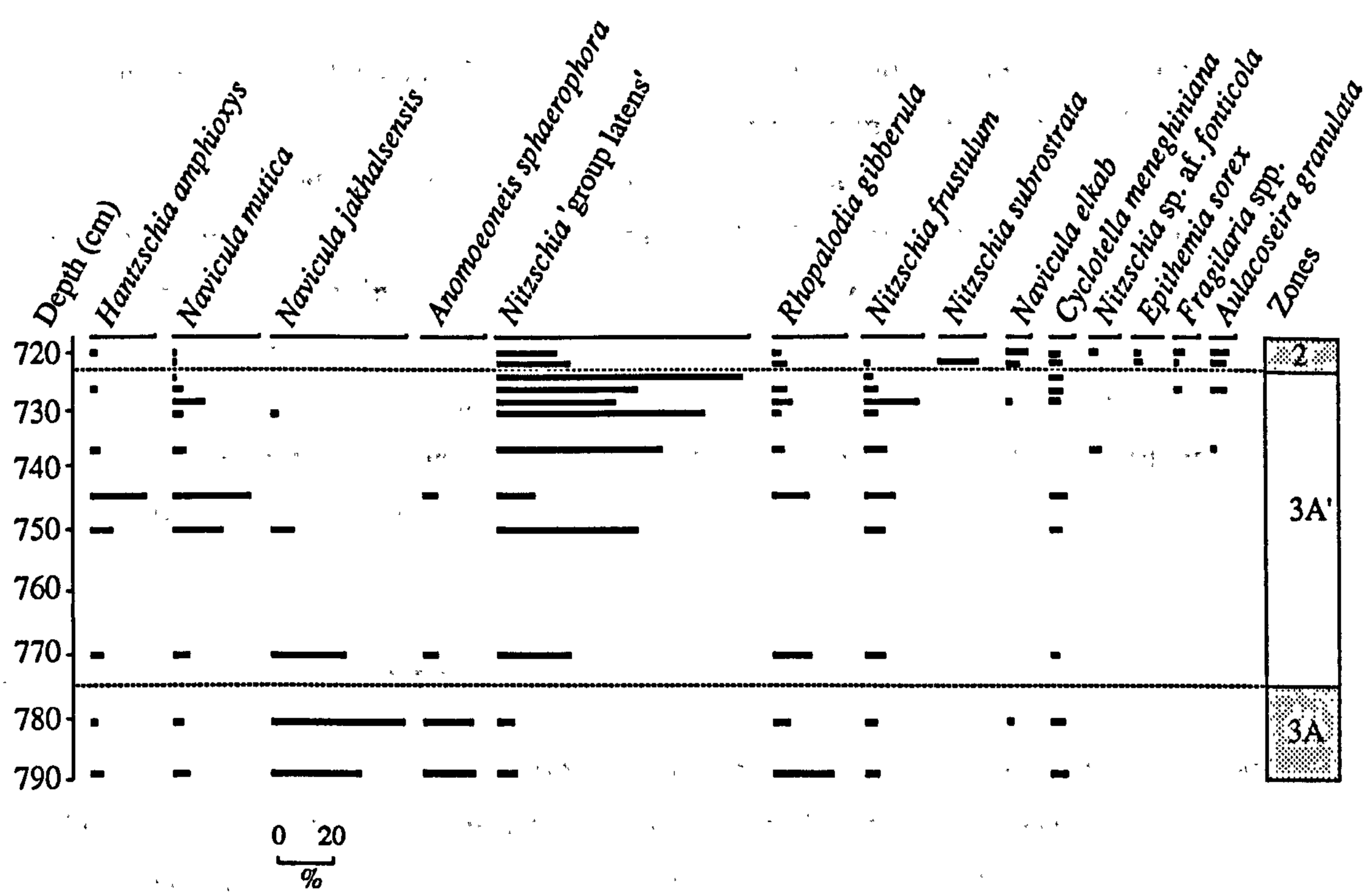
The second core from Flamingo Nursery spans several of the missing sections found in NF1, and allows for a more detailed investigation of the zone 3/zone 2, and zone 2/zone 1 boundaries to be made. Samples were collected at 1cm intervals from these sections, using the magnetic susceptibility and core lithology to correlate NF2 with NF1 and to identify the transitional zones. Twelve samples from the zone 3/zone 2 boundary were analysed between 721cm and 789cm, and six samples at 1cm intervals were studied from the zone 2/zone 1 transition (275.5-280.5cm).

Diatom abundance is highly variable through the lower boundary zone, ranging from the complete absence of valves at 760cm, to 2.9×10^7/g at 726cm. Counts had to be reduced to 380 at 728cm and 737cm and to between 150 and 200 for the samples at 730cm, 745cm, 770cm and 789cm due to low diatom abundance.

The zone 3/ zone 2 boundary is marked neither by an abrupt change, nor by a smooth transition, but with a complex series of intervening diatom assemblages termed here subzone 3A' (figure 3.5). Diatom assemblages within the samples at 789cm and



a) Zone 2/ sub-zone 1C boundary.



b) Sub-zone 3A/zone 2 transition.

Figure 3.5. Diatom analysis from core NF2: an examination of the zone boundaries.

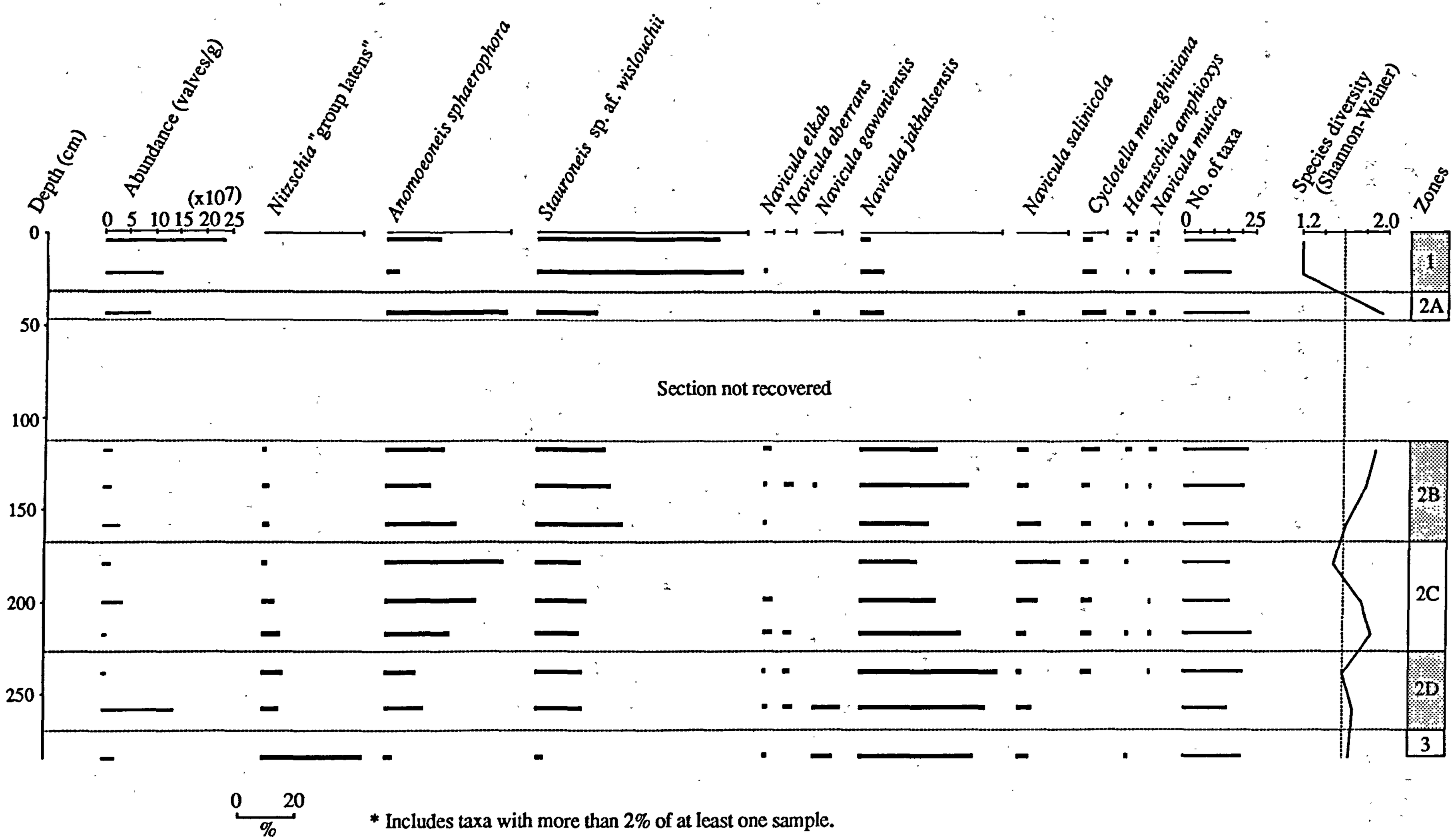
780cm are characteristic of those from zone 3 in having an abundance of *Navicula jakhalsensis* (as at 791cm in NF1) together with *Anomoeoneis sphaerophora, Rhopalodia gibberula, Nitzschia frustulum* and *Nitzschia* "group latens". Above these samples the diatom assemblages differ from those found in core NF1; *Anomoeoneis sphaerophora* dominant in much of zone 3 is reduced to less than 5%, and *Navicula jakhalsensis* declines gradually after being the most abundant taxa between 789cm and 770cm.

Aerophilous species are important in this transitional zone particularly in the samples at 750cm and 745cm, and *Navicula mutica* is the dominant species in the latter sample. *Nitzschia* group latens" is the most abundant taxa between 750cm and 726cm (with the exception of that at 745cm) occurring in proportions in the range 43% (730cm) to more than 90% at 726cm. Of the morphotypes within this taxon (see zone 1B of NF1), elliptical valves typical of *Nitzschia latens sensu stricto* are the most important in all samples except for those from 726-722cm where more elongate valves predominate. The final transition to zone 2 takes place between samples at 724cm and 726cm clearly shown by the marked increase in species diversity.

In contrast to the zone 3/ zone 2 transition, the zone 2/zone 1 transition was confirmed as abrupt by closer examination of the relevant section of NF2. Seven samples were studied between 275.5cm and 280.5cm allowing the boundary to be positioned precisely at 278cm. This is signalled by the simultaneous decline of taxa typical of zone 2 including *Navicula elkab, Cyclotella meneghiniana, Aulacoseira granulata, Epithemia sorex,* and various *Fragilaria* spp, with the rise in dominance of *Nitzschia* sp. af. *fonticola* characteristic of zone 1A. This abrupt transition occurs at exactly the same point that the lithology changes and strongly supports the contention that this represents an hiatus.

c) Northern Lagoon (NL1).

This 2.85m core was taken from a spring-fed perennial pool in the northern part of Magadi. Diatom preservation within the core is quite good and diatoms are present in high concentrations, particularly in the sample at 258cm and toward the top of the sequence. The changes in the diatom assemblages are small in comparison to those found at Flamingo Nursery with *Anomoeoneis sphaerophora, Stauroneis* sp. af. *wislouchii, Navicula jakhalsensis,* and *Nitzschia* "group latens" being abundant and ubiquitous throughout the core.



* Includes taxa with more than 2% of at least one sample.

Figure 3.6. Summary of diatom analysis from the Northern Lagoon (NL1).

Zone 3 at the base of the core is represented by a single sample in which the most abundant taxon is *Navicula jakhalsensis* (45%), but distinct from the remainder of the core in having a high proportion of *Nitzschia* "group latens" (37%) (figure 3.6). *Navicula jakhalsensis* maintains its share of the assemblage in zone 2 except for samples at 179cm and 42cm where it declines to 23% and 11% respectively. At 179cm it is replaced as the dominant species by *Anomoeoneis sphaerophora* reaching a peak of 44%, and *Navicula salinicola* rises to 10%. *Stauroneis* sp. af. *wislouchii* achieves its greatest importance in zone 2 at 159cm (31%), elsewhere in this zone its share of the assemblage lies in the range 14-24%. The uppermost sample in zone 2 at 42cm is notable for the return to dominance of *Anomoeoneis sphaerophora* (41%). Zone 1 includes the samples at 3cm and 22cm which hold assemblages of low diversity dominated by *Stauroneis* sp. af. *wislouchii* (58% and 64% respectively), with *Anomoeoneis sphaerophora* as an abundant element at 3cm.

All of the important species in the core from the Northern Lagoon are to be found in the modern samples collected from Magadi, and the degree of down-core variation in the diatom assemblages is no greater than that existing between the springs at the present time. In the absence of radiocarbon dates, it is difficult to estimate the age of this sequence, and in the absence of clear correspondence with the Flamingo Nursery core biostratigraphical correlation cannot be used to propose approximate dates for NL1. Although similar diatom floras to those of NL1 are found in zones 3 and 1A of NF1, correlation with the former is unlikely given that zone 3 is at the base of the Flamingo Nursery core and below two diatom zones that are not found in NL1. Moreover, the relatively high proportion of *Nitzschia* "group latens" at 285cm is insufficient to suggest a link with zone 1B of NF1 and similar proportions are found in the surface samples of Flamingo Nursery. Therefore, a Late Holocene-modern age is tentatively given to this short core pending radiometric confirmation.

Discussion.

Contrary to previous research which concluded that diatoms are relatively unimportant at Magadi (*e.g.* Eugster 1980), their frustules have been shown to be abundant in the modern and fossil sediments of Magadi, but their preservation is sporadic. Whilst high concentrations of valves are to be found in the cores of Flamingo Nursery and the Northern Lagoon, diatoms are absent in the core from Bird Rocks and scarce in many exposures of the High Magadi beds. Frustule dissolution in the more concentrated Magadi springs, with re-precipitation of the biogenic silica in the form of zeolites is the likely cause of this erratic diatom distribution. Support for a dissolution

hypothesis is provided by the modern samples from Bird Rocks, where diatoms were numerous if rather dissolved, whereas only zeolites and cherts are to be found in the core taken from the same site.

Partial dissolution of diatom frustules is also evident in the samples from zone 3 of core NF1, and could have altered the composition of these samples by selective removal of the more easily dissolved elements. Diagenesis of the diatom assemblages could profoundly distort the palaeoenvironmental conclusions reached, particularly those generated by quantitative methods, such as transfer functions, which are used in this study. Therefore, the problem of diatom dissolution is to be examined more closely in chapter 5, prior to the making of any palaeoenvironmental interpretation.

Elsewhere in the Flamingo Nursery cores diatom preservation is good especially in zone 2. However, here interpretation rests upon the resolution of the taphonomic processes that brought together seemingly incompatible diatom taxa. The fossil assemblages from this zone incorporate diatoms typical of saline environments (*e.g. Navicula elkab, Thalassiosira faurii* and *Nitzschia subrostrata*) alongside those more usually found in dilute conditions (*e.g. Aulacoseira granulata*, *Epithemia sorex*, and *Stephanodiscus minutus*). This situation is unusual although similar mixed assemblages have been found elsewhere, for example Guidimouni salt pond, Niger (Gasse 1987), and Lake Bogoria (Gasse and Seyve 1987). In the case of Magadi several competing hypotheses can be envisaged to explain this apparent paradox, these will be elaborated in chapter 6 alongside the environmental interpretation.

If the radiometric chronology of the Flamingo Nursery cores is reliable, the rate of sedimentation at the site has been highly variable, and is probably punctuated by several hiatuses. The possibility of up to three major hiatuses at Flamingo Nursery is suggested by abrupt changes observed between succeeding diatom assemblages, and nearly simultaneous changes in other measured parameters. The zone 3/ zone 2 transition studied in core NF2 may possibly be marked by an hiatus, after the sharp peak found in *Nitzschia* "group latens" gives way abruptly to the diverse assemblages of zone 2. However, this is not so clear as the unconformity occurring at the zone 2/ sub-zone 1C boundary where the diatom assemblages and lithology change abruptly at exactly the same point via a sandy horizon. Finally, a third hiatus is likely at the sub-zone 1B-1A boundary suggesting that most of the Holocene is missing from the Flamingo Nursery cores. The change from diatom zones 1C to 1B is equally abrupt as the others mentioned here, but this is considered to be an ecological, rather than a sedimentological change, as radiocarbon dates showing good agreement to each other fall on either side of this change and other parameters also continue across this boundary.

Chronological difficulties encountered in the Flamingo Nursery core make correlation of all but zone 1 to other lacustrine deposits in the basin uncertain. Zone 3, dating to between 50 and 30,000 years BP by U/Th and *c.* 17,000 by ^{14}C, cannot be precisely positioned into a chronological framework, and further problems arise in attempting to date zone 2 (U/Th age of *c.* 24,000 years BP). The homogeneity of this zone suggests substantial sediment mixing and / or rapid accumulation, but with the presence of a possible hiatus of uncertain length at the boundary with zone 1, no opportunity exists to assess the sedimentation rate. More encouraging is the good agreement shown between the ^{14}C and U/Th dates from zone 1. Furthermore, these show close accord to the ages proposed for both the High Magadi Beds, and the third generation of stromatolites, allowing palaeoenvironmental changes at Magadi during this time to be placed within a more secure time framework.

Despite their lack of chronological detail, the High Magadi beds contain at least three pieces of information which must be included in any palaeoenvironmental reconstruction of this period. The first concerns the abundant volcanic material in the exposures. Whilst most is undoubtedly derived from the reworking of older deposits (Surdam and Eugster 1976), some may result from increased volcanism in the area at the time of deposition (Hillaire-Marcel *et al.* 1986), potentially influencing the regional climate and biota. A second factor are the thick horizons of magadiite recurring throughout the High Magadi beds; the formation of this sediment is still unclear but two hypotheses have been proposed. Eugster (1980) considers magadiite to be a lake-wide precipitate forming in a stratified lake at the interface of a concentrated water body rich in dissolved silica, and dilute water of lower pH which upon contact with the former allows the precipitation of silica. Maglione (1970) favours an authigenic model for the formation of magadiite from Lake Chad resulting from the interaction of alkaline brines with siliceous sediments. Finally, the fish beds indicate a series of catastrophic events that must be reconciled within any model of palaeolimnological reconstruction.

Diatom analysis of the cores taken from Magadi can be used to reconstruct the former aquatic environments represented in the sediment record once difficulties of assemblage diagenesis and taphonomy have been overcome. Of particular interest is the period of Pleistocene/Holocene transition where several analyses converge and the chronology is the most secure. These issues will be considered in chapter 6.

CHAPTER FOUR: LAKE MANYARA, TANZANIA.

In contrast to the classical grabens and half-grabens of Kenya the Gregory Rift splits into numerous faults and troughs as it enters northern Tanzania. The eastern escarpment disappears far to the north of Manyara and the western fault diverges, one arm extending southwest to the Rungwe volcano, another southeast beneath Kilimanjaro and Meru (Baker *et al.* 1972, Grove 1986). The southern extension of this divergence has formed asymmetric structures occupied in the east by Lake Manyara (3° 35'S, 35° 50'E), and to the west by the vast drainage basin (65,000km^2) of hypersaline Lake Eyasi (3° 35'S, 35° 00'E). North of the catchment the dry Engaruka depression separates Manyara from the Magadi-Natron drainage basin.

Topography and geology.

The topography of the Manyara region was sculptured from Precambrian gneiss, schist and quartzite basement rocks by major tectonic evolution and volcanism during the Late Pliocene and Pleistocene. Volcanic deposits from the Plio-Pleistocene eruptions are found in the northwest of the catchment. These emanated from the volcanoes of the Ngorogoro Highlands and Oolmalasin which form the basin's watershed in the northwest, reaching altitudes of 3,440m and 3,468m respectively. At the foot of these volcanoes a plateau stretches almost to the shores of the lake itself, ending in the major western Manyara escarpment that climbs 200-900m from the lake's margin. The catchments northeastern boundary is also defined by volcanoes, Burko reaching 2136m and Monduli, 2660m. The Manyara drainage basin spreads 50km southwards to the volcanoes of Loya (2417m) and Kwaraha (2415m), and eastward 60km across a gently sloping plain at an altitude of 1000-1500m.

The areal asymmetry of the catchment is a result of the distinctive shape of the half graben in which it lies. This has a short steeply inclined arm to the west, manifested by the Manyara escarpment, with a longer more gently sloping eastward extension. The particular structural geology provides the over-riding control on the present hydrology of the lake and its sedimentation patterns.

Climate, hydrology and vegetation.

The major perennial rivers, the Endabash, Yambi, Marera, Garufa and Megara drain into the lake from the well-watered western highlands (figure 4.1). To the more arid east the rivers of Mkujunu and the Oltukai flow only ephemerally. Lake Manyara is at present shallow with a maximum depth of 3-4m that is known to have been highly variable even within the last century, the lake becoming almost dry as recently as 1960 (Greenway and Vesey-Fitzgerald 1969).

The water chemistry of some of the perennial rivers was sampled by Casanova (1986a). These have low salinities of 0.5‰, temperatures between 18 and 29 °C and pH values within the range 7.9 and 8.9. The river waters are rich in sodium and potassium carbonate and bicarbonates, with significant levels of calcium and magnesium. Hydrothermal springs enter the lake from beneath the western escarpment to the southwest near the Yambi delta. Casanova found the springs to have temperatures between 41 and 59 °C and pH levels of 9.5 and 9.7, a still higher temperature of 74 °C for the Maji Moto springs (southwest of the lake) have been reported by Njoga and Kinoti (1971).

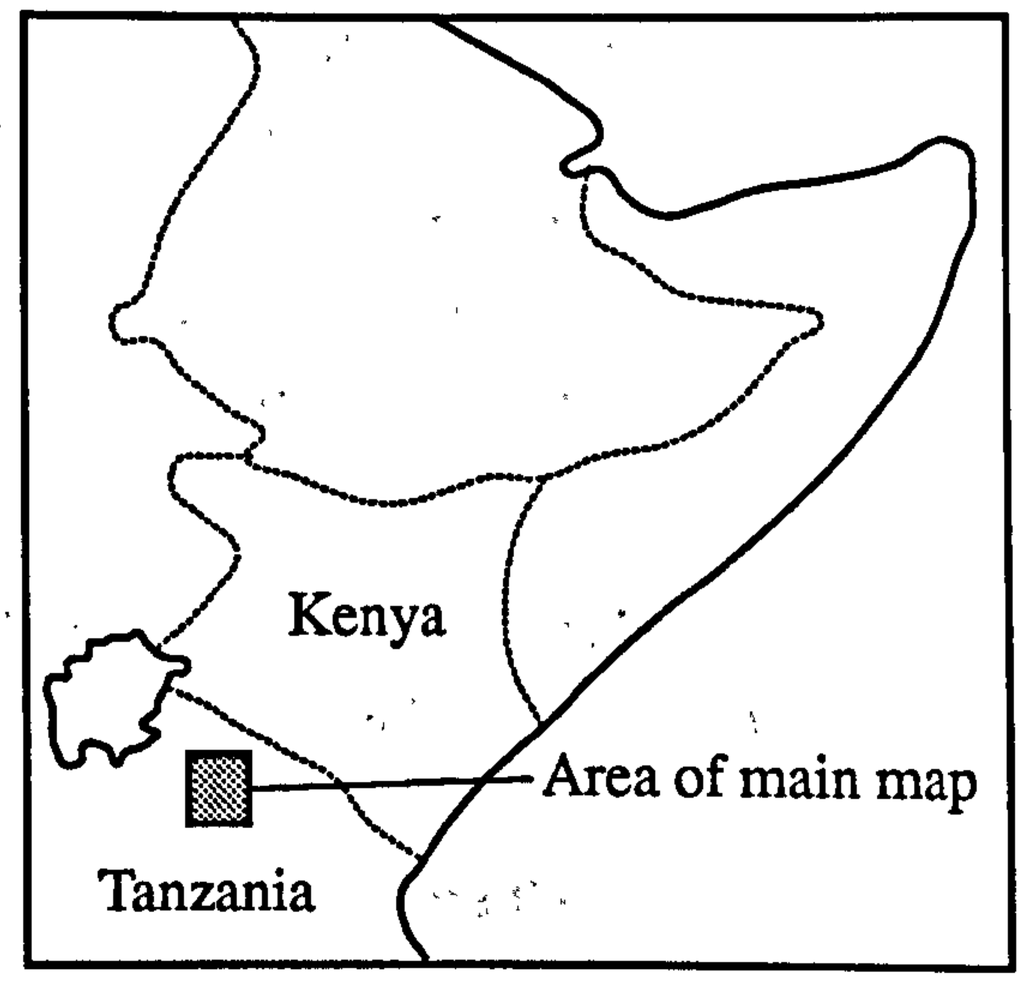
Lake Manyara is much less concentrated than Magadi or Natron. The lake water chemistry has been studied by Talling and Talling (1965), Kilham (1971), and Stoffers and Holdship (1975) (table 4.1).

TABLE 4.1. Lake Manyara water chemistry

Na	K	Mg	SO_4	Cl	HCO_3	CO_3	SiO_2	pH	Ref. and date
2,500	12	1	230	1,172	1,763	1,476	16	9.76	(1) June 1969
21,500	94	30	2,280	8,670	49,182	n. d.	19	n. d.	(2) June 1961
4,100	8	4	252	1,620	3,002	1,612	n.d.	9.86	(3) April 1971

(1) Kilham (1971); (2)Talling and Talling (1965); (3) Stoffers and Holdship (1975). Values in mg/l except pH.

The data shows that chemical concentration is highly variable and depends greatly on the precise level of the lake at the time of sampling. Casanova found salinities of 4-35‰ whilst the values obtained by Talling and Talling reached 82 ‰, the discrepancy



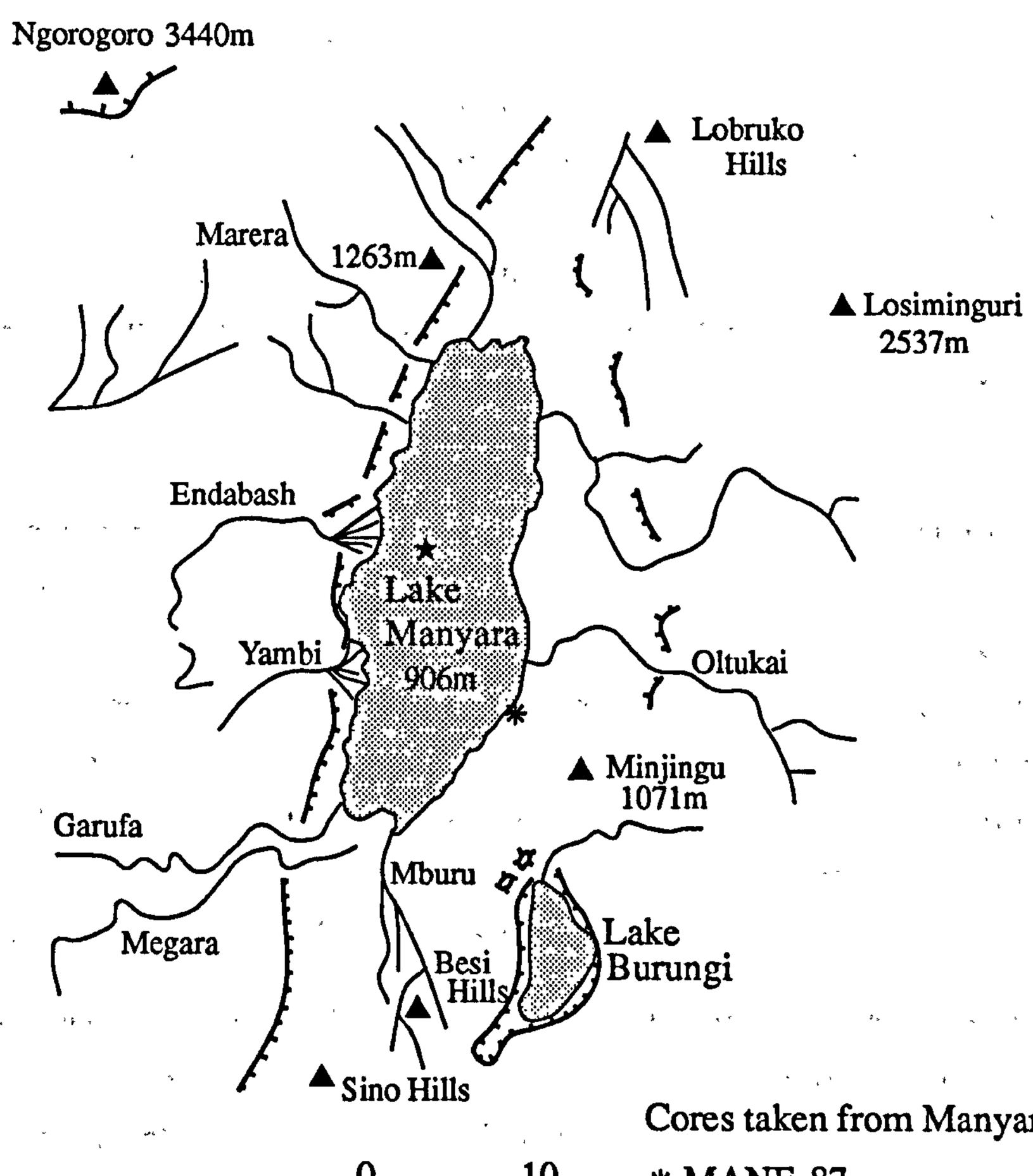


Figure 4.1. Lake Manyara; physiography and coring sites.

is probably a result of the latter samples being taken in 1961 following a period of extensive drought. Water temperatures have been recorded between 17 and 32.2 °C with pH at these temperatures being measured at 9.05 and 10.25 respectively. The dominant cation in the lake water is sodium with anions of carbonate, bicarbonate and chloride. The waters are supersaturated with respect to calcite and sepiolite and close to saturation for halite, trona and thermonatrite (Casanova 1986).

Rainfall in the Manyara catchment falls predominantly during a single rainy season between November and May (Griffiths 1972). This period can be divided into a minor rainfall peak in December the culmination of the short rains, and a major peak during the long rains in April (Prins and Loth 1988). The long rains are the result of the influence of topography on large-scale monsoonal circulation patterns, and are distributed with respect to altitude (figure 4.2). However, the short rains are less closely correlated to altitude and are due to convective cells within the monsoonal system (Prins and Loth 1988). Climate close to the lake and for the eastern plain may be described as semi-arid with mean annual rainfall of 500-600mm at Mto-wa-Mbu and mean monthly temperatures of 21-26 °C. Mean annual precipitation is much greater in the highland regions surrounding the catchment, figures provided by Casanova (1986a) indicates that Ngorogoro and Monduli receive more than 800mm/yr, whilst for Loya in the south mean annual precipitation is in excess of 1,500mm.

The vegetation reflects this uneven distribution of rainfall, ranging from montane forest in the well watered highlands, to *Acacia* dominated savanna in the drier east. The western plateau is covered by dense Marang woodland whilst more open *Acacia* woodland predominates in the lake trough itself. Gallery forest follows the drainage lines and mixed forest is supported close to the lake by groundwater emerging from the foot of the escarpment. Alkaline grasslands and *Typha* swamps fringe the lake with the former being particularly common on the seasonally exposed flats (Greenway and Vesey-Fitzgerald 1968, Prins 1988).

The northwestern quarter of the lake is given National Park status to protect the large number of game animals found in the Manyara region. Prominent amongst the large mammals are elephants which reached in the early 1970's reached densities of up to 12 per square mile, the highest levels recorded in Africa (Douglas-Hamilton and Douglas-Hamilton 1975). The elephant population has declined sharply since then due to poaching and habitat reduction caused by the expanding human population. The fauna of the lake itself includes hippopotamous and the cichlid fish species *Oreochromis amphimelas*[1].

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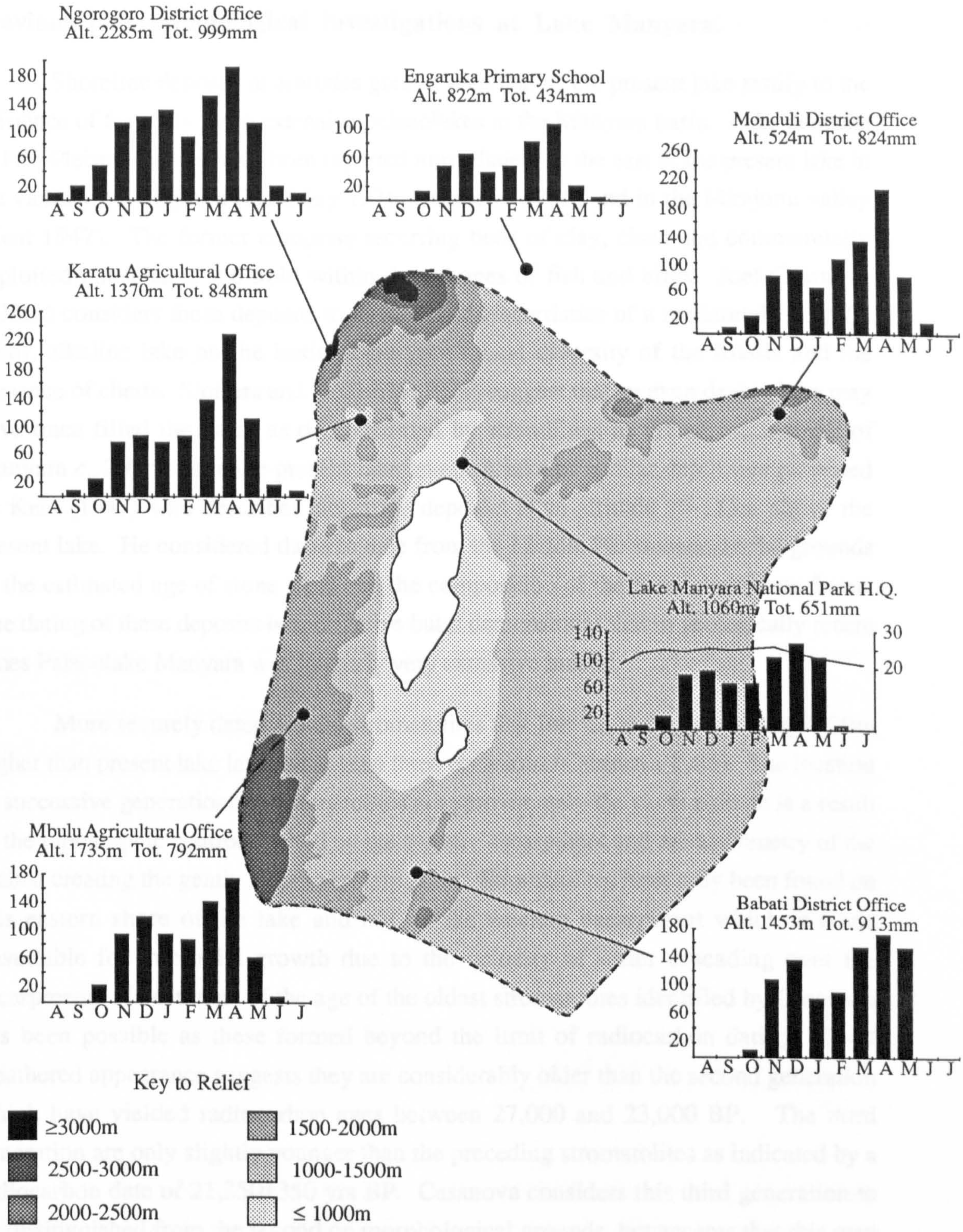
[1]Formerly *Tilapia manyarae*, Burgis and Symoens 1988



* Data Source: Prins and Loth 1988. Mean monthly Precipitation figures in mm based on records of at least 23 years duration. Mean Monthly Temperature at Manyara National Park H. Q. in °C.

Figure 4.2. Relief and precipitation in the Manyara catchment.

Previous palaeolimnological investigations at Lake Manyara.

Shoreline deposits at altitudes greater than that of the present lake testify to the existence of formerly more extensive palaeolakes in the Manyara basin. Lake deposits of Plio-Pleistocene age have been reported immediately to the east of the present lake in the vicinity of Minjingu (Holdship 1976, Casanova 1986) and in the Mkujunu valley (Kent 1947). The former comprise recurring beds of clay, chert and commercially exploited phosphates and hold within them bones of fish and birds. Joel Casanova (1986a) considers these deposits to have the characteristics of a moderately deep (*c.* 40m), alkaline lake on the basis of the low faunal diversity of the fossils and the presence of cherts. Stoffers and Holdship (1975) suggest that an even deeper lake may have once filled the basin as demonstrated by strandlines to the east and south of Manyara *c.* 100m above the present lake level. A lake of similar depth was proposed by Kent (1947) who describes lacustrine deposits at an altitude 90-115m above the present lake. He considered these to date from the Middle Pleistocene on the grounds of the estimated age of stone tools and the composition of the fossil vertebrate fauna. The dating of these deposits is speculative but it demonstrates that in geologically recent times Palaeolake Manyara was formerly very extensive indeed.

More securely dated are the stromatolites that formed at the lake's margin 20m higher than present lake level on at least three occasions (Casanova 1986). The location of successive generations of stromatolites at approximately the same altitude is a result of the topographic control exerted by the western escarpment and the asymmetry of the graben creating the gently sloping eastern plain. Stromatolites have only been found on this eastern shore of the lake and not on the western escarpment which is made unsuitable for microbial growth due to the velocity of water cascading over the escarpment. No estimate of the age of the oldest stromatolites identified by Casanova has been possible as these formed beyond the limit of radiocarbon dating. Their weathered appearance suggests they are considerably older than the second generation which have yielded radiocarbon ages between 27,000 and 23,000 BP. The third generation are only slightly younger than the preceding stromatolites as indicated by a radiocarbon date of 21,350±350 yrs BP. Casanova considers this third generation to be distinguished from the second on morphological grounds, but accepts that this may in fact be the final phase of the earlier growth.

Shoreline deposits are essential bathymetric indicators of lake-level maxima but they can only rarely be used to deduce periods of lower lake level. To establish a continuous register of the complete cycle of lake-level change necessitates the study of the lake sediments themselves, whether from exposed sections or from cores taken from the lake bed. A long core (57m) was taken from close to the centre of lake

Manyara in 1969 by a team from Duke University. Fourteen radiocarbon dates were obtained on total organic matter, the oldest finite age being 35,550±2,150, and by extrapolation of the sedimentation rate the base of the core was dated to *c.* 55,000 yrs BP. Recent U/Th datations from this core generally confirm the original ^{14}C chronology (Goetz 1990).

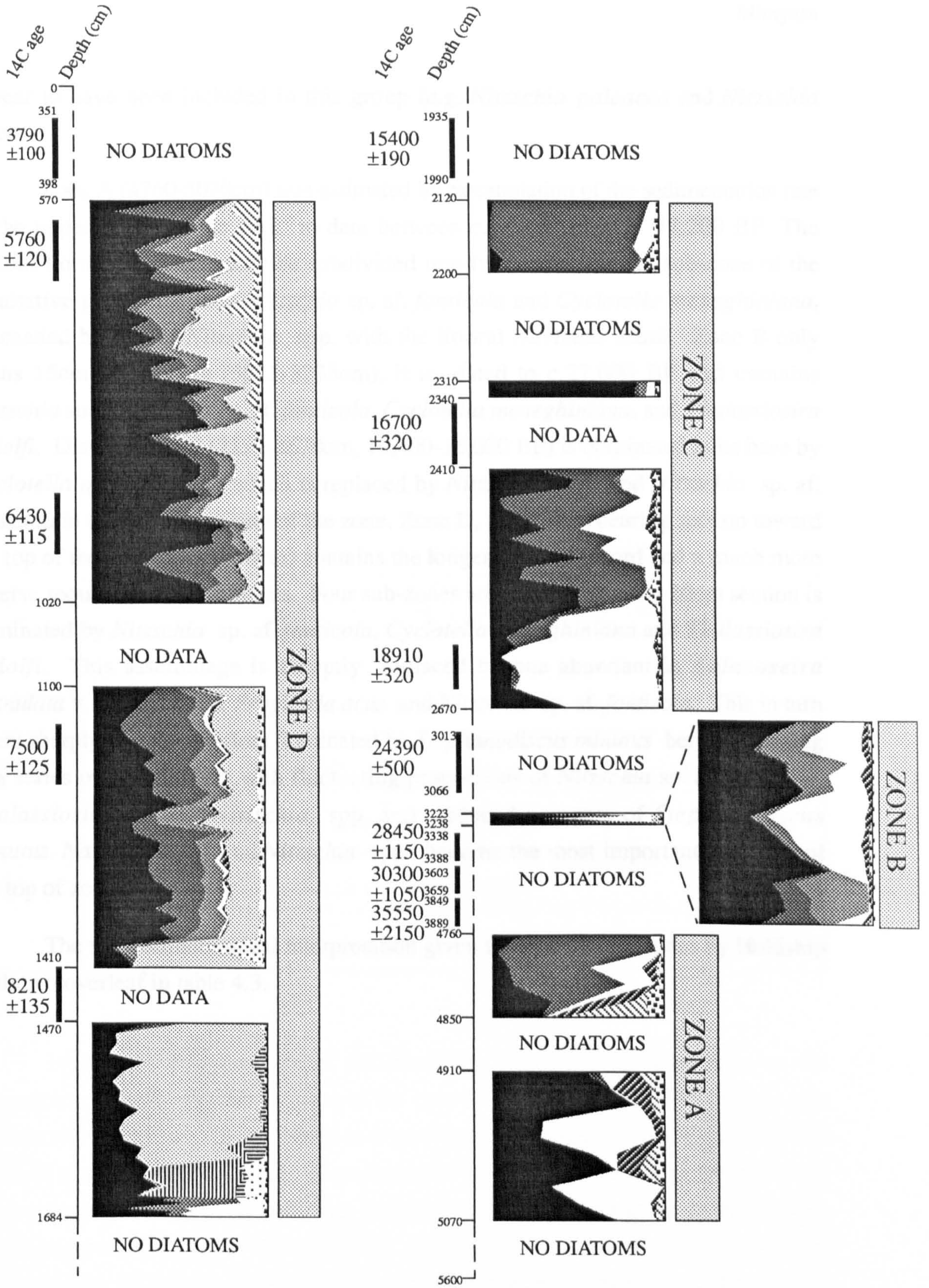
Although this core appears to be a continuous record of sedimentation throughout the Late Pleistocene, palaeoenvironmental interpretation is difficult as the diatom record (the indicator for which it has been most thoroughly examined) is fragmentary. The core contains four discrete diatom bearing zones (A-D) which were the subject of a thesis by Stephen Holdship (1976). The results of his study are shown in the summary diagram figure 4.3, constructed from raw data taken from Holdship's thesis and only altered to encompass the following recent changes in diatom taxonomy (table 4.2).

TABLE 4.2. Changes to diatom nomenclature.

HOLDSHIP (1976)	THIS WORK
Coscinodiscus	*Thalassiosira*
Stephanodiscus astrea	*Stephanodiscus rotula*[1]
Stephanodiscus astrea var. *minutula*	*Stephanodiscus minutus*
Melosira	*Aulacoseira*
Synedra	*Fragilaria*
Nitzschia fonticola	*Nitzschia* sp. af. *fonticola*

Prominent within Holdship's core is the taxon he refers to as *Nitzschia* spp. He describes this as 15-40 µm long, 3.5-5.0 µm wide, 15-22 fibulae/10 µm, striae indistinguishable under the light microscope, and with great morphological variation. This compares favourably with *Nitzschia* "group latens" *sensu* Gasse (1986a). The photographs provided by Holdship seem to confirm this designation but other species

[1] *Stephanodiscus rotula* is used here synonymously with *S. astrea* (Ehr.) Grun. *sensu* Gasse (1986).



*Note variations in vertical scale.

Figure 4.3. Diatom analysis of a core from Manyara. After Holdship (1976).

appear to have been included in this group (*e.g. Nitzschia paleacea* and *Nitzschia palea).*

Zone A (4760-5070cm) was estimated by extrapolation of the sedimentation rate in the upper levels of the core to date between *c.* 48,400 and *c.* 47,200 BP. The diatom flora it contained may be subdivided into two units, a lower sub-zone of the facultative planktonic taxa *Nitzschia* sp. af. *fonticola* and *Cyclotella meneghiniana*, succeeded by one of *Nitzschia* spp. with the littoral *Navicula elkab*. Zone B only spans 15cm of the core (3223-3238cm), it is dated to *c.*27,000 BP and contains *Nitzschia* spp., *Nitzschia* sp. af. *fonticola*, *Cyclotella meneghiniana*, and *Thalassiosira rudolfi*. Diatom zone C (2120-2670cm, 19,400-16,000 BP) is dominated at its base by *Cyclotella meneghiniana* which is replaced by *Nitzschia* spp. and *Nitzschia* sp. af. *fonticola* in the uppermost part of the zone. Zone D, the diatom bearing section toward the top of the core (570-1650cm) contains the longest diatom record and a much more diverse sequence of assemblages. Four sub-zones are clear, the lowest 20cm section is dominated by *Nitzschia* sp. af. *fonticola*, *Cyclotella meneghiniana* and *Thalassiosira rudolfi*. This assemblage is abruptly replaced by one abundant in *Aulacoseira granulata* v. *angustissima*, *Fragilaria acus* and *Nitzschia* sp. af. *fonticola*. This in turn alters sharply to a diatom flora dominated by *Stephanodiscus minutus* before changing to a series of assemblages with fluctuating proportions of *Nitzschia* sp. af. *fonticola*, *Thalassiosira rudolfi*, *Nitzschia* spp. and reduced amounts of *Stephanodiscus minutus*. *Navicula elkab* and *Nitzschia* spp. become the most important taxa toward the top of zone D.

The palaeolimnological interpretation given to these diatom zones by Holdship is shown overleaf in table 4.3.

TABLE 4.3. Interpretation of the diatom record suggested by Holdship (1976, table 9, p59).

Zone	Depth (cm)	Interpretation given by Holdship
ZONE D	570-1410	Moderately saline (i.e. "a wide range of intermediate salinities which are significantly less than that of the present lake"): salinity always less than present becoming fresh on occasions.
	1410-1620	Dilute: low dissolved silica.
	1620-1662	Dilute: high dissolved silica.
	1662-1685	Moderately saline: rapidly decreasing salinity.
ZONE C	2120-2550	Saline: usually close to present, rapidly fluctuating.
	2550-2670	Moderately saline: indicates rapid dilution prior to the deposition of this unit.
ZONE B	3223-3235	Moderately saline.
	3235-3238	Saline to moderately saline.
ZONE A	4760-4900	Saline close to present salinity.
	4900-5070	Moderately saline.

Holdship's interpretation of the remaining section of the core rests on the assumption that these sterile sections of the core formed at periods when the lake was sufficiently chemically concentrated to dissolve diatom silica and precipitate it in the form of alkaline zeolites. Under present conditions diatoms are not preserved in the sediments, nor in the sole limnological investigation at Manyara were they found in the water column (Melack and Kilham 1974). Therefore, the modern data do not allow confirmation of the suggestion that diatoms were once present and subsequently dissolved, but equally absence of evidence is not sufficient for falsification of the hypothesis. The former presence of diatoms in sterile sections of Holdship's core is supported by the presence of fragments of partially-dissolved frustules. It is also not clear whether (if diatoms were in fact present) dissolution occurred in the water column

on the point of death, at the water-sediment interface, or at some later phase by the action of interstitial waters.

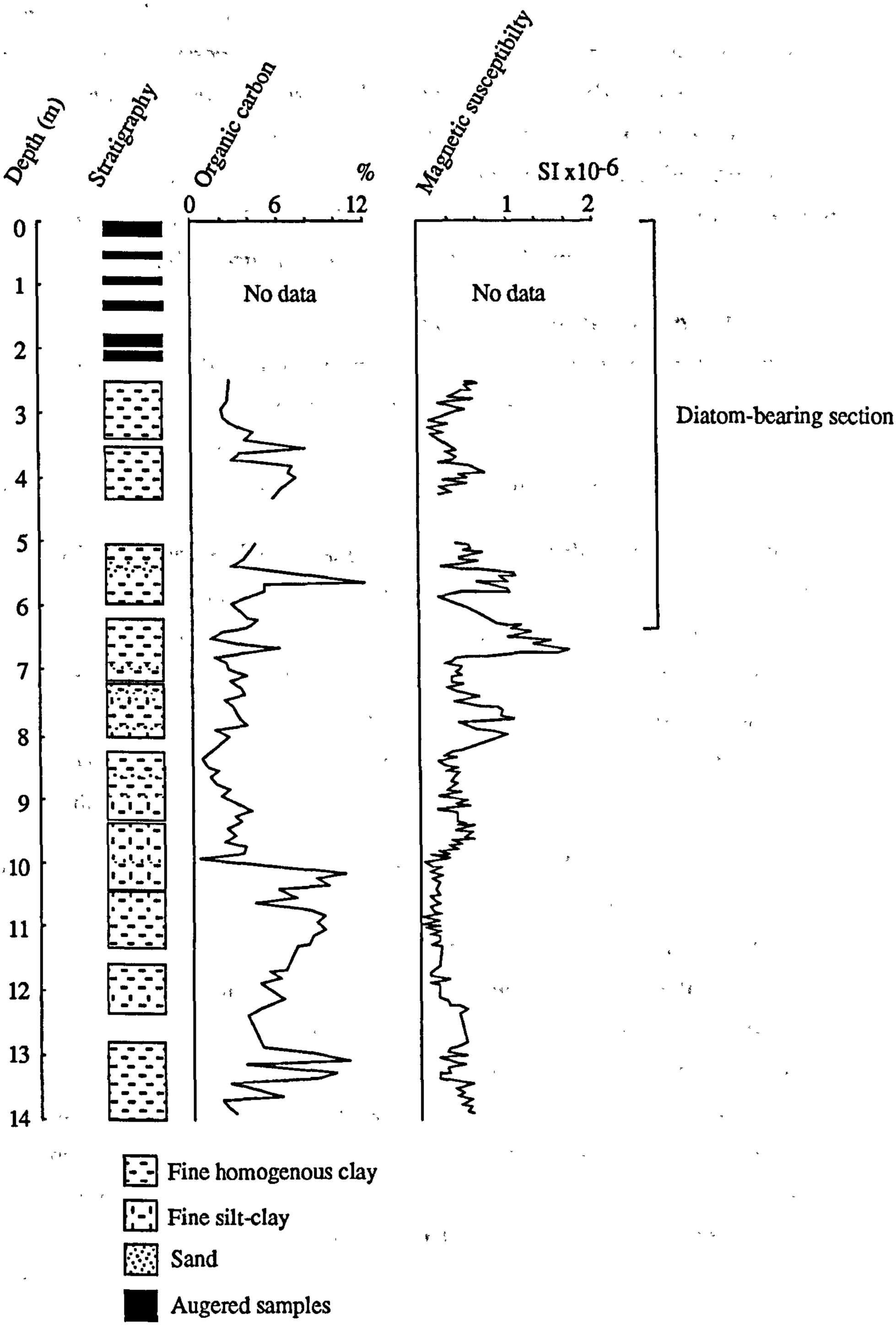
The sedimentology and mineralogy of this core tend to give further credence to the hypothesis concerning diatom frustule dissolution (Stoffers and Holdship 1975, and Holdship 1976). This has shown that the areas of the core devoid of diatoms are rich in the authigenic silicate mineral, analcime. This is also present in the surface sediments and it appears to be forming at the present time. Montmorillonite is found in the diatom zones and is abundant in zone D, however it is replaced in the sterile sections by illite, possibly by diagenesis of the montmorillonite (Singer and Stoffers 1980). The zeolites chabazite and erionite were found in conjunction with the diatom zones A, B, and C in the lower part of the core.

MANE-87: A new core from lake Manyara.

The core MANE-87 was taken from exposed mudflats at the southwestern edge of lake Manyara by a team from the Laboratoire de Géologie du Quaternaire (LGQ) in 1987. Fourteen metres of sediment were collected with the exception of sections between 435-505cm and 1241-1290cm. The uppermost 250cm had to be collected by auger rather than corer due to the hard, compact nature of these light green, silty clays.

The stratigraphy of the cored section is remarkably homogeneous, being comprised almost entirely of dark olive green-black silt or clay, interrupted only by very fine bands of slightly coarser sediment (figure 4.4). Organic matter content by weight is typically in the range 2-8% for the section of the core above 1000cm, apart from a peak of 12% at 530cm. In the lower part of the core (1000-1400cm), organic matter is generally higher, falling within the range 3-12%. Magnetic susceptibility of the sediments is quite low but shows several small peaks at 400cm, 550cm, 670cm, and 800cm, possibly indicating influxes in mineral material (D. Williamson pers. comm.).

Five conventional radiocarbon dates have been made at the LGQ on total organic matter within the core. At 405cm a sample produced an age of 26,300±1057 years BP and another at 535cm was dated at 27,056±852. Three further dates were also obtained, two of these at 1025cm and 1335cm were infinite, *i.e.* beyond the range of radiocarbon dating. Another of 23,021±1853 at 765cm appears erroneous, being younger than the two dates made above it and is therefore rejected.



*Data from EQUARIFT members (D. Williamson and M. Icole pers. comm.).

Figure 4.4. MANE-87; stratigraphy, organic carbon, and magnetic susceptibility.

An initial survey of the core material under the microscope at x600 magnification was conducted at 10cm intervals on untreated samples. This revealed well preserved pollen and spores throughout the 14m core. Ostracods too were noted in most of the samples analysed and were abundant at some levels. Their preservation was generally good but occasionally some fragmentation was observed. Unfortunately, diatoms were not so consistently found throughout the core, valves were abundant in the upper 635cm, and fragments were present in low numbers at 734cm, 831cm, 841cm and 910cm, elsewhere they were absent.

Counts of 500 valves were made from the diatom bearing section of the core at approximately 10cm intervals. No count was possible at 310cm where diatoms were absent and at 319cm the count had to be reduced to 161 valves due to very low diatom abundance. However, with the exception of these two samples the number of valves/g was generally high, particularly between 190cm and 50cm (figure 4.5).

Several difficulties can be envisaged in interpreting the samples collected by auger. Sub-samples taken from augered samples represent an amalgamation of diatoms from up to 20cm of sediment, and will reflect environmental conditions that prevailed over much longer time periods than the sub-samples from the cored section. Therefore, the use of these samples may exacerbate problems of taphonomic interpretation as they are more likely to contain highly mixed diatom assemblages indicative of very different environments within the same sample.

Qualitative zonation of the diatom sequence was aided numerically by using Principle Component Analysis as proposed by Birks (1986). The analysis produced sample scores for 5 factors of which factors one and two explained cumulatively over 90% of the variance. The sample scores from the two principle factors have been plotted against depth and zone boundaries were positioned by eye at the points of greatest vertical variance for each of these factors (figure 4.5). The first axis follows the *Cyclotella meneghiniana* curve as this is the most abundant and ubiquitous species, whereas the second axis shows a close relationship to *Nitzschia* sp. af. *fonticola*. Therefore, the zones and sub-zones are in the main distinguished according to the dominance of these two species, although other taxa which are less omnipresent but achieve abundance at certain levels are used in the zonation.

Results of diatom analysis.

Below 635cm in MANE-87 diatoms are sparse, and largely restricted to fragments of *Cyclotella meneghiniana* and *Rhopalodia gibberula*. A sample at 735cm

contained sufficient diatoms to count 151 valves, 86% of these were *Cyclotella meneghiniana* with *Thalassiosira rudolfi* , *Thalassiosira faurii, Nitzschia sp. af. fonticola, Rhopalodia gibberula,* and *Navicula elkab* also present. However, since this sample is isolated, with very poor preservation and low abundance of valves, it has been omitted from further analysis. This sample differs from those assigned to the lowest sub-zone 5C which contains a more diverse diatom assemblage, having *Cyclotella meneghiniana* and *Nitzschia* sp. af. *fonticola* as co-dominant species, cumulatively accounting for over 84% of the valves counted (figure 4.5). Also important are *Thalassiosira rudolfi* (16% in the 625cm sample) and to a lesser extent *Nitzschia paleacea.* In these two samples *Nitzschia sp. af. fonticola,* whilst otherwise displaying the characteristics typical of this taxa, has particularly attenuated apices. This may correspond to 'Type 2' of Gasse (1986a) (appendix 3). Sub-zone 5C is rich in alkaline zeolites and contains many frustules showing evidence of dissolution suggesting possible diagenesis of the diatom assemblage.

The samples at 604cm, 597cm, and 586cm are distinguished from 5C by the almost total absence of *Nitzschia* sp. af. *fonticola* (<0.2%) and are therefore labelled as a separate sub-zone, 5B. This taxon is replaced by *Cyclotella meneghiniana* which completely dominates the sub-zone, accounting for in excess of 87% of the assemblage in each sample counted. Sub-zone 5B contains only 7 taxa other taxa, all of which are found in small proportions with the exception of *Nitzschia paleacea*, occuring in levels of between 2 and 12%.

Species diversity increases once more in sub-zone 5A (samples 576cm, 567cm, and 557cm), returning to a level similar to that in sub-zone 5C. This is a result of a decline in the proportion of the assemblage occupied by *Cyclotella meneghiniana* (31-68%), and the increased percentage of *Thalassiosira rudolfi.* The latter species dominates at 557cm accounting for 49% of the assemblage, the highest levels achieved by this species in this new core from Manyara. The relatively freshwater species *Stephanodiscus minutus* increases to 17% of the sample at 567cm. Also present in this sub-zone are small amounts of *Nitzschia* sp. af. *fonticola, Nitzschia paleacea, Nitzschia frustulum,* and *Rhopalodia gibberula.*

Zone 4 (samples 547cm, 538cm and 528cm) incorporates the most diverse assemblages occuring in MANE-87 and represents a radical change in the diatom assemblages from those of zone 5. The change occurs abruptly between 557cm and 547cm and is marked by the declining proportion of *Cyclotella meneghiniana*, falling to less than 15% of the diatom assemblage from 31% and the sharp truncation of the *Thalassiosira rudolfi* curve between these two samples from 49% to just 1%. The dominant position occupied by *Cyclotella meneghiniana* in much of the core is

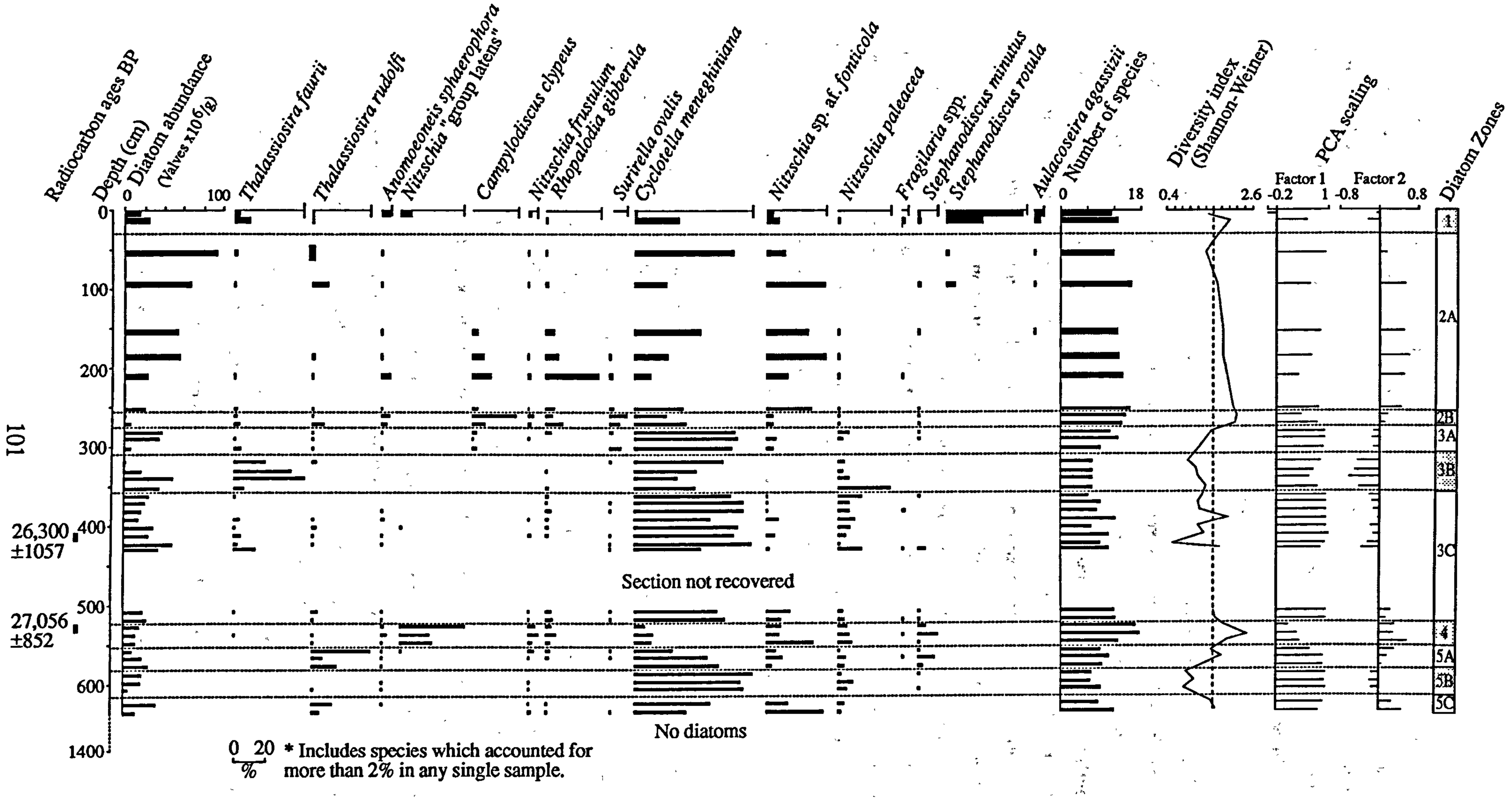


Figure 4.5 Summary of diatom analysis from Lake Manyara, core MANE-87.

supplanted in zone 4 by the genus *Nitzschia* (*Nitzschia* "group latens" 26-53% and *Nitzschia* sp. af. *fonticola* 11-39%) with smaller percentages of *Nitzschia paleacea* and *Nitzschia frustulum*. *Stephanodiscus minutus* reaches 15% at 537cm and *Rhopalodia gibberula* is also well represented in these samples. A small amount of aerophilous species (2%) are present in this zone suggesting very shallow or merely moist conditions existed at this time close to the coring site.

The zone 4/sub-zone 3C transition is as abrupt as that between sub-zone 5A and zone 4. *Cyclotella meneghiniana* increases its share of the assemblage from 8% at 528cm (zone 4) to 74% at 518cm (sub-zone 3C) whilst *Nitzschia* "group latens" which accounted for 53% of the sample at 528cm was not present at 518cm. Both diversity and the number of species counted per sample falls in sub-zone 3C (518cm to 361cm inclusive) from the relatively high levels reached in zone 4, because of the dominance of *Cyclotella meneghiniana* ranging from 53 to 94%. This sub-zone bridges the section between 435cm and 505cm that was not recovered during the coring, and although some discontinuities are evident in the species curves from above and below the missing section, the general assemblage composition is similar. *Nitzschia* sp. af. *fonticola* is well represented in 3C reaching 19% at 508cm and *Nitzschia paleacea* is found throughout this sub-zone at levels of up to 20%. *Thalassiosira faurii* is present in the upper section of sub-zone 3C reaching a maximum share of the assemblage of 17% at 429cm.

Sub-zone 3B includes four samples at 351cm, 338cm, 331cm and 319cm, that are distinguished from those of 3C by the presence in high proportions of valves of *Thalassiosira faurii*. The lowest sample of this zone at 351cm is a little anomalous to the sub-zone in general as the dominant diatom species here are *Cyclotella meneghiniana* (48%) and *Nitzschia paleacea* (43%). The latter species declines in the remaining three samples to less than 8% and is replaced by *Thalassiosira faurii* (25-57%) as the co-dominant species alongside *Cyclotella meneghiniana* (34-70%).

Diversity remains relatively low in sub-zone 3A (282cm, 291cm, and 301cm) despite containing a greater number of taxa than 3B. The dominant species is again *Cyclotella meneghiniana*, which maintains a share of the assemblage in excess of 78% in each of the three samples. The sample at 301cm is notable as it marks the first appearance of *Campylodiscus clypeus* in the core, and the first time *Surirella ovalis* occurs at levels greater than 1%. Other species present in smaller percentages include *Thalassiosira faurii*, *Nitzschia* sp. af. *fonticola*, and *Nitzschia paleacea*.

Sub-zone 2B (samples at 270cm and 261cm) is much more diverse than zone 3, chiefly as a result of a decline in *Cyclotella meneghiniana* which is reduced to

percentages of only 41% and 23% respectively. This is proportionally replaced by a range of species including *Rhopalodia gibberula*, *Anomoeoneis sphaerophora*, and *Campylodiscus clypeus*. The latter species becomes the dominant taxon at 261cm.

Sub-zone 2A (251-55cm) is separated from 2B by the abrupt rise of *Nitzschia* sp. af. *fonticola* which comprises between 15 and 49% of this zone and is the dominant taxa alongside *Cyclotella meneghiniana* (12-79%). *Rhopalodia gibberula* is also important, and is the most abundant species at 210cm (44%) where significant proportions *Campylodiscus clypeus* (12%), and *Anomoeoneis sphaerophora* (9%) are also found. The sample at 95cm differs slightly from the remainder of the zone in that it contains *Thalassiosira rudolfi* (12%) and *Stephanodiscus rotula* (6%) alongside the dominant species of *Nitzschia* sp. af. *fonticola* and *Cyclotella meneghiniana*. Diversity is higher in the top 250cm than in the cored section, although the cause of this may not necessarily be ecological, but may simply be an artifact of the use of the stratigraphically coarser augered samples.

Zone 1 contains the uppermost two samples at 2.5cm and 12.5cm. They are distinct from the other samples analysed in having high proportions of the freshwater planktonic diatom *Stephanodiscus rotula* and so are assigned to a separate zone because of the presence of this "indicator species". However, the two samples are also quite different from each other. That at 12.5cm has as its most important species *Cyclotella meneghiniana* (35%) and *Stephanodiscus rotula* (27%), with other species present including *Nitzschia* sp. af. *fonticola* (10%), *Thalassiosira faurii* (6%) and *Aulacoseira agassizii* (5%). In contrast, the sample at 2.5cm is dominated by *Stephanodiscus rotula* (56%) with *Nitzschia* "group latens" (10%), *Aulacoseira granulata* (7%), *Anomoeoneis sphaerophora* (7%), *Nitzschia* sp. af. *fonticola* (6%), and *Thalassiosira faurii* (6%). The autecology of the species within this zone would seem incongruous and the assemblages taphonomy will be discussed further in chapter 6.

Correlation with Holdship.

Correlation between cores is best resolved by the use of a wide range of analytical methods including a comparison of lithostratigraphy, magnetic susceptibility, biostratigraphy, or by using radiometric dating to establish a chronostratigraphy into which the cores can be placed. The problems of correlation become greater when a new core is being compared to published results of work from other research groups, who may have used different definitions, and studied different parameters. In the

specific case of Manyara problems of definition and terminology effectively preclude lithostratigraphic correlation, but leaves the methods of biostratigraphy by way of the diatom studies, and chronostratigraphy using the radiometric dates given to each core. Radiocarbon dating suggests that the central section of MANE-87 (zones 3C and 4) are *c.* 26-27,000 years old an equivalent age to Holdship's Zone B. However, problems with radiocarbon dates of this age range have recently been identified (Causse 1988), and the extrapolation of this rate of sedimentation would suggest breaks in MANE-87 above 4m. Therefore, detailed biostratigraphical analysis has been attempted both statistically and qualitatively using the diatom records of both cores to help aid correlation. However, it should be noted that inherent differences between the two cores exist, and the assumptions which have to be made make close correlation between the two cores problematical. Some of the difficulties are discussed below.

Site location. The sites of the two cores are *c.* 12km apart and from very different limnological settings. That of Holdship was taken from relatively deep water near to the western escarpment whilst MANE-87 was collected from a seasonally flooded littoral mudflat on the eastern shore. Therefore, assuming other factors to be equal the Holdship core would be expected to be relatively rich in planktonic forms whereas a higher proportion of littoral taxa could be anticipated in the new sequence. This expectation is confirmed by inspection of the species list given by Holdship which contains only 6 taxa generally considered littoral against the 22 found in the present study. The distance between the two cores makes the assumption that similar assemblages would have occurred even within the diatom planktonic community at the same time tenuous, given spatial patterns that have been observed amongst the phytoplankton of other African lakes (*e.g.* Kivu, Hecky and Kling 1986). Moreover, Hutchinson (1957) has written on the "paradox of the plankton" where species diversity in planktonic communities is often great despite the apparent homogeneity of the habitat. However, mixing processes and sediment redistribution will in part help to aid the correlation by diminishing the influence of spatial patterns occuring in the plankton. Finally, the distance between the sites is such that taphonomic processes will operate differentially. For example the Endabash river enters Manyara close to the site of Holdship's core and this will create local variation amongst the diatom community and may mix diatoms from different habitats.

Sedimentation patterns. The sedimentation rate for Holdship's core ranges from 0.5-4.7mm/yr (calculated between ^{14}C dates), although considerable

the variation is much less than for other lake sediment core sequences (*e.g.* Bogoria, Tiercelin and Vincens 1987; Abiyata, Perrott 1979; Kivu, Degens and Hecky 1974). However, with MANE-87 being from a site that is at present seasonally exposed it is not possible to make this assumption of continuity. Sediment will only accumulate on the mudflat when the lake level is higher than that at present and it may be lost by wind erosion during periods of low lake-level. Therefore, the expected presence of unconformities in the new sequence could render the core incomplete making correlation between the two cores difficult.

Diatom assemblage diagenesis. Correlation will be greatly hindered by differential dissolution of diatom frustules which may substantially alter the composition of the diatom assemblage or remove completely a section of the diatom record (see chapter 5). Dissolution will affect the cores to different degrees due to hydrochemical variations in the lake and evidence of this is found at various levels in both cores from Manyara. Whilst Holdship's core may well be a relatively continuous record of sedimentation, its diatom record is far from complete. The sections of the core in which diatom frustules are absent are explained by Holdship as having formed during periods of chemical concentration equal to or greater than those of the present lake. Conditions conducive to silica dissolution will impede the preservation of any diatoms present in the lake at that time, and groundwater circulation could dissolve the frustules of diatoms already within the sediment. The sterile sections cannot be expected to coincide with similar zones in the new core as when the lake brines become sufficiently concentrated to allow silica dissolution the water level will generally be below the site of the new core and sedimentation will cease. Therefore, sterile sections in Holdship's core are likely to be marked by hiatuses in MANE-87.

Taxonomy. Fundamental to achieving a biostratigraphic correlation between the two cores is the assumption that the the taxonomy used is the same. A particular problem is given by Holdship's "*Nitzschia* spp." which is important in many levels of his core and which according to the description given (see above) could encompass several of the *Nitzschia* found in the new diatom assemblages and firm correlation is impossible with this taxon. In the analysis which follows two further assumptions regarding the taxonomy were made, Holdship's "*Coscinodiscus rudolfi* " was taken to include both *Thalassiosira rudolfi* and *Thalassiosira faurii* as

the latter is a recent addition to the taxonomic literature, and the taxonomic designation of *Stephanodiscus* spp. was used for correlation purposes to avoid the problem of different identifications of *Stephanodiscus minutus* (*Stephanodiscus astraea* v. *minutula*, Holdship 1976) and *Stephanodiscus rotula* (*Stephanodiscus astraea* of Holdship).

An initial qualitative examination of the similarities in the diatom assemblages intimates two probable points of correlation between the cores (figure 4.6). The first of these is a relationship indicated by the *Stephanodiscus* assemblages of zone 1 in MANE-87 to the corresponding assemblages from the lower section of zone D in Holdship's core. Zone 1 in MANE-87 is more diverse than this section of Holdship's core, and this may be explained by differences in location of the cores and the operation of taphonomic processes. *Stephanodiscus* is not found in such high proportions in other parts of the two cores which would tend to support this assignment. The second correlation indicated by the diatom sequences exists for the *Thalassiosira* dominated sub-zones 3B and 5A and Holdship's zone B. The proposed biostratigraphical relationship is corroborated by the radiocarbon ages already established for the two cores. Therefore, these correlations permit other possible relationships existing elsewhere in the diatom sequences to be examined.

Zones 2A, 2B, and 3A of MANE-87 have a similar planktonic diatom flora to both Holdship's zone C and also to the samples at the base of zone D, having as abundant taxa *Cyclotella meneghiniana* and *Nitzschia* sp. af. *fonticola*. The major discrepancy from the otherwise close correlation is the abundance of "*Nitzschia* spp." in Holdship's core. No equivalent to this taxon is found within this section of the new sequence, the only abundant species of *Nitzschia* being *Nitzschia* sp. af. *fonticola* which is quite different taxonomically to the description given by Holdship of "*Nitzschia* spp.". Therefore, sub-zones 2A and 2B could be associated with either zone C or the bottom of zone B, although sub-zone 3A equates well with the almost monospecific *Cyclotella meneghiniana* assemblage found at the base of Holdship's zone C.

On the basis of the correlation established between sub-zone 5A and the base of Holdship's zone B, the lowest sub-zones 5B and 5C again *Cyclotella meneghiniana* dominated should correlate to Zone A. An assemblage dominated by *Cyclotella meneghiniana* is found at the base of zone A but given the ubiquity of this species in both cores this is an highly speculative association. It is also possible that these zones have no equivalent recorded by Holdship as a result of the dissolution process.

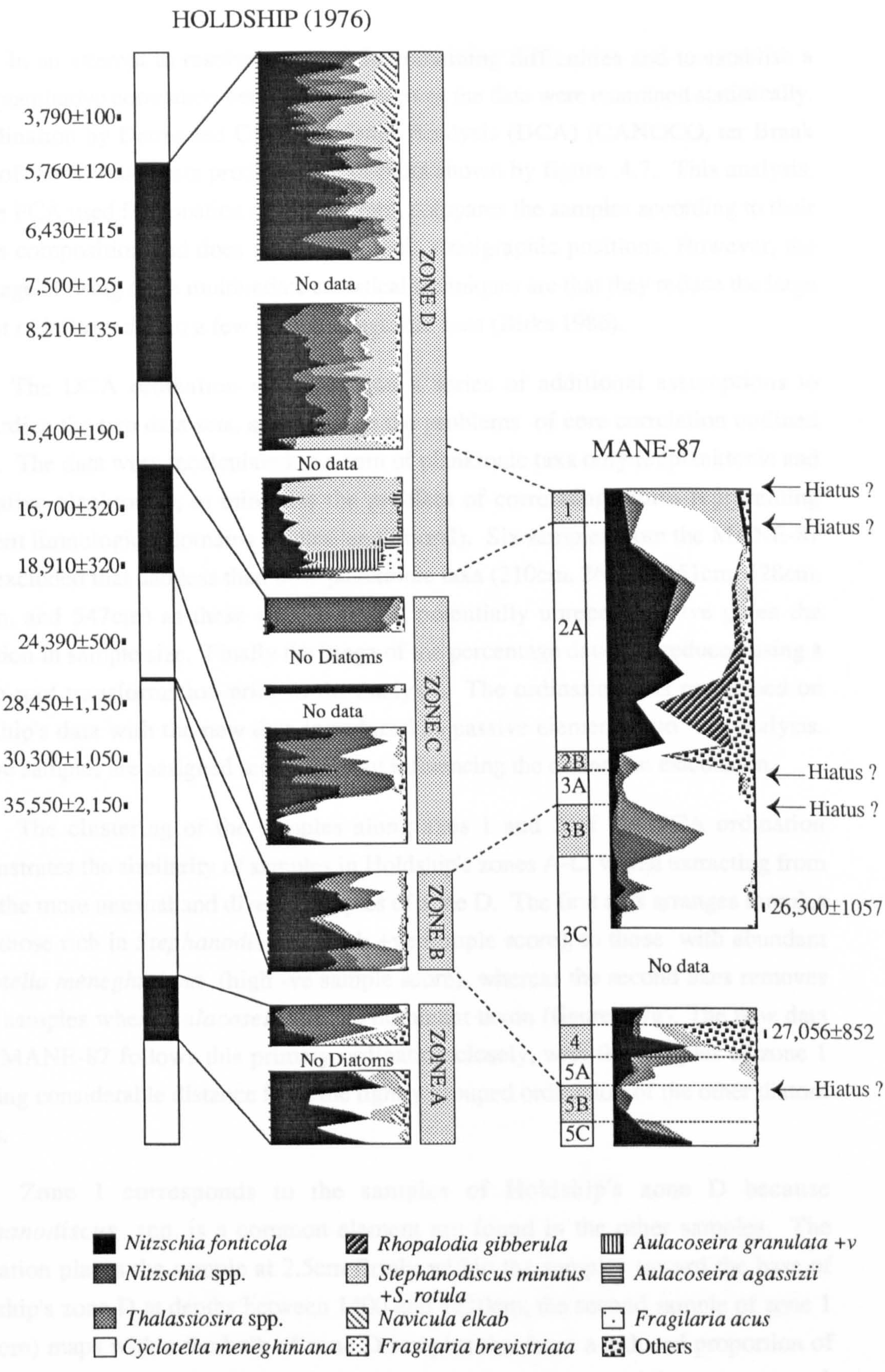


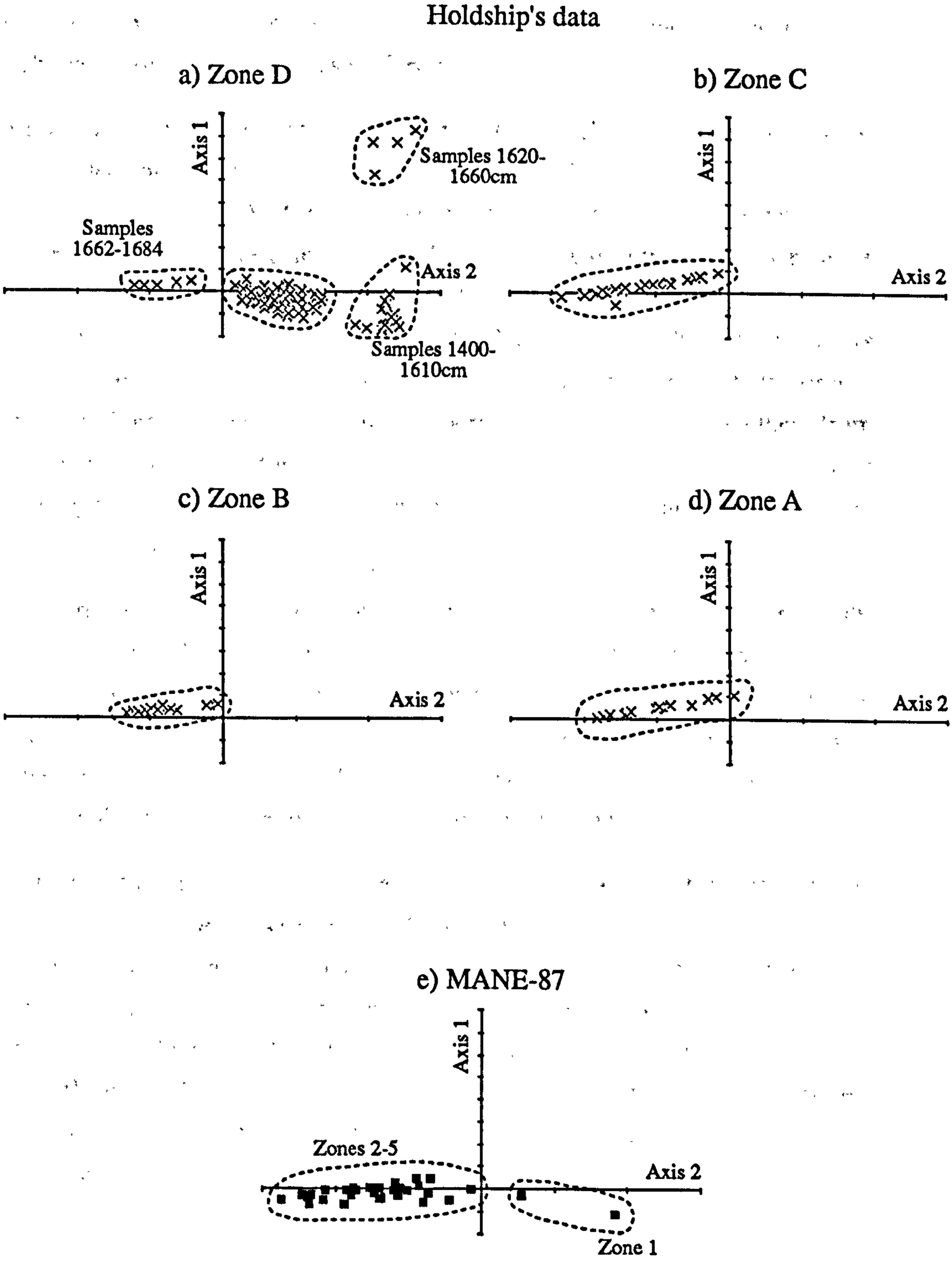
Figure 4.6. Tentative correlation of the two cores from Lake Manyara.

In an attempt to resolve some of the remaining difficulties and to establish a more quantitative correlation between the two cores the data were examined statistically. An ordination by Detrended Correspondence Analysis (DCA) (CANOCO, ter Braak 1988) of the two data sets produced the bi-plots shown by figure 4.7. This analysis, like the PCA used for zonation of the diagram, compares the samples according to their species composition and does not respect their stratigraphic positions. However, the advantage of using these multivariate statistical techniques are that they reduce the large amount of information to a few more manageable axes (Birks 1986).

The DCA ordination was based on a series of additional assumptions to standardize the two data sets, and to offset the problems of core correlation outlined above. The data were recalculated as a sum of planktonic taxa only (euplanktonic and facultative planktonic), to minimise the problem of correlating cores representing different limnological domains (central and littoral). Six samples from the MANE-87 were excluded that had less than 60% planktonic taxa (210cm, 261cm, 351cm, 528cm, 538cm, and 547cm) as these were regarded potentially unrepresentative given the reduction in sample size. Finally the range of the percentage data was reduced using a square-root transformation prior to the analysis. The ordination was performed on Holdship's data with the new data introduced as passive elements into the analysis. Passive samples are assigned scores without influencing the ordination calculation.

The clustering of the samples along axes 1 and 2 of the DCA ordination demonstrates the similarity of samples in Holdship's zones A-C, whilst extracting from these the more unusual and diverse samples of zone D. The first axis arranges samples from those rich in *Stephanodiscus* (high +ve sample score), to those with abundant *Cyclotella meneghiniana* (high -ve sample score), whereas the second axes removes those samples where *Aulacoseira* is the dominant taxon (figure 4.7a). The new data from MANE-87 follows this primary ordination closely, with the samples of zone 1 showing considerable distance from the tightly grouped ordination of the other diatom zones.

Zone 1 corresponds to the samples of Holdship's zone D because *Stephanodiscus* spp. is a common element not found in the other samples. The ordination places the sample at 2.5cm firmly within the samples toward the base of Holdship's zone D at depths between 1400 and 1610cm, the second sample of zone 1 (12.5cm) maps within the bulk of zone D samples that have a reduced proportion of *Stephanodiscus* spp. with respect to *Thalassiosira* spp. and *Nitzschia* sp. af. *fonticola*. If the statistical results are taken literally a stratigraphical reversal would have to be envisaged according to this correlation, however this could more easily be



* The samples were recalculated as a sum of planktonic taxa prior to the analysis. Six samples from MANE-87 that have less than 40% planktonic taxa have been excluded (see text for details).

Figure 4.7. DCA ordination of Holdship's data with samples from MANE-87 introduced as passive elements.

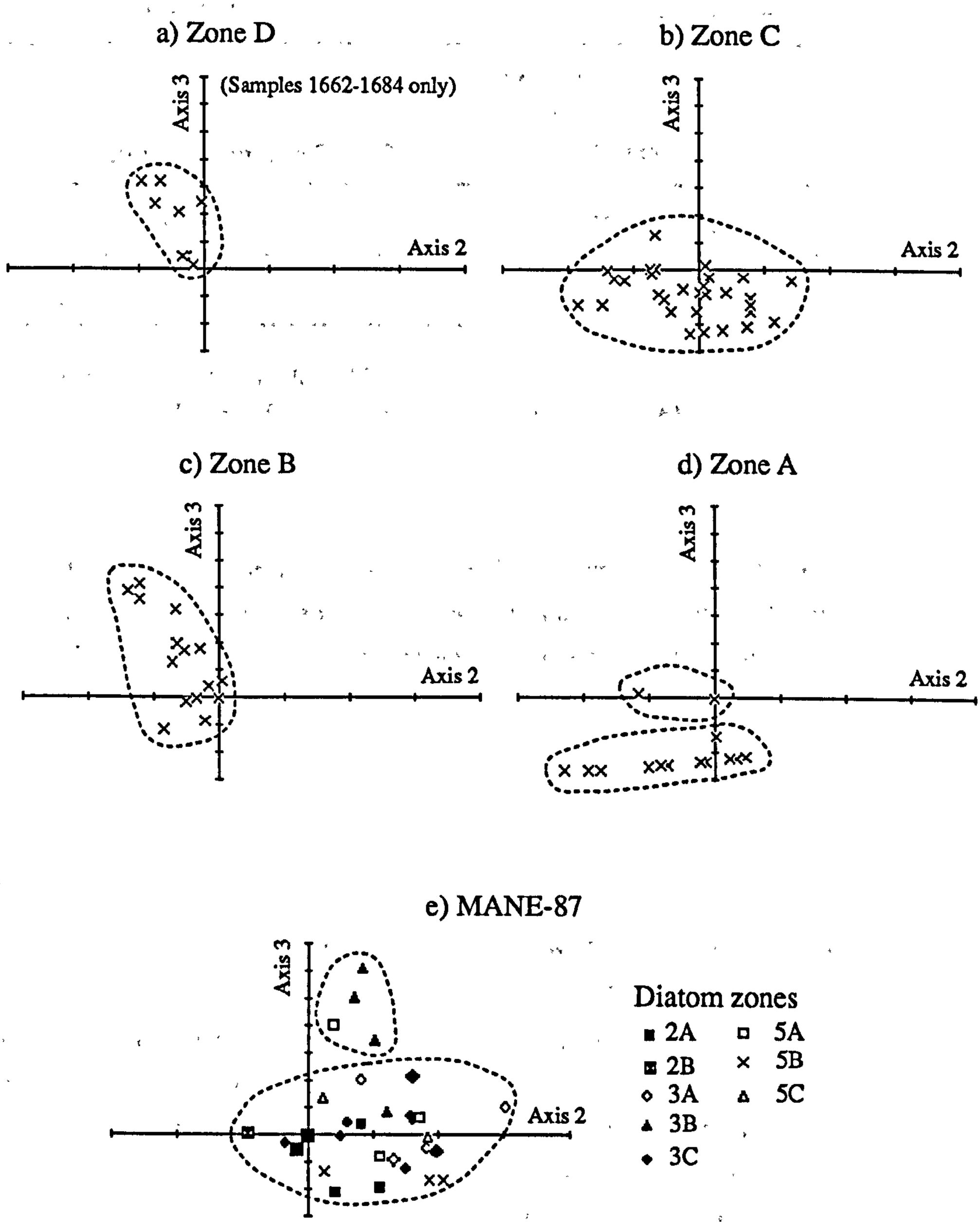
explained by reference to mixing processes, sampling strategies, and the assumptions under which the statistical analysis was performed.

In order to help differentiate the remaining tightly clustered assemblages the DCA was repeated following the removal of the samples (570-1600) from Holdship's zone D and zone 1 of MANE-87 for which a correlation has already been established. As in the first ordination exercise the MANE-87 data was introduced as passive elements into the analysis and the data were transformed by square-root. The first axis extracted the remaining six samples (five from MANE-87) in which *Stephanodiscus* spp. was found, leaving the majority of the samples tightly clustered close to the origin. The second axis of ordination split the samples more successfully, arranging them from those rich in *Nitzschia* sp. af. *fonticola* (-ve scores) to those with abundant *Cyclotella meneghiniana* (+ve scores). Samples containing *Thalassiosira* spp. are ordinated along the third axis (figure 4.8).

The third axis of ordination supports the relationship suggested between sub-zones 3B and 5A of MANE-87 and Zone B of Holdship on the basis of having *Thalassiosira* spp. as a common element in each of these. It also would seem to suggest that zone 2 of MANE-87 shows a greater resemblance to Holdship's zone C than D. The latter has more abundant *Thalassiosira* spp.and *Nitzschia* sp. af. *fonticola* than zone 2 in which *Cyclotella meneghiniana* is more important.

However, the second axis also emphasises the major difference existing between the two cores, *i.e.* those from MANE-87 are greatly enriched in *Cyclotella meneghiniana* and deficient in *Nitzschia* sp. af. *fonticola* relative to Holdship's core. This may result from ecological differences amplified by the distance between the sites, or it could be the product of differential dissolution, a question to be addressed more fully in the following chapter. Despite these difficulties it is possible to propose a preliminary table of correlations existing between the two cores and therefore to construct a more substantive chronology for MANE-87.

Holdship's data.



* Data recalculated as in figure 4.8 with the additional exclusion of zone 1 from MANE-87 and samples 570-1600 from Holdship's Zone D as explained in the text.

Figure 4.8. DCA ordination of Holdship's data excluding samples 570-1600 from Zone D with MANE-87 introduced as passive elements.

TABLE 4.4. Possible correlation with Holdship (1976).

MANE-87	HOLDSHIP	Possible radiocarbon age[1]
Zone 1	Zone D (samples 1400-1610)	8,000-12,500 yrs BP
Zones 2A -3A	Zone C (samples 2310-2670)	16,500-19,000 yrs BP[2]
Zones 3B-5A	Zone B	26,000-27,500 yrs BP[3]
Zones 5B + 5C	?	>27,500

[1] Interpolated from ^{14}C dates of Holdship (1976).
[2] U/Th dating suggests these ^{14}C dates are too young, Goetz (1990).
[3] From MANE-87.

Suggesting an age for the base of the diatom sequence is difficult, the radiocarbon age of *c.* 27,000 from zone 4 gives a minimum age for zone 5 but with the possibility for discontinuities zone 5C may prove to be much older than an extrapolated sedimentation rate might suggest, especially if a correlation with Holdship's zone A is correct.

Conclusion.

The chronological framework outlined above implies marked variation in the sedimentation rate of MANE-87, almost certainly involving the discontinuous accumulation, or erosion of sediments from the coring site resulting in hiatuses. Abrupt changes in the diatom assemblages found at each of the zone and sub-zone boundaries might point to the location of hiatuses in the core, but may also (given the potential for diatom communities to change very rapidly) simply indicate ecological changes with the transitional phases not detected by the sampling interval employed. The early Holocene age suggested for the top of the core means that the last 8,000 years of sediments are missing, either due to the cessation of sedimentation, or more likely from a combination of this and subsequent erosion. If the correlation between zones 2 and 3A and Holdship's zone C is valid, a major hiatus is likely at the zone 2/zone 1 transition. Some evidence for this is presented by the discontinuity in the diatom assemblages, and also by a sandy horizon at this depth in a 1m box core taken from close to the same site. Other abrupt changes in the diatom sequence occur at the boundaries of sub-zones 2A/2B and 3A/3B, and even potentially within sub-zone 2A

itself. Therefore, at least one further significant hiatus is likely here but, closer chronological control is necessary before any break in sedimentation can be conclusively identified in this section of MANE-87.

Correlation with the core studied by Holdship allows the complex chronology of MANE-87 to be better understood. In addition the new core may also be useful to the interpretation of Holdship's sequence, especially for Holdship's zone B which is thought to be the equivalent of zones 3B to 5A of MANE-87. The more extensive diatom record from this section shows several abrupt changes not found by Holdship, and zones for which he has no equivalent. The greater depth of sediment representing this diatom zone in the new core could be a consequence of changing depo-centres within the lake, or the later eradication of diatoms from Holdship's core by silica dissolution.

Species abundance in MANE-87 is low with only 32 different diatom taxa identified, in a diatom record comprising for the most part *Cyclotella meneghiniana* dominated assemblages. This compares well to the 34 taxa found in the much longer core of Holdship. The restricted number of species is not unusual in saline lakes (Hammer 1986) and is also a function of the location of the core site, but in Manyara an additional factor could be assemblage diagenesis selectively removing certain species. Diagenetic processes could, by differential removal of particular taxa, serve to enhance the apparent similarity of the assemblages and may serve as an explanation for the recurrence of similar diatom assemblages.

Therefore, environmental reconstruction of this new core depends critically on an understanding of the extent to which the diatom assemblages have been modified by the diagenetic processes operating within the lake. These must be distinguished from the environmental processes initially responsible for supporting the particular diatom communities represented by the fossil assemblages in the core. Furthermore, the biostratigraphical correlations proposed between the two cores could be undermined if the assemblages have been greatly altered by the differential dissolution of diatoms. These questions and the process of dissolution in general will be addressed more fully in the following chapter and the palaeoenvironmental significance of the diatom changes in MANE-87 are discussed in chapter 6.

CHAPTER FIVE: DIATOM DISSOLUTION -EXPERIMENTAL STUDIES.

The physico-chemical alteration of diatom assemblages by forces operating in the water body and the sediment column, is a major hindrance to diatom based palaeoecology. The recognition that diagenesis of the fossil assemblage may be a source of error in diatom based environmental reconstructions has been stated by many authors (*e.g.* Hecky and Kilham 1973, Battarbee 1978, Gasse *et al.* 1989a), but has received little direct attention except from marine diatomists (Lawson *et al.* 1978, Mikkelsen 1980, Shemesh *et al.* 1989). Evidence of frustule degradation in terrestrial freshwater environments has been reported (Meriläinen 1971, Bradbury and Winter 1976, Parker *et al.* 1977, Schelske *et al.* 1983) but it has been considered unlikely to lead to serious palaeoecological misinterpretations (Round 1964). More problematic in this respect are athallasic saline-alkaline environments which may preserve only a partial record of the diatom death assemblage (Holdship 1976, Bradbury 1989, Gasse and Seyve 1987). Under these conditions the fossil diatom assemblage must often be treated as merely a window onto a formerly more complete diatom community. The problem of diatom frustule destruction is also severe in the context of marine waters, and it is here that the issue has received the most attention. Lisitzin (1971) estimates as much as 90-99% of marine diatoms are dissolved even before they reach the deep sea floor. Once deposited the destructive processes continue and up to 90% of all particulate material may be subsequently re-dissolved (Hurd 1973).

The destruction or partial destruction of diatom assemblages creates a series of problems for diatom-based palaeoecology. These include the poor state of preservation of some frustules, which can make identification more difficult and may limit the level of taxonomic precision possible (Meriläinen 1971). More extremely it can create sterile levels in cores and sections thereby limiting the value of diatom based reconstructions (*e.g.* Holdship 1976). However, perhaps most dangerous to palaeoenvironmental interpretations are those processes that lead to subtle diagenesis of fossil assemblages. It has been suggested that these may preferentially remove small and weakly silicified species (*e.g.* Battarbee 1988) leaving no trace of them in the sediment. This differential destruction of certain species can result in bias in percentage calculations which may not be detected during routine counting. Such errors can be passed on to the environmental interpretation stage of diatom analysis and can significantly alter the conclusions made. This may be especially true if quantitative techniques such as transfer functions are used to reconstruct environmental variables (Shemesh *et al.* 1989, Beyens and Denys 1982).

These are usually based on the entire fossil assemblage and the loss of even a small number of taxa can be very important for the values calculated.

The destruction of diatom frustules in saline lakes.

Physical, chemical and biological processes are all likely contributors to the destruction of diatoms in saline lakes. These may operate on living communities, on the death assemblage at the sediment-water interface, or at some later stage within the sediment column. Physical destructive processes such as the degree of water turbidity, the sedimentation of particles, and post-depositional sediment mixing, can result in the fragmentation of frustules. These tend to preferentially break elongate and spicular taxa and may lead to bias in percentage calculations unless allowance is made in the counting strategy adopted (*cf.* chapter 2). Fragmentation will also contribute greatly to the chemical dissolution of valves by increasing the specific surface area (Glover 1982).

Biological factors are often allied to these strictly physical means of destruction. These include the mixing of sediment by organisms which might cause the physical destruction of diatom frustules in the surface sediments. Bioturbation and subsequent resuspension will increase the rate of chemical dissolution by re-exposing the sedimentary silica to undersaturated waters (Rippey 1983). Grazing by predators and sediment browsers may also fragment valves through their digestive processes and remove the protection to the frustule provided by cell protoplasm (Hurd 1972). Paradoxically, the actions of predators can also serve to preserve the frustule by protecting it within faecal pellets, which can increase its rate of sinking through the water column, thus protecting it against chemical attack at this stage and providing it with a protective covering against physical and chemical processes operating in the sediment (Hurd 1972, Haberyan 1985). However, chemical destruction is probably the most important diagenetic process at work on the diatom assemblages of saline-alkaline lakes. This is a result of the dissolution of frustule silica in alkaline waters, a process discussed in the remainder of this chapter.

The chemistry of silica dissolution.

Diatom frustules being comprised almost entirely of amorphous silica (about 86% by weight, the remainder being water and a few metal ions; Oehler 1979), are subject to the processes that dissolve silica in natural waters. The catalyst for the solution of silica is provided by the hydroxyl ion which liberates oxygen from the

silicate molecule (SiO_2) leaving silica in its dissolved state ($SiOH_4$) (Iler 1979). The solubility of silica in an aqueous solution is determined by several controlling factors (Oehler 1979).

1. The degree of crystallinity. Silica is present naturally in various crystalline forms ranging from an amorphous state to quartz, each of which has a different level of solubility. For example, Iler (1979) has estimated that the equilibrium solubility of amorphous silica is 110ppm at 25 °C compared to that of quartz which is only approximately 10ppm at 25 °C. These differences are a function of the surface area of the crystal; the larger crystals have a smaller surface area/ volume ratio available for dissolution.

2. Specific surface area. The rate of dissolution of silica particles increases in proportion to the square root of their specific surface area (Goto 1958). Hence, narrow needle-like structures are more prone to dissolution than spheres of the same volume. In the case of diatoms the degree of sculpturing is a major control of specific surface area. Hurd *et al.* (1981) have shown how diatom and radiolarian frustules have a microporosity in addition to their normal sculpturing and this is very important in determining the solution rate.

3. Adsorbed metal cations. These may inhibit dissolution by forming polymeric coverings around the silica particles. In the natural situation these are likely to involve chiefly the polyvalent metal cations of iron and aluminium although other metals such as berium, germanium, and yttrium can also retard dissolution. The amount of metal ion required to decrease silica solubility is very small, Iler (1979) reports that the adsorption of only one aluminium ion can drastically reduce the equilibrium solubility of the silica. Magnesium can also combine with amorphous silica to produce magnesium silicates, a process which may involve the dissolution of the silica. Calcium has no effect on the solubility of silica up to pH 9.5 above which calcium silicates are formed. It should be noted however that Hurd and Theyer (1975) consider that the role of metal ions is only to delay the dissolution process rather than to influence the final outcome.

4. The role of organic matter. Organic compounds may also retard dissolution of amorphous silica by forming protective films over the surfaces of particles. In other circumstances they can accelerate the dissolution rate by absorbing soluble silica and helping to convert it to a

soluble complex (Iler 1979). Living diatom cells may have some protection against dissolution afforded to them by their organic membrane.

Silica solubility is also dependent on the characteristics of the solution in contact with it. Of particular importance are the following properties.

1. pH. The solubility of amorphous silica varies greatly with the pH of the solution. This is not linear and it appears that solubility decreases slightly as pH increases to 7, it then rises gradually to pH 9 above which the solubility increases exponentially to 1000ppm at pH 10 (Iler 1979 and references therein).

2. *Salinity.* The solubility of amorphous silica in various salt solutions has been investigated by Marshall and Warakomski (1980). They found that the addition of any salt decreased the solubility of silica although this varied for different salts. Sodium bicarbonate and sodium sulphate solutions produced the smallest decrease in silica solubility with salt concentration whilst the largest decline was found in magnesium chloride, calcium chloride and magnesium sulphate salts. Sodium chloride occupied an intermediate position with silica solubility declining by approximately 25% as the solution approached one molar concentration.

3. Temperature. The solubility of amorphous silica and the rate of the dissolution process are both positively correlated to the temperature of the solution. For example, the solubility of silica at 22 °C is only 30% that at 73 °C in a neutral solution (Goto 1955 cited in Iler 1979).

4. Impurities in the water. The dissolution of silica in natural waters is often greatly reduced from that in pure water due to the presence of impurities such as metal ions. Iler (1979) has shown that the addition of soluble aluminium to a solution of pure water reduces the solubility of amorphous silica greatly from 110ppm to 10ppm.

5. Pressure. This increases the solubility of silica. It has been shown that in sea water at 0 °C the solubility of silica at 1atm is 65 ppm whilst at 150 atm solubility rises to 71 ppm after which solubility increases linearly (Willey 1974 cited by Iler 1979). The effect of pressure may be important in very deep lakes and in the oceans.

6. Flushing and turbulence. The factors mentioned above all refer to the bringing of solid phase silica into solution. In order for this to be removed

from sediments and not simply redeposited in another form, it is necessary to have an open system of water flow. Turbulence at the water sediment interface may also help to increase the solution rate by removing the dissolved silica away from the sediments (Rippey 1983) and therefore preventing saturation levels of silica being reached. This has been demonstrated experimentally by Hurd (1972).

Previous experiments concerning the dissolution of diatom silica.

Laboratory studies cannot hope to precisely model the process of diatom frustule dissolution due to the immense time periods over which this can potentially occur in nature. Also the complexity of natural systems dictates that the conclusions reached may only be valid for the environments where they were developed. Nevertheless, several laboratory studies have begun to isolate the parameters critical to diatom dissolution and these may provide a general framework within which to answer site specific problems.

The first rigourous assessment of the variables that contribute to diatom dissolution was made by Joyce Lewin (1961) who performed a series of experiments, primarily on cultured diatoms, but also used natural phytoplankton and some fossil material. Her first conclusion was to reaffirm the results of Jorgensen (1955) which had demonstrated the importance of pH to the solubility of diatom silica. She showed that both the rate and the amount of dissolution increase as pH rises above neutrality. This could then be further accelerated by increasing the temperature of the solution, such that at 35 °C the amount of dissolution was 75% greater than at 15 °C, everything else being equal. The next stage of her research was to investigate the factors responsible for retarding dissolution and whether these were primarily of organic or inorganic origin. Valves that were cleaned in nitric acid which oxidises organic matter, dissolved much more quickly than those which were not cleaned. However, when the nitric acid extract was evaporated, re-dissolved in water and then reapplied to the cleaned diatoms (*i.e.* without the oxidised organic matter) the dissolution process was retarded back to the level found when intact valves were used. This suggested that the major factor reducing the dissolution rate was not the organic material itself but some inorganic compound which was thought to be a metal ion. The addition of aluminium, barium, iron, gadolinium, gallium and yttrium were all successful in reducing dissolution in solutions of pH 8. Further tests showed that the aluminium had become adsorbed to the frustule surfaces, providing a protective coating against dissolution.

Experiments performed on living diatoms (grown in starvation conditions to prevent uptake of silica from the solution) showed dissolution to proceed slowly until the point of death after which it accelerated greatly. This suggests that living diatoms have some physio-chemical means of preventing dissolution which is lost on death. The fossil samples behaved in a similar fashion to the cultured diatoms in that their dissolution could be greatly accelerated by acid cleaning. It was also noted that the solubility of a sample from the late Pleistocene was far greater those from Pliocene and Miocene deposits, and it was therefore suggested that diatom frustules become less liable to dissolution with age.

Mikkelsen (1980) examined Pliocene diatom assemblages from the Pacific and attempted to dissolve these experimentally in sea water. Raw sediment showed no evidence of dissolution after 250 hours exposure to sea water at 25 °C and so samples were chemically pre-treated with 10% HCl and 10% H_2O_2. The results of this showed clearly that differential dissolution occurs between species, as samples taken at different times during the experiment had different assemblage compositions. The number of species present also declined almost logarithmically during the course of the experiment. It was possible to identify morphological changes in the surviving valves at various stages of dissolution and it was smaller phenotypes that had been selectively removed. Interestingly, it was found that in samples from sites at different latitudes, the abundance of one *Coscinodiscus* species increased relative to another during the experiment in samples from high latitudes, but the same species had an inverse relationship in samples from low latitudes. According to Mikkelsen this reflects the influence of different environments on valve formation and she suggests this may limit the applicability of dissolution studies to particular regions. This may suggest that solubility can vary due to differences in the fossilization processes at disparate sites.

More recently Shemesh *et al.* (1989) have dealt experimentally with the dissolution of fossil diatoms from the Southern Ocean. They considered two experimental temperatures, 85 °C and 60 °C. Dissolution was greatly enhanced at the higher temperature which led them to suggest that kinetic effects dominate the process of dissolution in alkaline solutions. They found that differential dissolution occurred between species, and that this can lead to misleading palaeoenvironmental interpretations. They then suggested a means of reinterpreting palaeoecological data using a preservation index developed from the results of dissolution experiments.

Aims, hypotheses and objectives.

Previous research on marine sediments has established that the solution of silica selectively removes certain diatoms from an assemblage while proportionally enhancing it with others. A knowledge of this and the changes to the marine thanatocoenoses resulting from the diagenetic process have enabled adjustments to palaeoecological interpretations to be made. In the saline lakes of tropical Africa conditions conducive to diatom dissolution also exist, and an hypothesis can be advanced that this will also operate differentially between species as has been found in the oceans.

According to the factors controlling the dissolution of silica the solubility of a diatom frustule is in part a function of surface area and the density of silica relative to valve volume. Those valves with a large surface area to volume ratio and a low silica density are expected to be the first to be dissolved. Table 5.1 provides estimates of the volumes (V) and surface areas (SA) of selected taxa.

TABLE 5.1 Morphological measurements of selected diatom species.

Species	V (μm^3)	(SAμm^2)	SA/V
Thalassiosira faurii	7,540	1,177	0.16
Epithemia sorex	6,341	1,972	0.31
Cyclotella ocellata	849	259	0.31
Cyclotella meneghiniana	3,328	1,165	0.35
Aulacoseira granulata	1,382	636	0.46
Aulacoseira granulata v. *angustissima*	198	175	0.88
Fragilaria brevistriata	296	316	1.07
Navicula elkab	374	421	1.13
Nitzschia subrostrata	205	303	1.48
Cymbella microcephala	108	161	1.49
Nitzschia sp. af. *fonticola*	90	137	1.52

These values were calculated from morphometric measurements of at least 10 complete frustules of each species made using an eyepiece graticule on the light microscope. The volume and external surface areas were then calculated by approximating the frustule to its nearest geometric shape of the measured dimensions (*cf.* Einsele and Grim 1938, Battarbee 1973, Sicko-Goad *et al.* 1984). This method provides only an approximation of these quantities and does not consider the frustule sculpturing. However, despite these limitations table 1 shows how great the range of volumes and surface areas are for different diatom species. Solubility depends not only on the size of the frustule but also on factors such as the microporosity (Hurd *et al.* 1981), impurities within the silica, and the frustule thickness. This latter property is highly variable even within species (Glover 1982, Sicko-Goad *et al.* 1984, Tuchman *et al.* 1984) but overall silica content of the cell is closely correlated to cell volume (Sicko-Goad *et al.* 1984). Since volume and surface area are amongst the most important factors in governing the rate of silica dissolution this may provide a theoretical basis for predicting the propensity for dissolution of particular diatom species. This hypothesis will be tested by the experiments described below.

A series of dissolution experiments (DE1-5) have been conducted to examine the relationships between African diatom assemblages and the dissolution process. The first group of experiments (DE1-4) was performed to establish a suitable experimental procedure and to test some of the previously held assumptions relating to the factors affecting dissolution. An appropriate methodology to investigate diatom dissolution must result in frustules dissolving slowly enough so as to allow adequate samples to be taken without being unreasonably long. Experiment 5 (DE5) applies the methodology established by DE1-4 to a more diverse fossil flora with the intention of producing a spectrum of individual species dissolution potential. The aim is to make recommendations regarding the recognition of assemblage diagenesis and to aid the palaeoecological interpretation of partially dissolved fossil diatom assemblages found in the cores from Magadi and Manyara.

General methodology.

The dissolving medium. Silica solubility is determined largely by the characteristics of the dissolving medium. Of particular importance is the alkalinity of the solution as this increases the solubility of silica exponentially above pH 9. Several alkaline solutions have been used in dissolution experiments including TRIS buffer

(Lewin 1961), sodium chloride (Mikkelsen 1980) and sodium carbonate (Shemesh *et al.* 1989). The most appropriate dissolving agent for these experiments is sodium carbonate as this is the dominant anion in the saline lakes of Africa from where the samples were obtained. This was used in a 2M solution with a pH of 12 and a conductivity of 80,000 µS/cm. Whilst these values are high, they are found naturally in the most concentrated saline-alkaline lakes.

The sediments. DE1-4 were conducted on Late Pleistocene sediment from Lake Manyara, Tanzania. The samples were taken from the following depths of the core described in chapter 4, 150-160cm (DE1), 90-100cm (DE2), 50-60cm (DE3) and 275-295cm (DE4). Samples from different levels had to be used in order to have sufficient sediment for each experiment. These samples were low in species diversity but they contained significant proportions of large, heavily silicified species (*e.g. Cyclotella meneghiniana*) as well as some smaller, more delicate diatoms (*e.g. Nitzschia* sp. af. *fonticola*). The ratio of these two taxa should indicate whether dissolution occurred differentially with respect to frustule size during the course of these experiments. Late Pleistocene material from Lake Magadi was used for DE5. Samples were taken from 300-350cm of core NF1 from Flamingo Nursery (see chapter 3). The diatom flora of this material was much more diverse with 69 taxa being identified. The untreated samples were oven dried at 60°C and homogenized in a pestle and mortar prior to weighing into 20 mg sub-samples (DE1-4 only). In DE5 sub-sampling was undertaken after cleaning the bulk sample with acid, therefore the weight of sample used was reduced to 10mg.

Experimental temperature and duration. In nature, dissolution is not confined to the duration of a research project to substantially alter an assemblage, and so it is necessary to employ a catalyst in laboratory simulations. As so often in chemistry, temperature has been found to be useful in this respect and previous workers have employed a variety of experimental temperatures and durations. The studies by Shemesh *et al.* (1989) were completed within 240 minutes at 60 and 85°C, Mikkelsen (1980) experimented for 450 hours at 25°C, whilst those of Lewin (1961) were allowed to run for up to 130 days at 19°C. In the experiments conducted here, the lead of Shemesh *et al.* (1989) was taken with temperature fixed at 85°C (DE1 and DE3) and at 60°C (DE2, DE4, and DE5). Therefore, the assumption is made that the changes produced in the diatom assemblage are the same at these high temperatures as those from experiments at lower temperatures allowed to run for longer durations.

Pre-treatments of samples. The experiments required the cleaning of some samples prior to the dissolution stage. Three treatments were used, a) heating the sample in 10% HCl for 2 hours and washing three times in deionised water, b) heating

the sample in H_2O_2 for 2 hours and washing three times in deionised water, c) both of these. Figure 5.1 describes the pre-treatments applied to the various samples of DE1-5.

The dissolution experiment. Samples of fossil material were oven dried and weighed into 20mg sub-samples, these were placed in 50ml polypropylene centrifuge tubes and 40ml of 2M sodium carbonate was added at the experimental temperature. The tubes were then heated in a water bath for the experiment duration, one tube being removed at selected intervals. This was immediately placed in a centrifuge and spun at 3000rpm for 15 minutes. The supernatant solutions were decanted into plastic tubes and saved for determination of the dissolved silica content. The use of plastic vessels throughout was imperative to prevent the sodium carbonate dissolving the glassware.

Post-experiment procedure. After each experiment the residual solids were acidified in 10% HCl to remove remaining carbonate and repeatedly washed in deionised water. If the sample had not been oxidised as part of the pre-treatment the sample was washed in 30% H_2O_2 to remove organic matter in order to facilitate counting. After final washing the samples were diluted and a known quantity of polystyrene microspheres were added to enable "absolute" counts to be made (Battarbee and Kneen 1982). The sample was then placed in an ultrasonic bath for a few seconds to disperse the microspheres, an aliquot was immediately drawn off and evaporated onto a coverslip at room temperature, finally a permanent slide was made using Naphrax high resolution diatom mountant. Counts of at least 300 valves were made for each sample of experiments DE1-4, broken valves being counted only if more than half remained. This was increased to 500 valves in DE5 due to the greater species diversity in these samples. Calculation of species abundance and percentage representation were made with confidence intervals constructed accordingly.

Determining the percentage of silica dissolved. A 10ml subsample of the supernatant liquid was decanted into a plastic beaker and acidified using 20ml of 1N sulphuric acid. This was then transferred into a flask and diluted to 1 litre with deionised water. The dissolved silica content of a 10ml aliquot of this mixture was determined using a Palin water test kit based on molybdbate blue phototometry. Therefore, the amount of dissolved silica in the supernatant liquid (Sd) was calculated as Sd=Sp-Sb, where Sp is the result of the Palin test[1], Sb is the result of a Palin test performed on a "blank" sample of deionised water plus reagents. The initial silica content of the sediment was calculated to allow the percentage dissolution at various stages of the experiment to be estimated. A 5mg sample of oven dried sediment was weighed into a nickel crucible with 50mg of sodium carbonate. The crucible was

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[1]*Palintest* Water tests, Wilkinson and Simpson Ltd. Gateshead, Tyne and Wear.

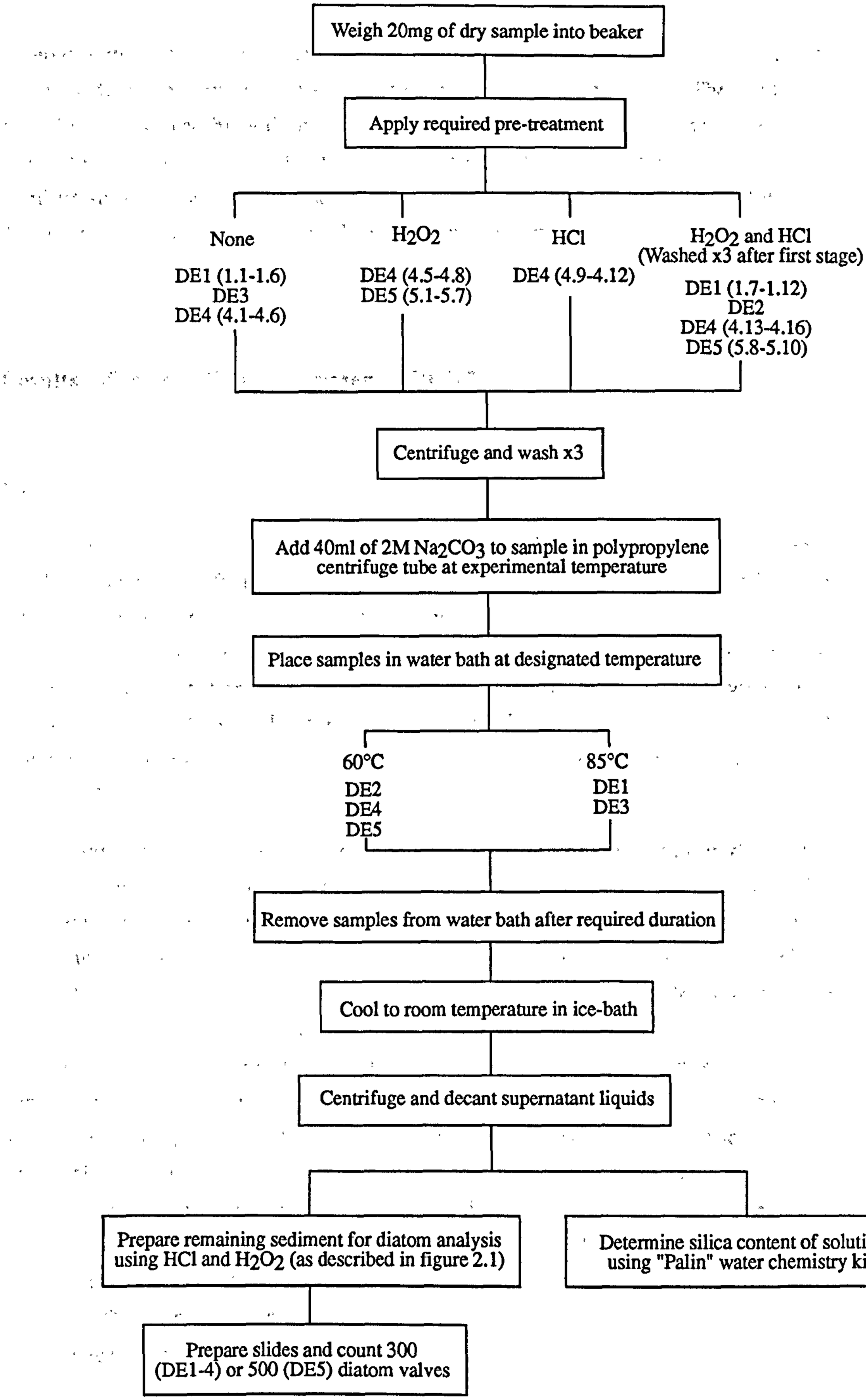


Figure 5.1. Summary of experimental procedure for DE1-5.

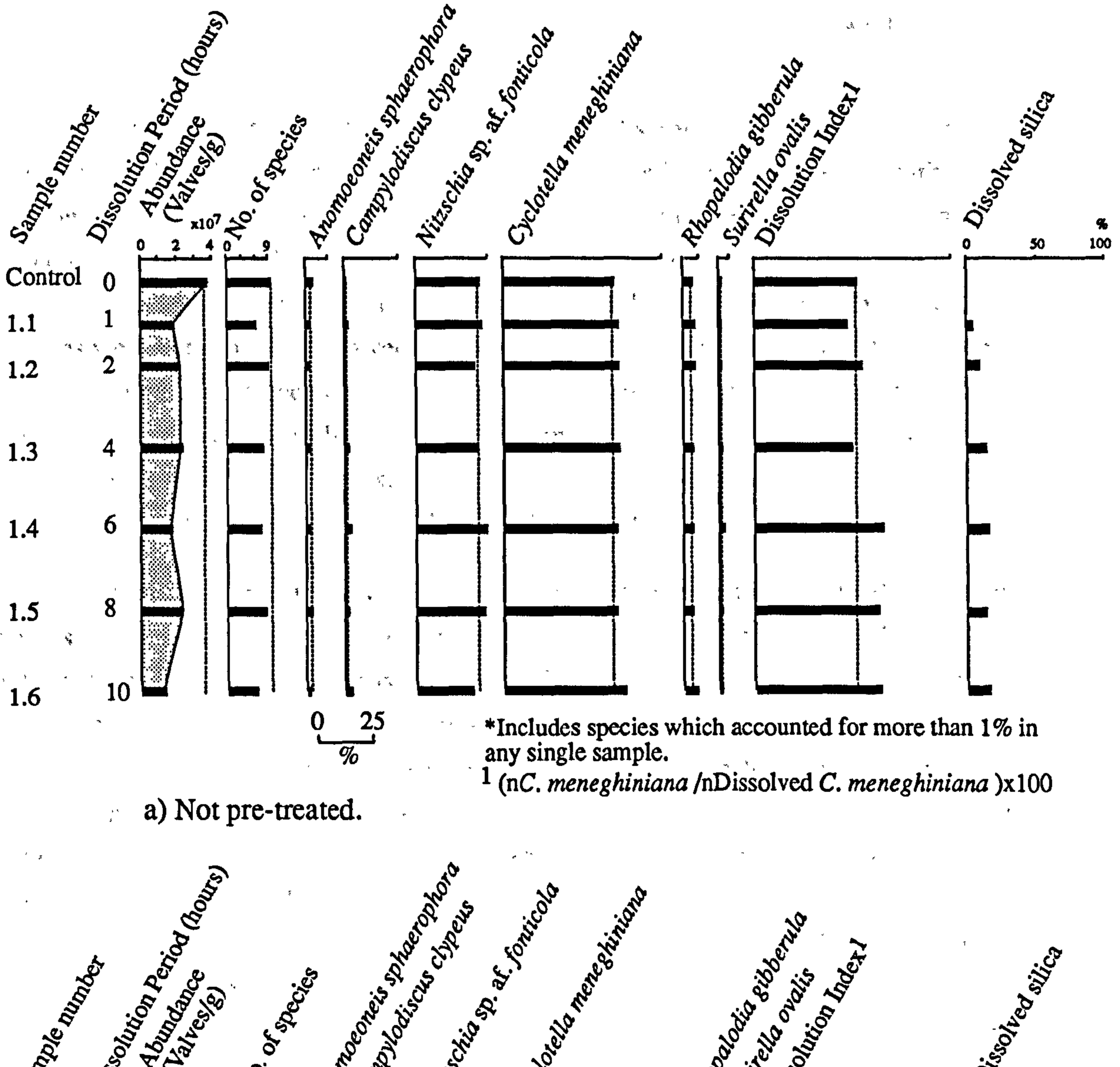
covered with a lid and heated at maximum temperature for 5 minutes over a Bunsen burner to fuse the sodium carbonate with the silica in the sediment. The melt was cooled and dissolved by adding 10ml of deionised water and heating on a hot plate. When the melt had dissolved the mixture was cooled in an ice bath and acidified with 10ml of sulphuric acid. This was transferred to a flask and diluted to 1 litre with deionised water. A Palin test on a 10ml aliquot was performed as for the supernatant liquids.

Results of dissolution experiments DE1-5.

DE1

Previous work has shown that acid cleaned diatom frustules dissolve more quickly than those left in their raw condition (Lewin 1961, Hurd 1972, Mikkelsen 1980). Therefore, experiment one (DE1) was designed to test the effect that acid cleaning has on the rate that these sediments dissolved and to establish whether this or un-treated sediment should be used in following experiments. A parallel experiment was performed with samples pre-treated in 10% HCl and 30% H_2O_2 (1.7-1.12) compared to those left un-treated (1.1-1.6). One sample from each group was removed after 1,2,4,8, and 10 hours.

Samples 1.1-1.6 showed little evidence of differential dissolution during the course of the experiment despite the overall abundance of diatoms falling to only 37% of the control sample after 10 hours (figure 5.2a). However, the silica determinations for samples 1.1-1.6 indicate that only 17% of the initial silica had been dissolved during the experiment. This discrepancy suggests the silica test is underestimating the amount of dissolution which may be due to the immediate resorption of dissolved silica on alumino-silicate mineral surfaces. Changes in the assemblage composition of these samples were small and not statistically significant. However, a significant increase is shown in the proportion of *Cyclotella meneghiniana* frustules which had lost their marginal ring of areolae in the samples left longest in the experiment. This is displayed in the "dissolution index" of figure 5.2a and 5.2b, calculated as the percentage of *Cyclotella meneghiniana* without their marginal areolae. Therefore, it is possible that given a longer period of experimentation significant differential dissolution may have resulted. This is in accordance with the relatively small changes observed in the diatom assemblages of these samples.



*Includes species which accounted for more than 1% in any single sample.

[1] (n*C. meneghiniana* /nDissolved *C. meneghiniana*)x100

a) Not pre-treated.

*Includes species which accounted for more than 1% in any single sample. No count was possible for sample 1.11 as too few valves remained.

[1] (n*C. meneghiniana* /nDissolved *C. meneghiniana*)x100

b) Samples pre-treated with HCl and H_2O_2.

Figure 5.2. Dissolution experiment 1.

In contrast to samples 1.1-1.6 the acid cleaned samples dissolved very rapidly indeed, and only 13% of frustules remained after just one hour in the sodium carbonate solution (figure 5.2b). Very low numbers of frustules survived in the other samples and no count was possible at all for the sample 1.11. Moreover, the count size had to be reduced to 150 valves in 1.8 and 1.12 due to very low abundance. The surviving frustules were very badly dissolved and were almost unidentifiable, the determination of species would have been difficult, if not impossible for many valves had the initial composition of the assemblage not been known. This is a weakness in the methodology, and a "blind" test would have been preferable using independent analysts, although this would have added greatly to the time involved.

Several species increased their share of the assemblage as dissolution progressed. These included *Cyclotella meneghiniana*, which appeared highly resistant to dissolution, increasing proportionally from 57% in the control sample to 72% after 1 hour of the experiment (1.7), and remaining between 67% and 77% in samples 1.8-1.10 and 1.12. However, this species was not immune to the effects of dissolution, as was demonstrated by the increasingly poor state of preservation of *Cyclotella meneghiniana* frustules with time in the experiment. In the control sample 54% of these frustules had lost their marginal areolae, whilst for the pre-treated samples the proportion of poorly preserved frustules rose to in excess of 93%. The most pronounced increase in proportion of any species was shown by *Campylodiscus clypeus* which rose from less than 1% of the assemblage in the control sample, to almost 12% in 1.7, and 23% in the sample 1.12. A significant increase (at the 90% confidence interval) was also shown by *Anomoeoneis sphaerophora* which rose from less than 2% to nearly 6% of the count after 1 hour. *Rhopalodia gibberula* also increased in importance but this was not statistically significant.

These proportional increases were matched by a corresponding decrease in several of the other taxa and the number of taxa per sample fell gradually to just 5 after 10 hours (sample 1.12). *Nitzschia* sp. af. *fonticola*. was reduced from an initial 33% of the diatom assemblage to only 3% in sample 1.7 and accounted for 2% or less in each of samples 1.8-1.12. This offsets almost all of the corresponding increases shown in the species mentioned above. The absolute abundance of *Nitzschia* sp. af. *fonticola* also declined sharply with estimated abundance being reduced by two orders of magnitude.

The acid cleaned samples produced much greater levels of silica in the supernatant solutions than the samples which were not pre-treated. Each of samples 1.7-1.12 had lost in excess of 70% of its silica into solution. This demonstrates that the diagenesis of samples 1.7-1.12 was not progressive during the course of the

experiment but occurred very rapidly at first (within an hour) after which subsequent changes happened much more slowly. This may be as a result of the sodium carbonate solution approaching an equilibrium saturation with respect to silica or due to the greater resistance of the remaining larger particles.

DE2

In the light of the rapid dissolution shown by the acid cleaned samples in DE1, the experiment was repeated on samples pre-treated in a similar fashion, but dissolved at a lower temperature and with finer sampling resolution. This was intended to produce a more detailed record of the dissolution process which occurred during the first hour of the previous experiment. The experimental temperature was reduced to 60 °C, the lower of the two temperatures used by Shemesh *et al.* (1989). The sampling interval was also reduced with tubes being removed from the water bath at 15, 30, 45, 60, 120, and 240 minutes (samples 2.1-2.6 respectively).

Unfortunately dissolution of silica was again rapid and insufficient valves remained to be counted even after only 15 minutes (sample 2.1). Almost all the initial silica was dissolved by the time of the extraction of this first sample as detected in the supernatant liquids. One source of error that may become significant when short sampling times are being used is the 15 minutes spent by the sample in the centrifuge. During this time the dissolution process will be continued, thus extending the actual time of the experiment. To verify this, the experiment was repeated with another sample (2.1a) which was removed from the water bath after 15 minutes but then immediately cooled in ice prior to centrifuging to slow down or stop the dissolution. Although badly dissolved a count was possible of the surviving frustules, the results of this are shown in table 5.2.

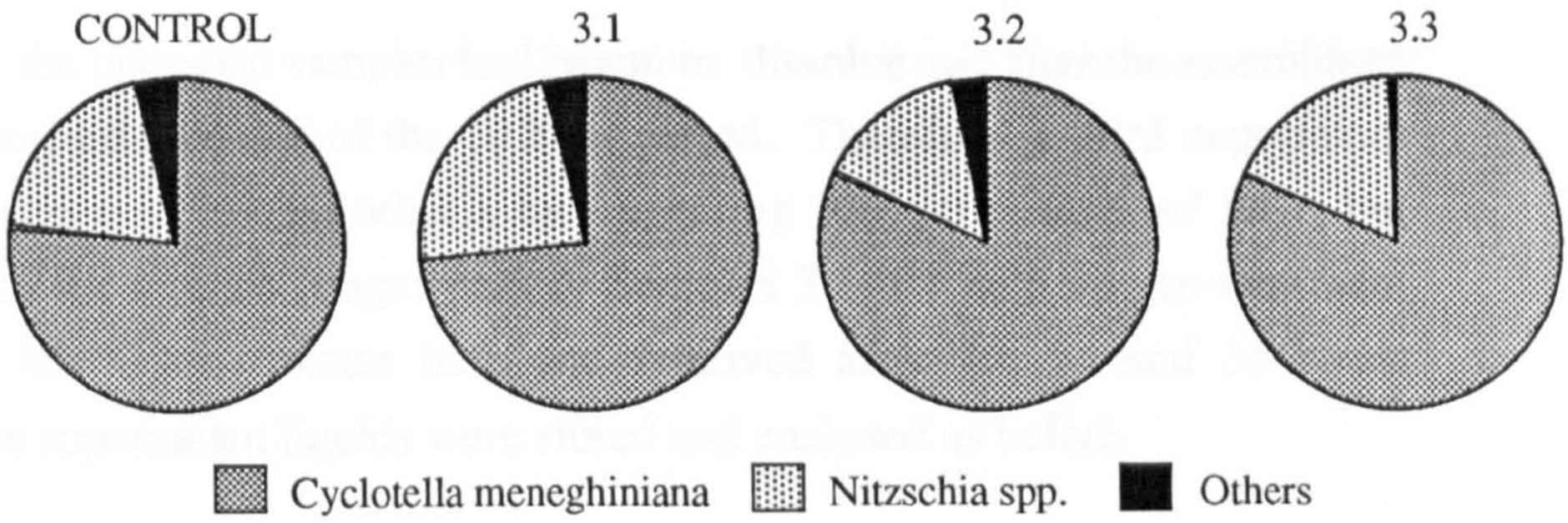
TABLE 5.2. Results of DE2

Species	Control %	2.1a %
Anomoeoneis sphaerophora	0	1.7
Cyclotella meneghiniana	29.9	76.7
Nitzschia sp. af. *fonticola*	37.0	7.3
Nitzschia rostellata	5.4	0
Rhopalodia gibberula	6.2	7.3
Stephanodiscus minutus	5.1	2.3
Surirella ovalis	0.1	1.0
Thalassiosira faurii	0.1	1.0
Thalassiosira rudolfi	11.9	1.7
Others	4.3	1.0
Abundance ($x10^6$)	25.0	4.5

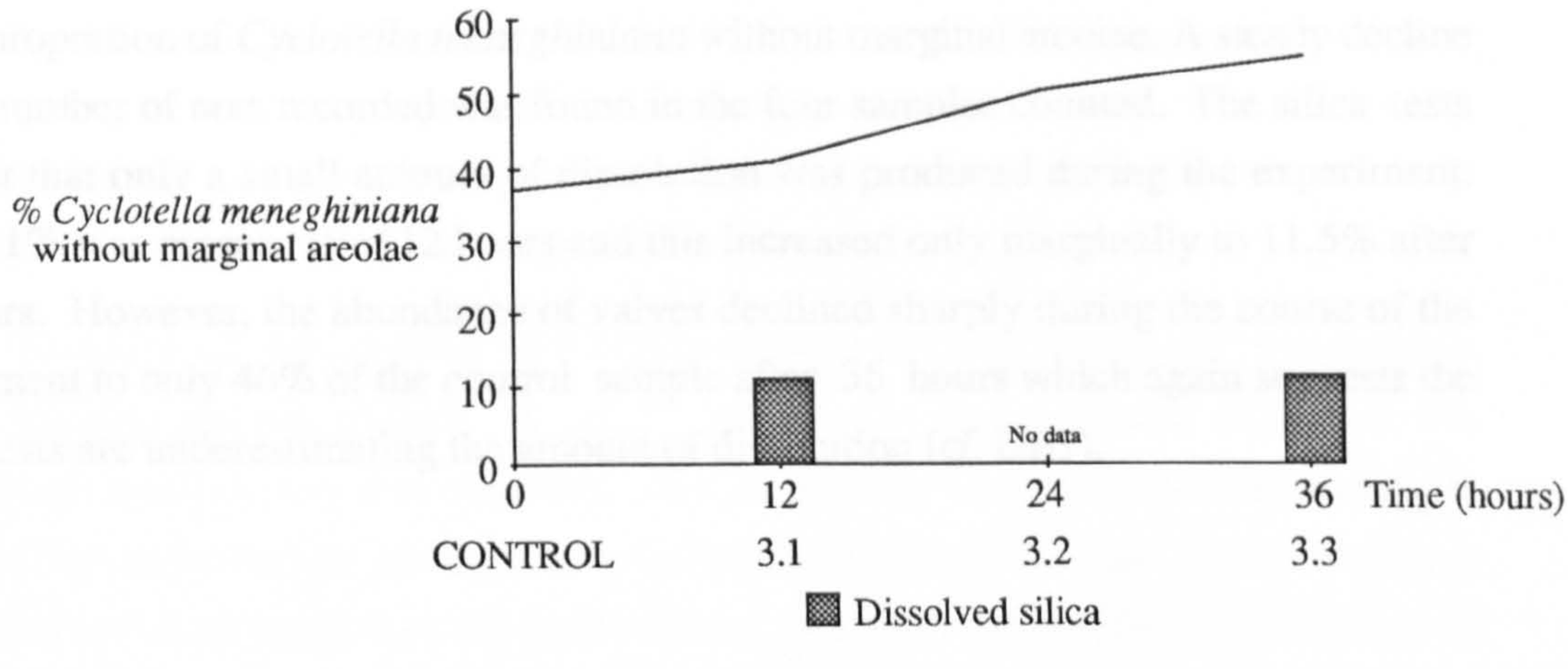
The silica dissolution resulted in inter-specific changes in sample 2.1a which show great similarity to those found in DE1. Most significant is the inverse relationship found between the proportions of *Cyclotella meneghiniana* which increased by 61%, and *Nitzschia* spp. which fell by 82%. Other species which increased in percentage were *Anomoeoneis sphaerophora, Rhopalodia gibberula, Surirella ovalis* and *Thalassiosira faurii.* Losses occurred in the proportions of *Stephanodiscus minutus* and *Thalassiosira rudolfi.*

DE3

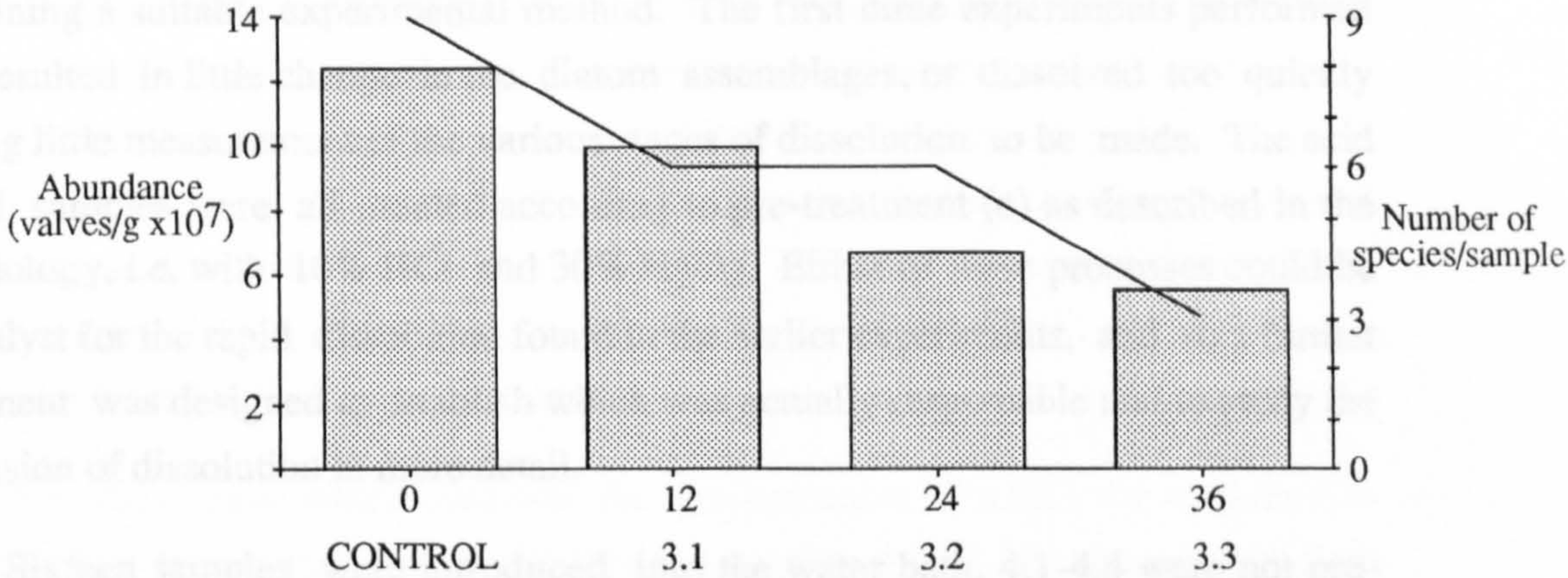
The two previous experiments served to demonstrate that acid cleaning the samples before adding them to the sodium carbonate greatly accelerated the dissolution process. This precluded observation of intervening phases even when temperature and time were both reduced. An alternative approach is to proceed with no pre-treatment but, over allowing the experiment to run for a greater time period. DE1



5.3a Results of DE3.



5.3b Dissolution Index and dissolved silica.



5.3c Diatom abundance and number of species.

Figure 5.3. Dissolution experiment 3.

did suggest that the untreated samples had begun to dissolve and alter the assemblage in composition towards the end of the 10 hour period. Therefore, a third experiment was undertaken to test this hypothesis by repeating the procedure of DE1, but allowing it to run for a much longer period. Samples 3.1-3.3 with no pre-treatment were heated at 85 °C in a water bath and removed after 12, 24 and 36 hours respectively. The supernatant liquids were stored and analysed as before.

As is shown in figure 5.3 no significant changes were found in the diatom assemblage composition. The proportion of weakly silicified species such as *Nitzschia* sp. af. *fonticola* remained relatively constant, whilst *Cyclotella meneghiniana* continued to dominate the assemblage. Some suggestion of dissolution is shown by the increase in the proportion of *Cyclotella meneghiniana* without marginal areolae. A steady decline in the number of taxa recorded was found in the four samples counted. The silica tests suggest that only a small amount of dissolution was produced during the experiment. Only 11% was present after 12 hours and this increased only marginally to 11.5% after 36 hours. However, the abundance of valves declined sharply during the course of the experiment to only 46% of the control sample after 36 hours which again suggests the silica tests are underestimating the amount of dissolution (*cf.* DE1).

DE4

The remarkable difference in the solubility of silica depending on whether it has been cleaned with acid before the experiment or left un-treated is critical in determining a suitable experimental method. The first three experiments performed either resulted in little change in the diatom assemblages, or dissolved too quickly allowing little measurement of the various stages of dissolution to be made. The acid cleaned samples were all treated according to pre-treatment (c) as described in the methodology, *i.e.* with 10% HCl and 30% H_2O_2. Either of these processes could be the catalyst for the rapid dissolution found in the earlier experiments, and so a further experiment was designed to establish which was actually responsible and to study the progression of dissolution in more detail.

Sixteen samples were introduced into the water bath, 4.1-4.4 were not pre-treated in any way, 4.5-4.9 were cleaned in H_2O_2, 4.9-4.12 were acid-cleaned with HCl, and 4.13-4.16 were treated with both HCl and H_2O_2. Given that rapid dissolution of the acid cleaned samples was anticipated, the duration of the experiment was kept short, with one sample from each group removed after 20, 40, 60 and 80

minutes. As in 2.1a the samples were immediately cooled in an ice bath before centrifugation to halt the dissolution process.

The analyses of the supernatant liquid of samples 4.1-4.4 revealed only small quantities of dissolved silica (<10%) (figure 5.4). Despite these low levels of dissolution the diatom assemblages altered considerably with increasing proportions of *Cyclotella meneghiniana* and *Rhopalodia gibberula* being found, whilst *Nitzschia* sp. af. *fonticola* , *Nitzschia paleacea*, and *Thalassiosira* spp. all declined in relative terms. This compares favourably with the outcome of the previous experiments, although greater variation is shown than in samples of DE1 or DE3 which were dissolved for a longer period. A likely explanation for this is that the sediment used for this experiment was at a more advanced stage of dissolution than that of the earlier experiments. The fact that only a small amount of silica had been dissolved is confirmed by the analysis of the supernatant liquids which showed that even after 80 minutes only 9.6% of the initial silica had been dissolved.

Samples 4.5-4.8, cleaned with H_2O_2 showed levels of dissolution comparable to the samples not pre-treated. A small, (statistically insignificant) change in the assemblage composition was observed after 20 minutes into the experiment (sample 4.5) and no reduction in abundance was found (figure 5.4). This gradual change continued in 4.6 although here the proportion of *Nitzschia* had fallen to just 55% of its original value. This progressive decline of *Nitzschia* spp. continued in the samples left in the bath for 60 and 80 minutes (4.7 and 4.8), finally reducing to only 39% of the control sample. Sample 4.7 does not conform to the patterns shown by the other samples due to an increase in the percentage and of *Thalassiosira rudolfi*. This may be an error due to insufficient mixing of the sediment before the experiment began, a small aggregate containing many valves of this small taxon (less than 10µm in diameter) might easily be introduced. The percentage of silica in the supernatants corresponds well with the values found in the raw sediment samples (4.1-4.4). Only 2% of the total silica in the sediment was taken into solution after 20 minutes and this had only increased to 7.6% after 80 minutes.

The dissolution which followed the pre-treatment with HCl for samples 4.9-4.12 greatly resembles that which occurred for samples 4.13-4.16 (cleaned with both HCl and H_2O_2). In 4.9 (after 20 minutes) *Nitzschia* spp. were reduced to less than 7% of the assemblage compared to over 31% in the control sample. This absolute decline in *Nitzschia* was matched by a proportional increase in *Cyclotella meneghiniana*. *Rhopalodia gibberula* remained constant whilst *Thalassiosira* declined slightly. Similarity between 4.9-4.12 and those pre-treated with HCl and H_2O_2 is also shown in the figures for total abundance of valves/g. Abundance falls

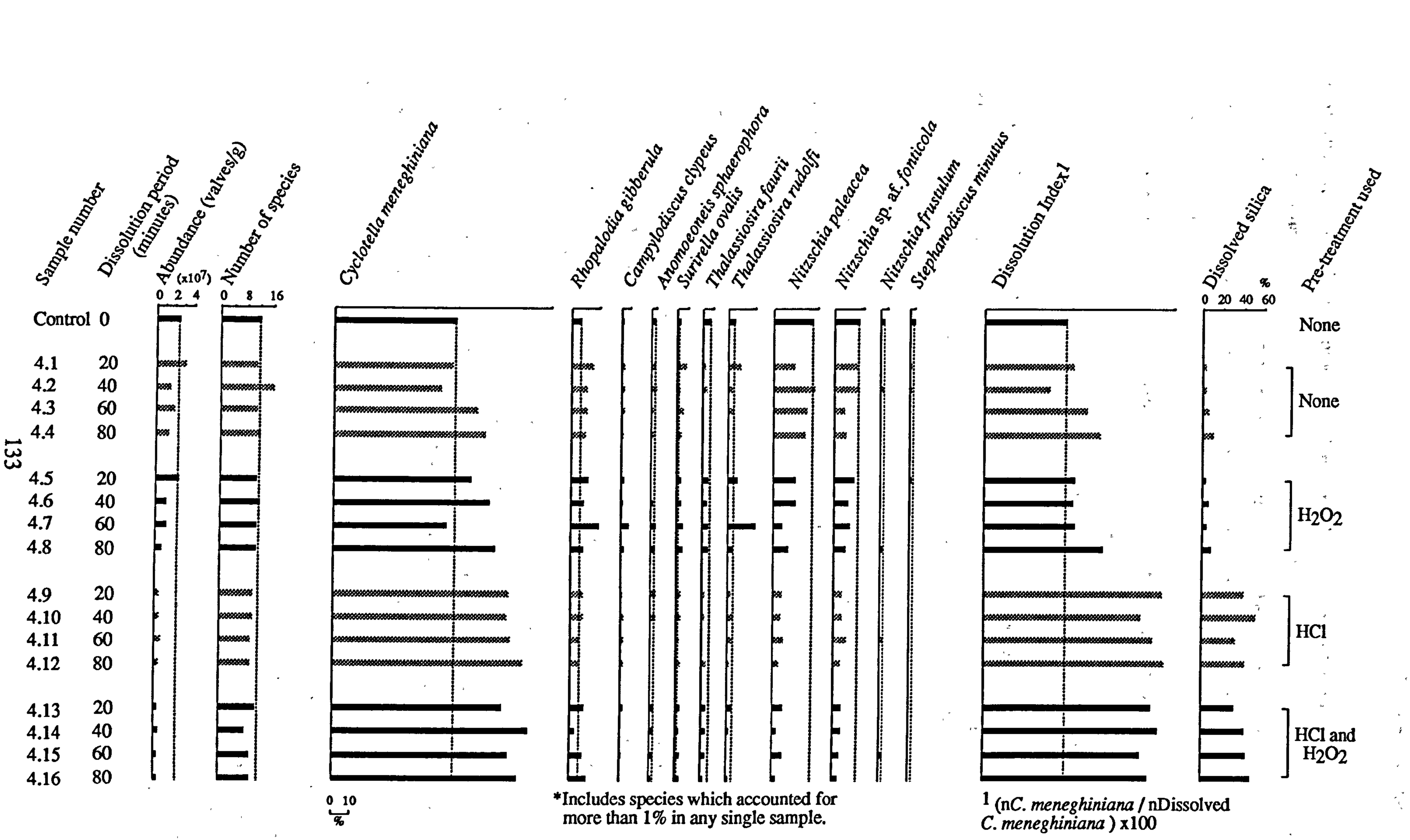


Figure 5.4. Dissolution experiment 4.

markedly from the high number of valves found in the control sample to less than 25% of this value in the partially dissolved samples. These values are a little higher than those found when both pre-treatments were used. The number of taxa fell from 12 to 9 as is found in experiments described above. Dissolved silica values fluctuated remarkably from 40% in sample 4.9 , 52% in 4.10 , 34% in 4.11, to 42% in 4.12.

The results of those samples pre-treated with both HCl and H_2O_2 (4.13-4.16) also showed good agreement with the earlier experiments in dissolving very rapidly. Indeed, the abundance of species decreased to less than 22% of the control in all of the samples, whilst the total number of taxa dropped from 12 to 9 after 80 minutes (figure 5.4). The percentage of the assemblage occupied by *Cyclotella meneghiniana* increased significantly in sample 4.13, after which it remained relatively constant at this new high level. This was accounted for almost entirely by a decline in *Nitzschia* sp. af. *fonticola* and *Nitzschia paleacea*, together with a smaller fall in *Thalassiosira* spp.. *Rhopalodia gibberula* increased slightly during the experiment although this was not statistically significant (at the 90% level). The percentage silica in solution increased from 33% in sample 4.13 to 48% in 4.16.

DE5

Experimental dissolution of samples from lake Manyara has demonstrated that weakly silicified species such as *Nitzschia* sp. af. *fonticola* will eventually be proportionally replaced by robust species such as *Cyclotella meneghiniana* and *Campylodiscus clypeus*. It is necessary to verify that similar assemblage diagenesis will result when material from other lakes is investigated. This was tested on sediment from Lake Magadi which holds a much more diverse diatom flora comprising 66 taxa. Sediment was cleaned in H_2O_2 on the assumption that this would allow dissolution to take place over a suitable experimental period as suggested in experiment four. Samples (5.1-5.7) were extracted after 60, 135, 240, 360, 480, 1200 and 1620 minutes respectively.

The silica that was measured in the supernatant liquids of these samples was slight and never exceeded 6.2% of the total silica in the sample. In order to investigate more advanced assemblage diagenesis the rate of dissolution had to be increased. This was achieved by treating the sediment which had already been cleaned in H_2O_2 with HCl prior to dissolving in the sodium carbonate. As in previous experiments this produced very rapid dissolution. The percentage of dissolved silica reached 38% after just 10 minutes (5.8), 63% after 20 minutes (5.9) and 65% after 30 minutes (5.10).

Although the total amount of dissolution was small in samples 5.1-5.7, diatom abundance and species diversity did fall with respect to the control sample. After only 60 minutes the number of diatoms present had fallen to only 19% of the control sample but the effect on species composition was negligible in comparison. This dramatic fall in abundance may be accounted for largely by a loss in fragmented valves. Fragments are included in the count but have a high propensity toward dissolution and may therefore be quickly lost. Changes in assemblage composition were initially much more subtle, but undoubtedly differential. Samples 5.1-5.7 showed declining percentages of *Cyclotella* spp. (excluding *Cyclotella meneghiniana*), *Cymbella* spp., *Fragilaria* spp., *Navicula* spp. (excluding *Navicula elkab*) and *Nitzschia* sp. af. *fonticola* as is shown in figure 5.5. The most significant gains for these samples are the proportional increases of *Nitzschia subrostrata*, *Cyclotella meneghiniana*, *Navicula elkab*, *Thalassiosira faurii*, *Epithemia* spp., and *Nitzschia* "group latens".

Samples 5.8-5.10 dissolved much more readily and demonstrated much clearer changes in species composition (figure 5.5). Sample 5.8 resembles closely the changes described above for samples 5.1-5.7 with the major losses shown by *Fragilaria* spp and *Cyclotella* spp. (excluding *Cyclotella meneghiniana*). These are replaced by the increasing relative importance of *Nitzschia subrostrata*, *Navicula elkab* and *Cyclotella meneghiniana*, although even these decline in absolute abundance. The first decline in percentage of *Nitzschia subrostrata*, *Nitzschia* sp. af. *fonticola* and *Navicula elkab* is found in sample 5.9. Corresponding proportional increases occur in *Cyclotella meneghiniana*, *Epithemia* spp., *Aulacoseira granulata* and *Thalassiosira faurii*. The species that decline most rapidly in sample 5.10 are *Navicula elkab*, *Nitzschia* sp. af. *fonticola* and *Thalassiosira faurii*, which are replaced proportionally in the assemblage by *Cyclotella meneghiniana*, *Epithemia* spp. and *Aulacoseira granulata*.

The pattern of dissolution of *Nitzschia subrostrata*, *Nitzschia* sp. af. *fonticola* and *Thalassiosira faurii* is quite similar. Initial exposure to the sodium carbonate resulted in the loss of a large number of valves of all three species after which a period of equilibrium is reached when the number of valves in the sample remains relatively constant. This new level is at 19% of the original value for *Nitzschia subrostrata* and 16% for *Thalassiosira faurii*. The initial loss of *Nitzschia* sp. af. *fonticola* is greater than for the other two species and this stabilises at a level of only 7% of the number of valves in the control sample. All three species then declined rapidly when the samples were cleaned with HCl prior to the dissolution experiment. *Fragilaria* spp. (*Fragilaria brevistriata*, *Fragilaria construens*, *Fragilaria pinnata*, *Fragilaria ulna*, *Fragilaria ulna* v. *acus*) were much more susceptible to dissolution and 97% of valves of these taxa had dissolved even by the point that only 4.5% of the silica had been taken into solution

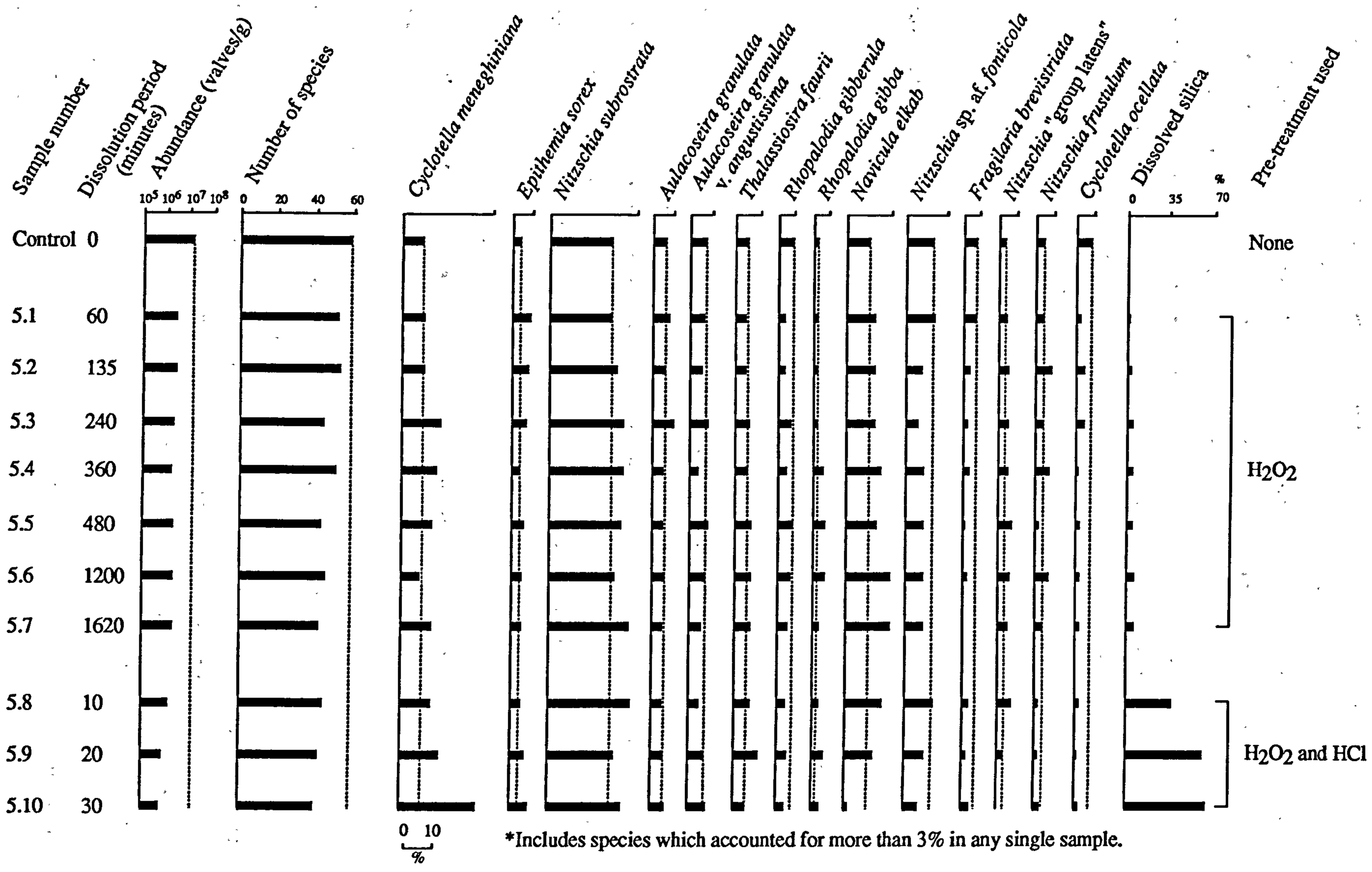


Figure 5.5. Dissolution experiment 5.

(sample 5.4). Dissolution was most rapid for *Fragilaria ulna* and *Fragilaria acus* which were usually encountered as fragments, but proceeded more slowly for the relatively robust *Fragilaria brevistriata.* The dissolution curves of *Aulacoseira granulata* and *Epithemia* spp. (*Epithemia sorex* and *Epithemia zebra,* are both less steep than for *Fragilaria* spp. indicating a much slower rate of dissolution. As in previous experiments the most resistant taxa to dissolution appears to be *Cyclotella meneghiniana.* The initial fall in abundance was large (80%) but slightly above the average for all species. Following this decline only a further 6% of *Cyclotella meneghiniana* frustules were lost to dissolution. The share of the assemblage occupied by this species increased from 7.3% to 26.1% during the course of the experiment.

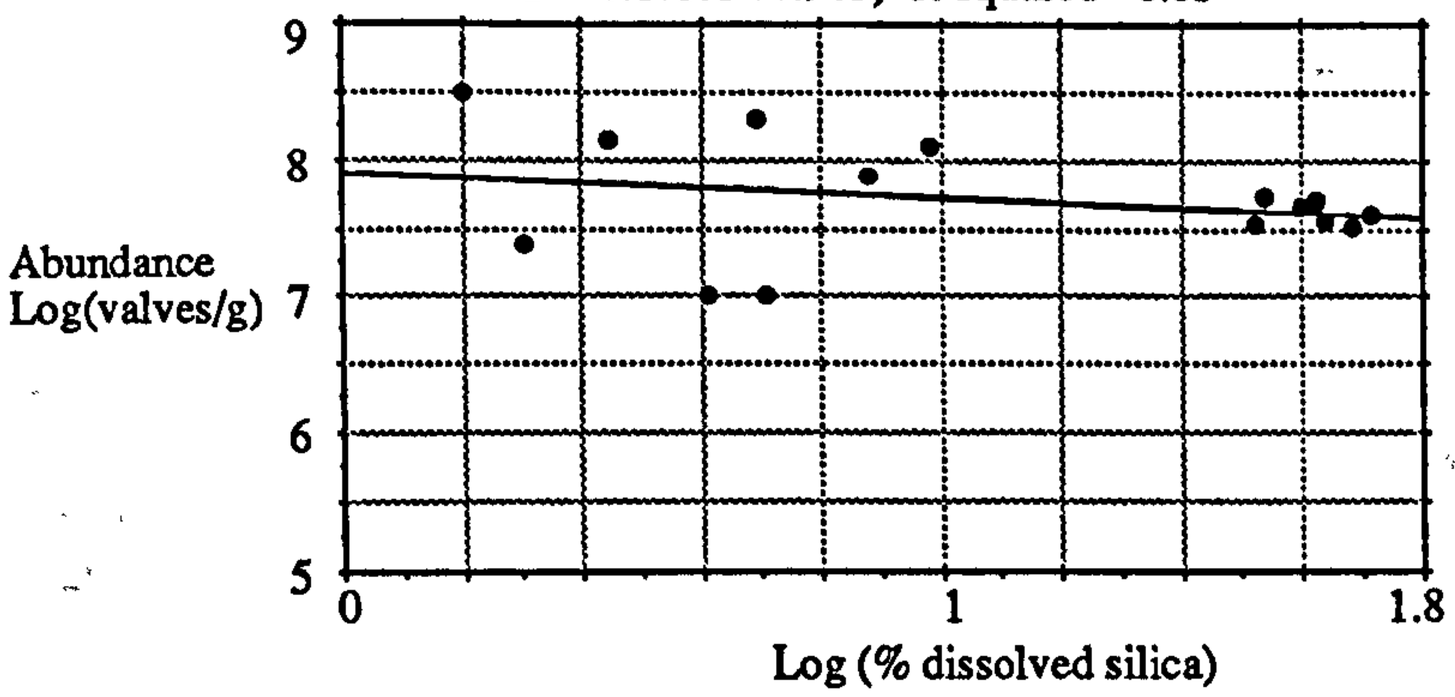
Discussion.

It is impossible for experiments of this kind to faithfully mirror the natural limnological situation and a number of assumptions have had to be made in establishing the laboratory method. Particularly unrealistic is the use of pre-treatments to hasten dissolution since these have no obvious natural counterpart. However, the samples used for DE1-4 initially had similar diatom floras but as dissolution progressed they became dominated by the same few highly resistant species, and the direction of assemblage diagenesis was largely the same irrespective of the pre-treatment used to stimulate the dissolution. This appears to justify the use of pre-treatments as they only control the rate of dissolution and not the outcome. A further methodological problem is that the sediments used in the experiments are themselves from the tail-end of a dissolution chain. This makes comparison between different experiments difficult as the rate of dissolution is variable although the progression of dissolution in DE1-4 was the same despite differences amongst the sediments used.

Subjecting diatomaceous sediment to dissolving conditions can radically alter the species composition of the fossil diatom assemblage through differential dissolution. This is clearly demonstrated by figures 5.6 and 5.7 which show the changing abundance of the most important taxa in DE4 and DE5 against the proportion of the silica in the sample dissolved. The regression coefficients for many species are statistically insignificant and so the gradient of the curves only offers a tentative estimate of the rate of dissolution. Moreover, a direct relationship between the two variables is assumed, although for certain species *e.g. Navicula elkab* (figure 5.7) a more complex curve could be drawn. The relationship between the variables could be improved by increasing the number of samples in which 10-50% of the silica has been lost, since the majority of samples lie outside this range. Error may also be introduced

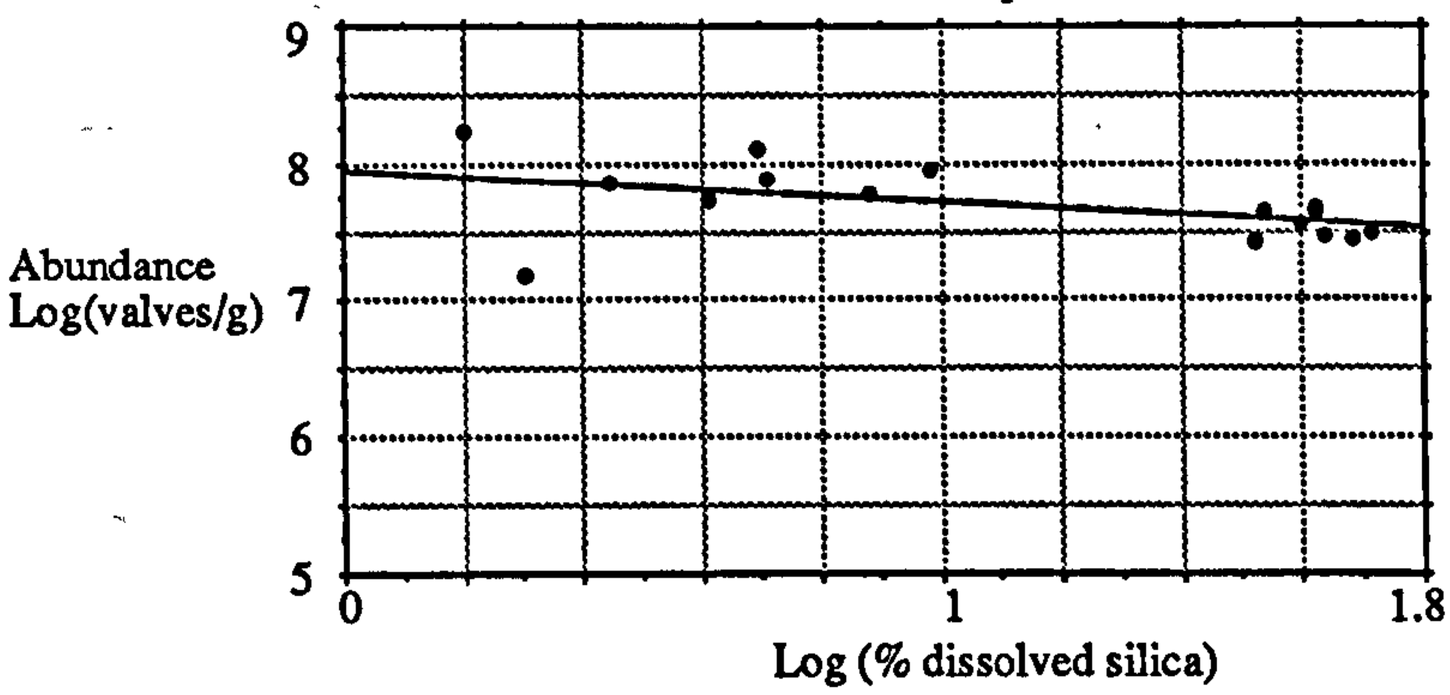
All species

Y =-0.175X +7.903) R-squared =0.05



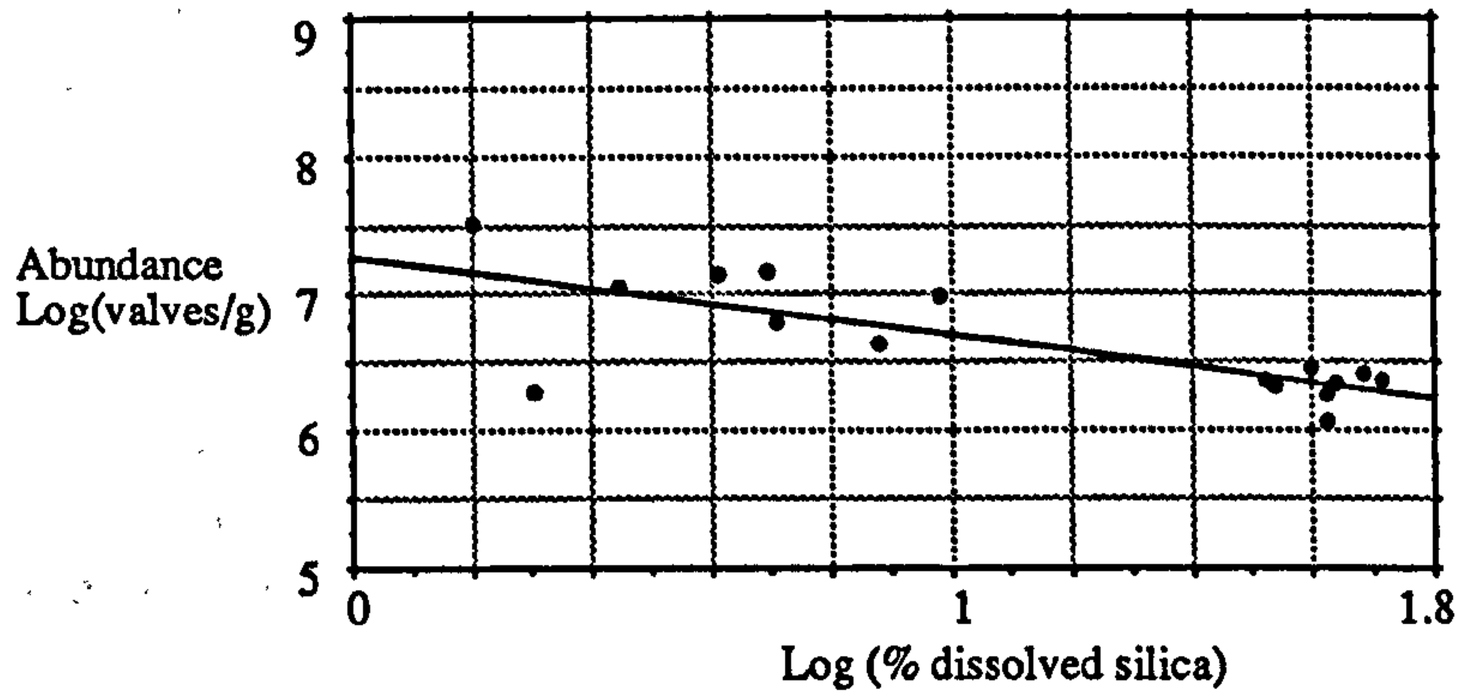
Cyclotella meneghiniana

Y = -0.241X +7.959 R-squared 0.24



Rhopalodia gibberula

Y = -0.562X +7.264 R-squared 0.57



Nitzschia sp. af. *fonticola*

Y = -0.935X +7.619 R-squared 0.92

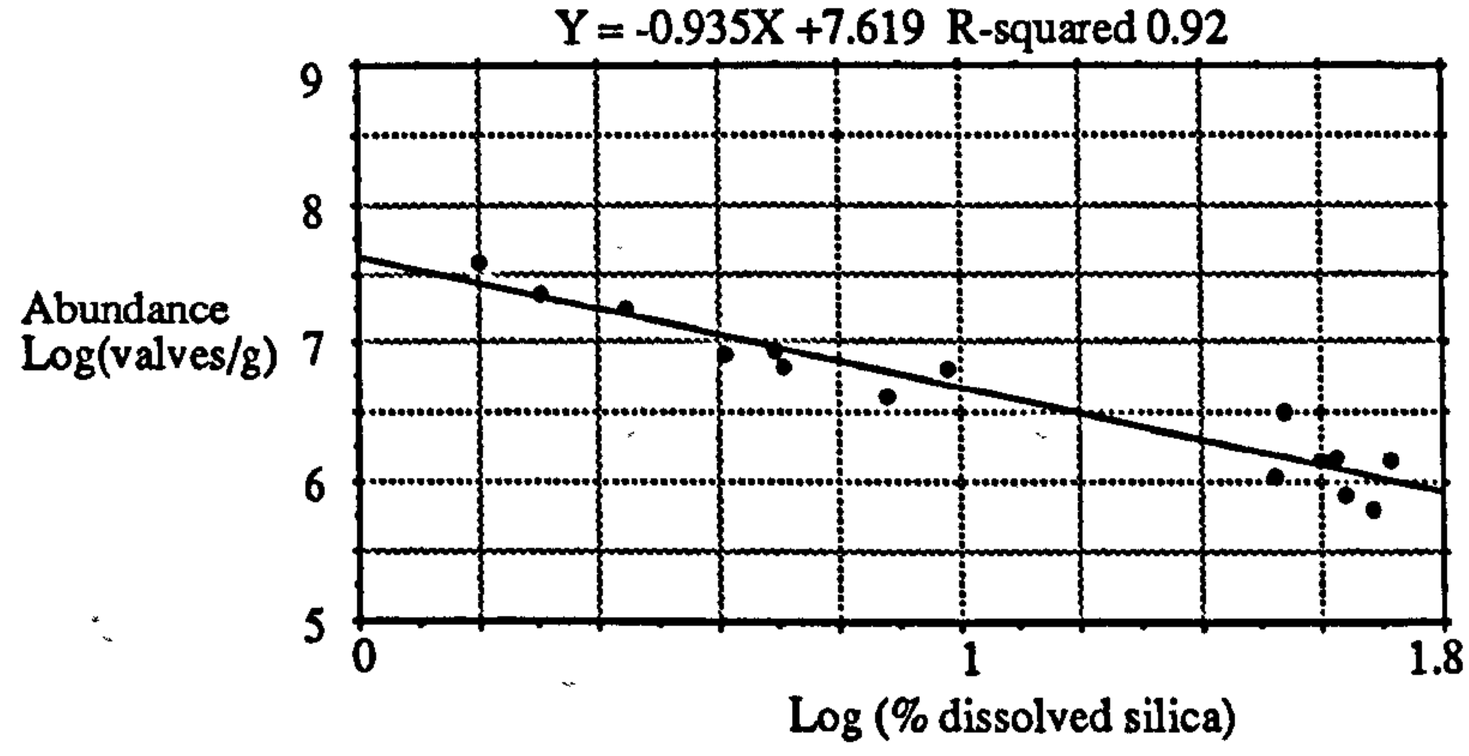


Figure 5.6. Changing abundance of diatom species from DE4 with increasing dissolution.

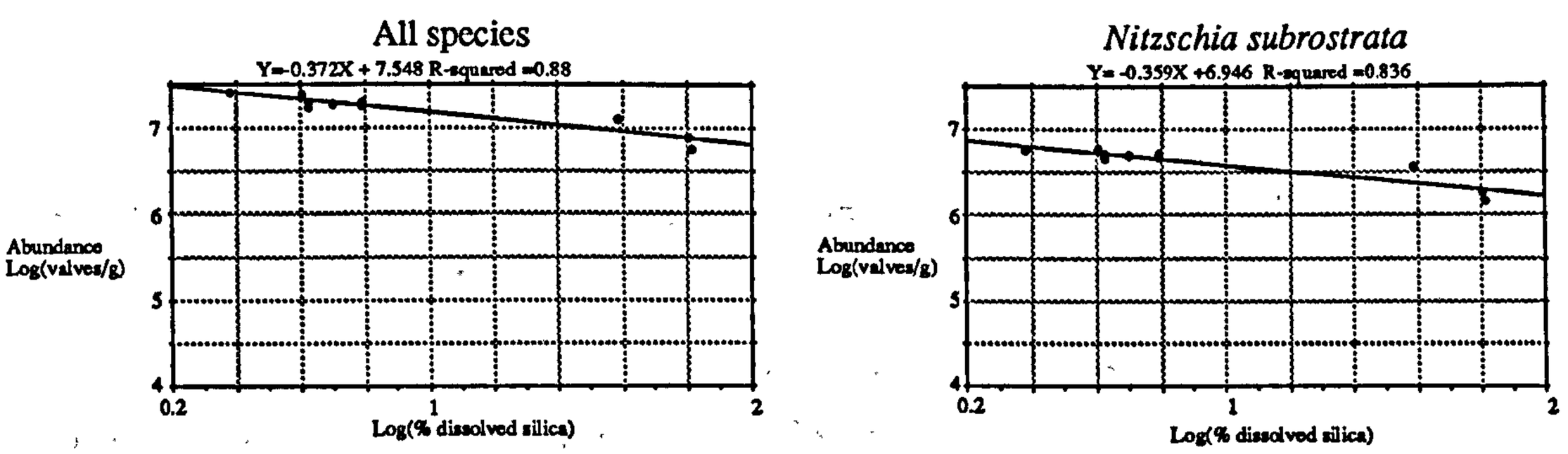


Figure 5.7. Changing abundance of diatom species from DE5 with increasing dissolution.

when estimating the abundance of those species found in low frequency and the count size could be increased to offset this.

For DE4 *Cyclotella meneghiniana, Rhopalodia gibberula,* and *Nitzschia* sp. af. *fonticola*, represent the full range of dissolution rates for the species recorded. *Cyclotella meneghiniana* has the lowest propensity for dissolution and its abundance declines gradually, whereas the curve for *Nitzschia* sp. af. *fonticola* describes a much more rapid decline. The dissolution rate of *Rhopalodia gibberula* occupies an intermediate position to these two taxa. *Cyclotella meneghiniana* and *Nitzschia* sp. af. *fonticola* are also common in the sediments used for DE5, where they again are found at different ends of the dissolution spectrum. However, for DE5 the curves for *Cymbella microcephala, Navicula elkab* and *Cyclotella ocellata* suggest that these species are more prone to dissolution than *Nitzschia* sp. af. *fonticola*, although the validity of this conclusion is compromised by the rather low regression coefficients. Following *Cyclotella meneghiniana* as the most resistant taxa comes *Thalassiosira faurii, Fragilaria brevistriata, Aulacoseira granulata* v. *angustissima, Epithemia sorex, Nitzschia subrostrata* and *Aulacoseira granulata.* The position of *Fragilaria brevistriata* is extremely tenuous as no clear relationship is found between the two variables for this species.

To what extent can the pattern of differential dissolution found in these experiments be explained by the relative valve volumes (V) and surface areas (SA) as hypothesized in the aims of this chapter? Figure 5.8 shows plots of the dissolution of species in rank order following DE5, against V, SA, and SA/V (*Fragilaria brevistriata* is excluded due to the uncertain position of this species in the dissolution spectrum). To test the strength of these relationships Spearman's rank correlation was used and coefficients (R_s) of 0.49 were found for dissolution against V, 0.52 for this against SA and 0.44 for SA/V. None of these values for R_s reach the 95% confidence level which for 10 samples which is 0.56 and it is not possible to accept any of the parameters as statistically significantly correlated with dissolution rate. The plots of figure 5.8 reveal that the closest relationship is found between SA/V, contrary to the calculated values for R_s. If *Cyclotella ocellata* is excluded from the calculation as an outlier, the correlation coefficient Rs increases to 0.63 and becomes significant at the 95% confidence level.

In order to explain the ranking of species dissolution rate derived from DE5 it is necessary to incorporate additional factors to valve morphometry. The position of *Cyclotella ocellata* and *Cyclotella meneghiniana* at opposite ends of the spectrum is particularly instructive since morphometrically they are similar. This may be a function of frustule volume since *Cyclotella meneghiniana* is much larger, but *Cyclotella ocellata* is also more densely sculptured and perhaps more lightly silicified. The presence of 3-

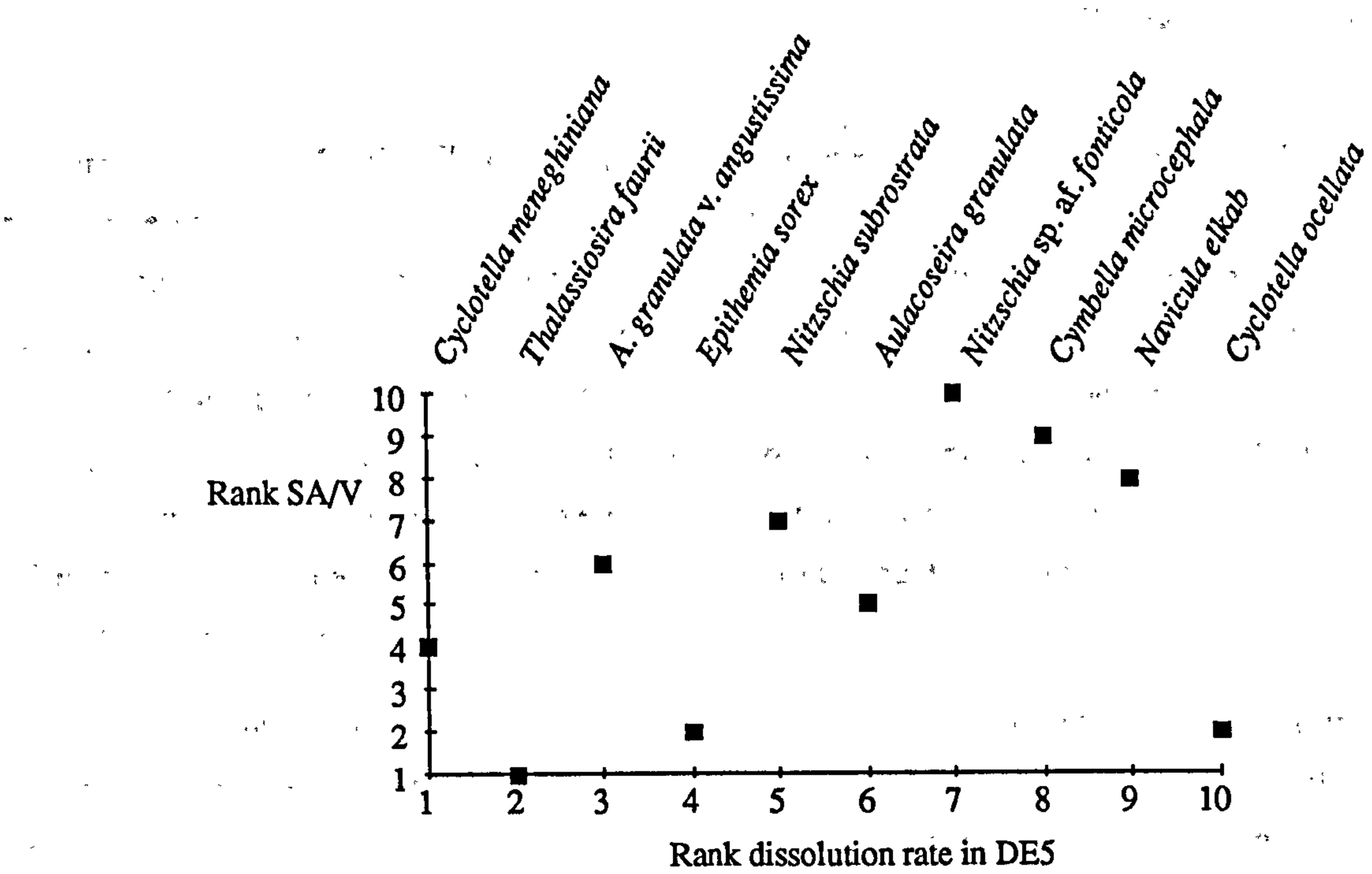


Figure 5.8. Rate of dissolution of selected taxa from DE5 against valve volume (V), surface area (SA), and surface area /volume (SA/V) by rank order.

6 central areolae in *Cyclotella ocellata* will greatly increase the surface area and lessen resistance to dissolution. In contrast to *Cyclotella ocellata, Nitzschia subrostrata* is more resistant than its morphometry would suggests. Moreover, its sculpturing is similar to that of *Nitzschia* sp. af. *fonticola* which was much more readily dissolved. One possible explanation for this enhanced preservation may be the degree of valve separation which is noticeably less in these samples for *Nitzschia subrostrata* than for many other species thus reducing the effective surface area. Factors such as the degree of microporosity may also be important in explaining the surprising resistance to dissolution of this taxon.

Differential dissolution need not entirely remove a given taxon from the sample to alter the composition of the assemblage; it need only dissolve it to the point at which it becomes unidentifiable to the diatomist or it ceases to be counted under the strategy employed for dealing with fragments, this is different for each species and for each observer. In this study a policy was adopted for dealing with broken valves that they should only be counted if more than half was present. That is, if a broken valve including the central area was found, it would be included in the count. This is a standard procedure (*cf.* Battarbee 1986) and it ensures valves are not counted more than once. In badly dissolved assemblages such as those that resulted from these experiments this strategy may lead to bias since the central areas of some species are more easily dissolved than others. For example when the frustule of *Anomoeoneis sphaerophora* becomes dissolved this frequently removes the exterior of the valve first, leaving the more heavily silicified raphe and central area intact. This is distinctive and would normally be included in the count. However, if in proportional terms an equivalent amount of dissolution occurred to a frustule of *Thalassiosira faurii* it would almost certainly be excluded as it is difficult to assess whether at least half the valve was present without the outer edge to gauge the dimensions of the valve (the sculpturing on the valve face is irregular giving no indication of the centre). Allied to the problem of counting strategy is that of identification which may preferentially bias the count toward those species whose major identifiable characteristics happen to be well preserved. This is exemplified by *Cyclotella meneghiniana* which dissolves to leave a largely unsculptured disc of silica (*cf.* Battarbee 1988), but which can still be recognized either by the radial punctae which often remain, or by the presence of some marginal ribs which are the last part to dissolve of the outer ring of the frustule.

The recognition that dissolution has altered an assemblage is vital in order to reassess environmental interpretations and to avoid erroneous conclusions. The experiments have produced information which may be used to recognise the degree

of dissolution to which a fossil assemblage has been subjected. Amongst the most valuable and direct indicators of assemblage diagenesis is the appearance of the diatom frustules themselves. Partially dissolved frustules tend to become more transparent when viewed under the light microscope. The valve margins suffer the most, and they can often be removed completely, as in *Cyclotella meneghiniana* (plate 5.1 g-i). Destruction by dissolution can be distinguished from that as a result of physical breakage as the latter creates sharp fractures in contrast from the more indistinct outlines caused by the dissolution process. Narrow pennate diatoms appear to dissolve by first losing their apices, this has been found in weakly silicified, very attenuated species such as *Nitzschia rostellata*, as well as for more robust species such as *Rhopalodia gibberula* (plate 5.1 d-f). Individual species may also dissolve to leave highly characteristic features. For example, the final part of *Mastogloia* spp. to dissolve is the partecta adjacent to the mantle, perhaps due to this being the most highly silicified part of the frustule.

Conclusion.

The isolation of the factors responsible for the dissolution of silica in sediments is beyond the scope of this thesis, but the results of these experiments allow some comments to be made. Dissolution of silica even under highly alkaline, high temperature conditions was limited unless the sediments were cleaned in acid before the experiment. This then resulted in dissolution which proceeded very rapidly indeed. The most pronounced dissolution followed treatment with a strong acid such as HCl (pH 1) but even a mildly acidic reaction as produced by H_2O_2 (pH 5-6) was partially effective in this respect. H_2O_2 is also a strong oxidant and effectively removes organic material from sediments. However, given the slow dissolution of the samples pre-treated with H_2O_2 relative to those cleaned in HCl it appears that the presence of organic matter is not the principle control on the preservation of silica. Instead it appears that in order for dissolution to progress rapidly, some inorganic material must first be removed from the sediments by the acid cleaning. This is very much in line with the results of Joyce Lewin (1961) who suggested that adsorbed metal cations, principally of iron and aluminium could reduce the rate of dissolution. These might then be removed by being made soluble under acid conditions and lost from the sediment during the washing process. Translating these results to the problem of dissolution and silica diagenesis found in the sediments of Magadi and Manyara (chapters 3 and 4) is difficult due to the potentially long time periods over which dissolution could occur. It would appear to require not only a knowledge of the

Captions for plates overleaf.

a) *Surirella ovalis*; well preserved specimen.

b) Partially dissolved *Surirella ovalis*.

c) Highly dissolved fragment of *Surirella ovalis* ?

d) *Rhopalodia gibberula* well preserved specimen.

e) *Rhopalodia gibberula* without apices. Damage caused by dissolution and/or breakage.

f) Dissolved *Rhopalodia gibberula*.

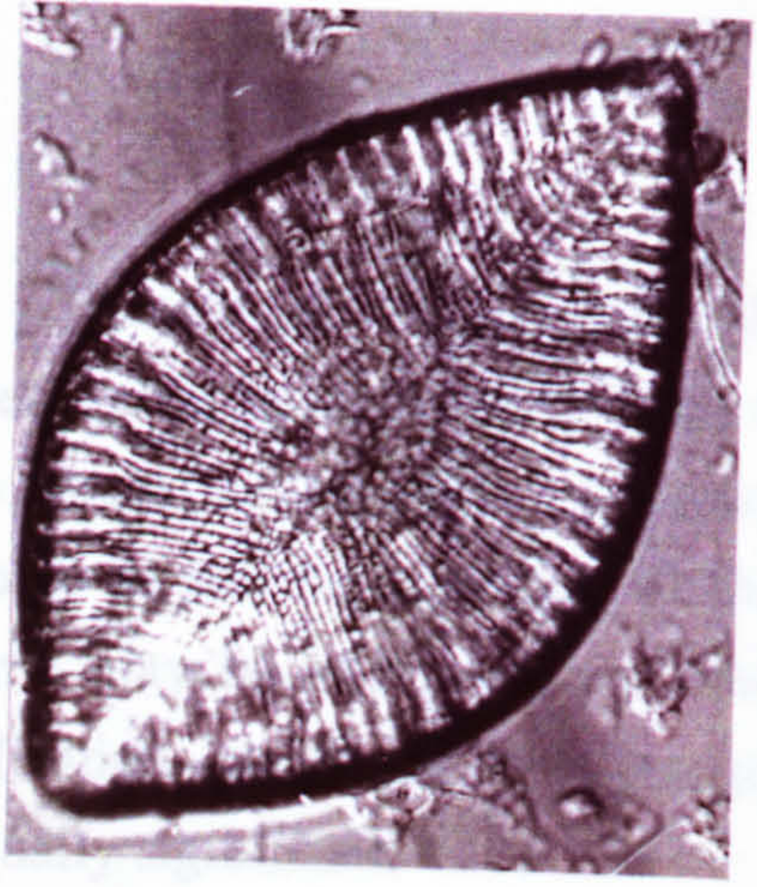
g) Partially dissolved *Cyclotella meneghiniana*.

h) More advanced dissolution of *Cyclotella meneghiniana* beginning with the marginal areolae.

i) Highly dissolved *Cyclotella meneghiniana* leaving behind featureless disc.

j) *Campylodiscus clypeus* showing slight dissolution.

k) Highly dissolved fragment of *Campylodiscus clypeus* ?



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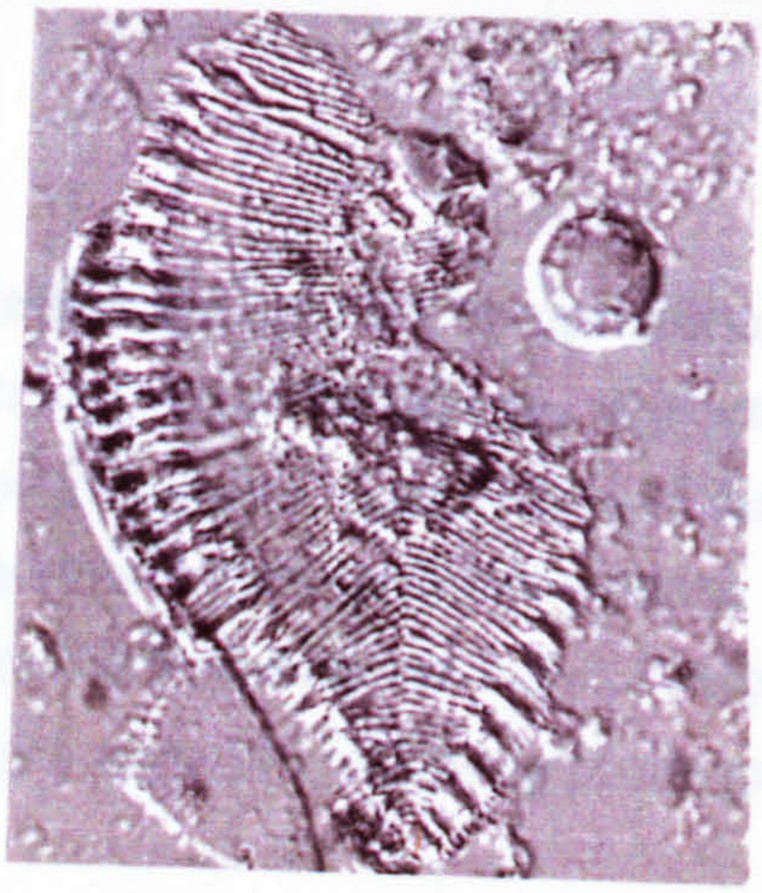

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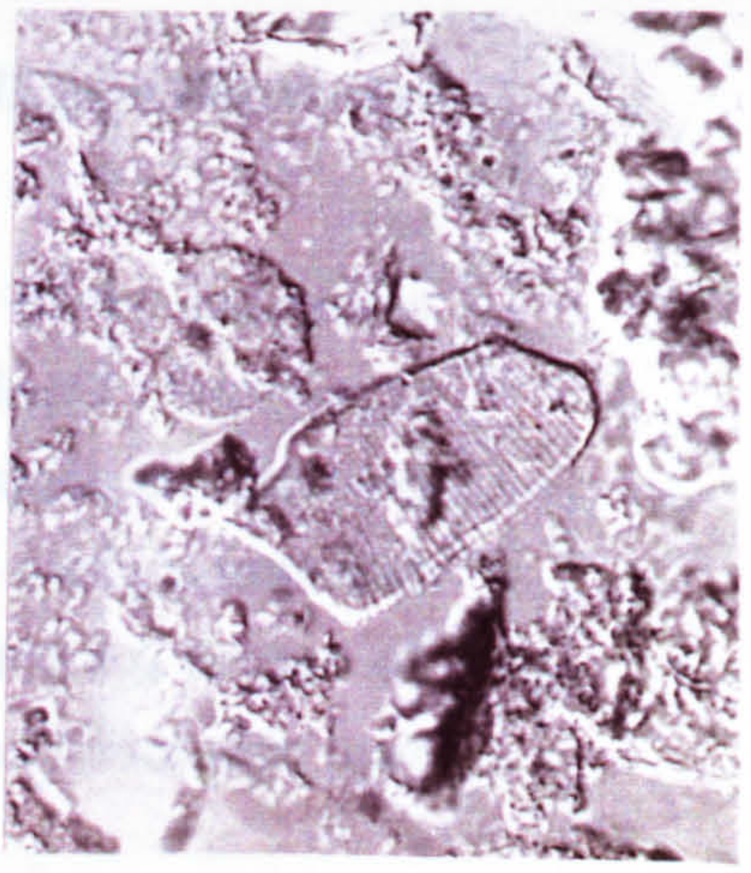

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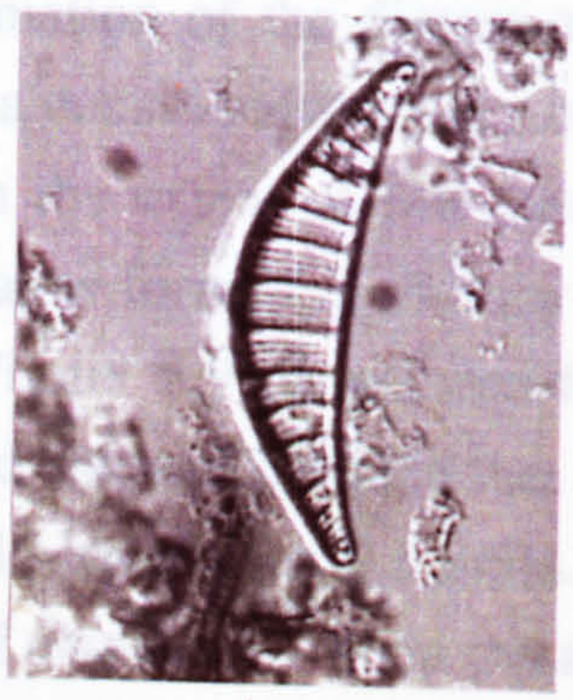

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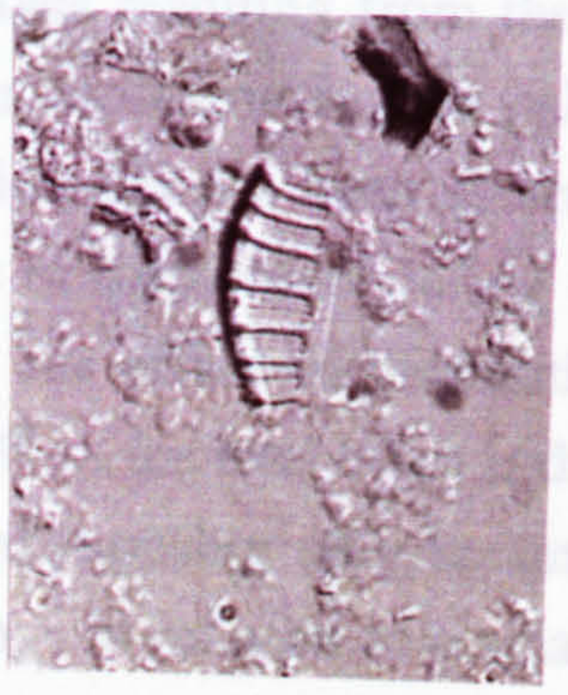

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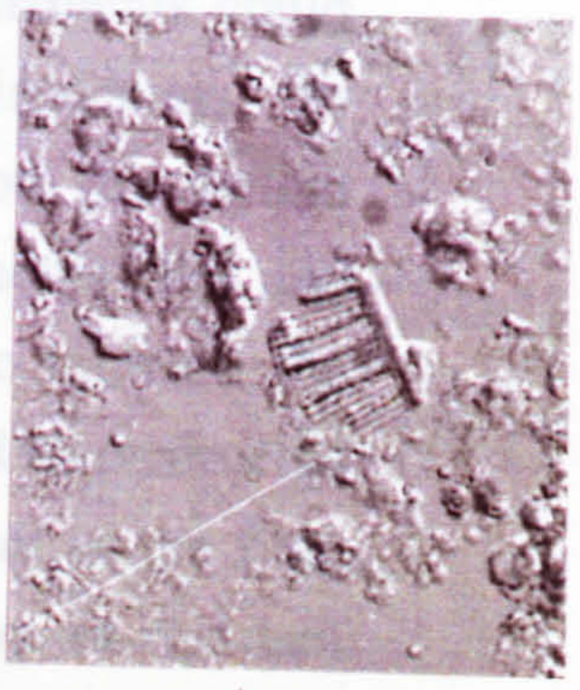

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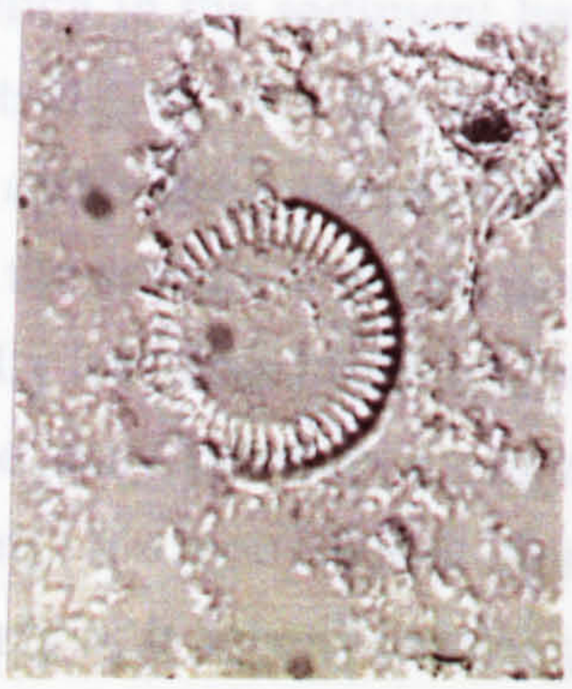

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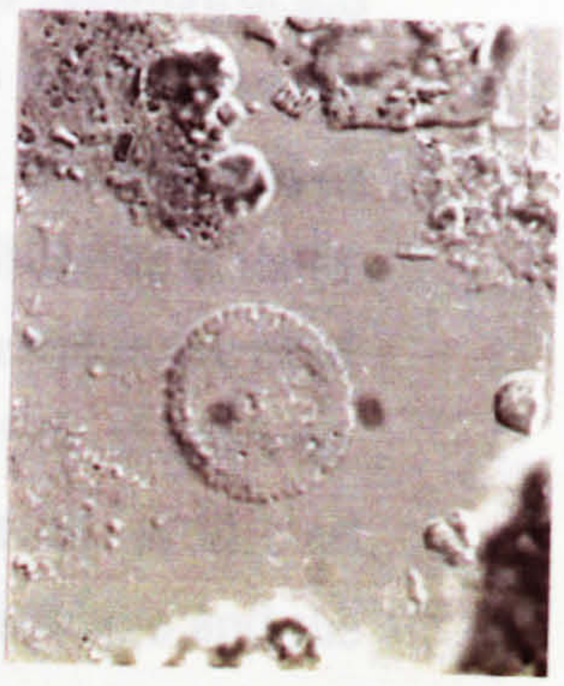

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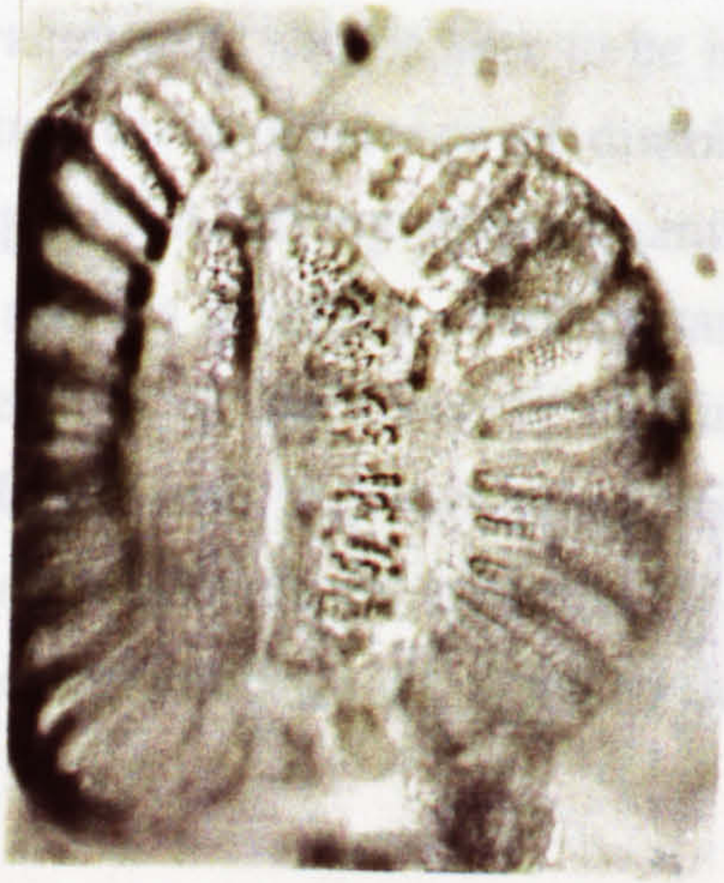


(j)

(k)

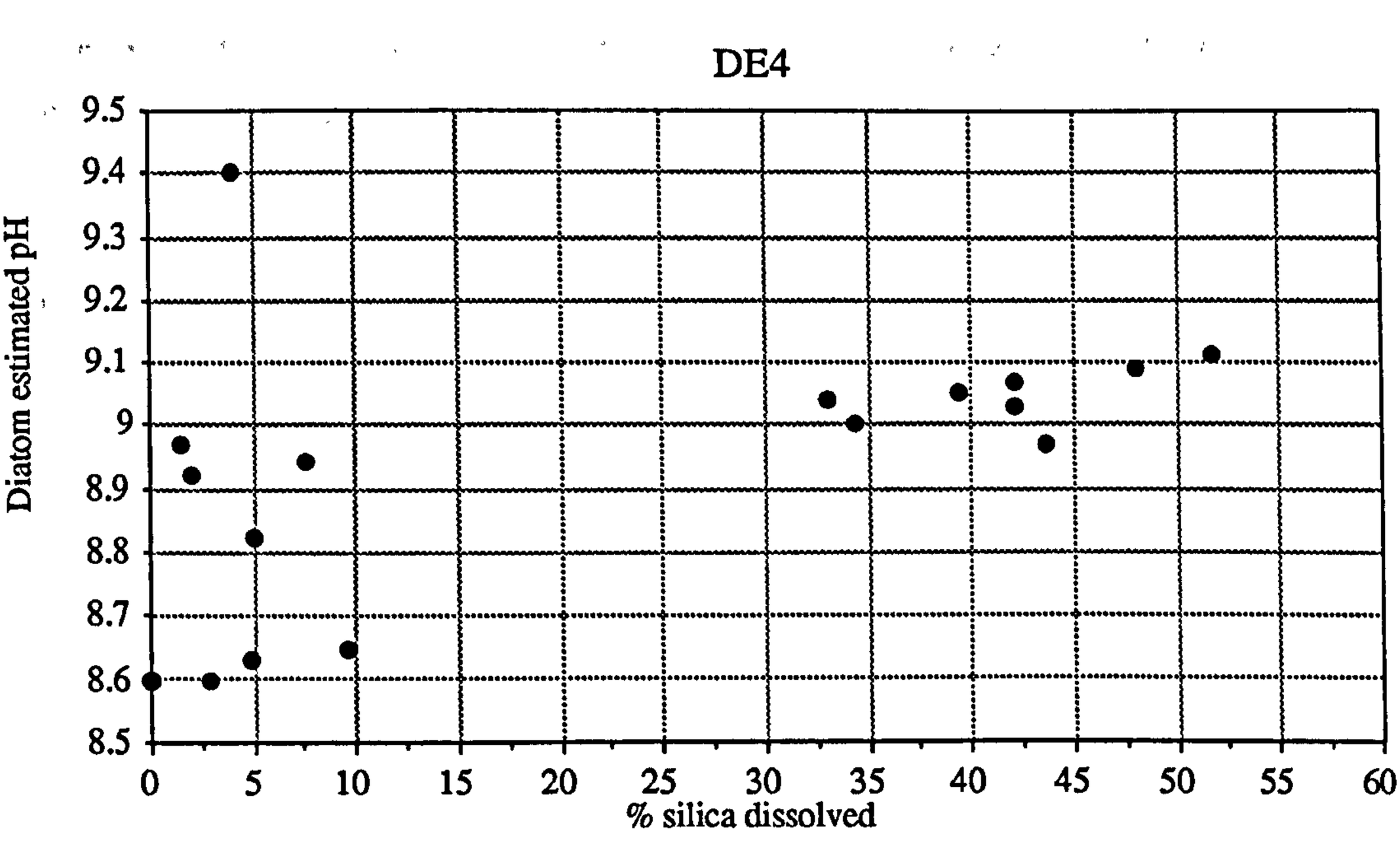
0 10 20
µm

Plate 5.1

Dissolution differentially altered the species composition in the sediments studied by replacing small delicate taxa (*e.g. Nitzschia* sp. af. *fonticola*) with larger more robust ones (*e.g. Cyclotella meneghiniana*). The pattern of dissolution observed can only in part be explained by the relative valve morphometry. Surface area and volume may be important but other factors such as valve sculpturing, degree of silicification, and the ability to recognize a species following prolonged dissolution may be equally significant.

The initial motivation behind these experiments was to examine the implications of diatom dissolution for palaeoecological interpretation. The pronounced transformation of the diatom assemblages resulting from these experiments could provide a considerable source of error in reconstructing the palaeoenvironments. To establish the extent of this potential bias, pH has been estimated from the diatom assemblages formed at various degrees of dissolution during experiments DE4 and DE5. Figure 5.9 shows that for DE4 the effect of dissolution is to increase the estimated value of pH such that after 52% of the total silica is dissolved reconstructed pH would have risen 0.5 units. This relationship only becomes linear in the final stages of dissolution when the assemblage is reduced to a small number of resistant species. Indeed the predicted value is much more erratic when only a small amount of silica has been lost as some species are selectively removed. Strikingly, when only 2% of the silica in the sediment has been dissolved the estimated pH was reconstructed 0.36 units higher. The pH reconstruction from the samples of DE5 also varied greatly. Initially dissolution caused estimated pH to rise sharply by 0.5 units as in DE4, but as more of the sample was lost to solution the reconstructed pH also declined to a value marginally less than in the control sample. Paradoxically when these samples are 60% dissolved they provide a closer estimate for pH than when only 10% dissolved. Therefore, the conclusion must be drawn that dissolution cannot be predicted definitively as it depends entirely on the composition of the starting assemblage and the amount of dissolution that has taken place.

Dissolution may be recognised in a sample by the presence of certain characteristics shown here to be indicative of partially dissolved assemblages. These include direct evidence of dissolution on the frustules, changes in the assemblage composition leaving predominantly large, robust taxa, low total valve abundance and low species diversity. Circumstantial evidence of dissolution can be drawn from the presence in the sediments of alkaline silicate minerals such as zeolites as has been found in Magadi and Manyara (chapters 3 and 4). When the possibility of dissolution has been established the assemblage can be qualitatively reinterpreted according to the species remaining. In order to do this it is necessary to consider what other species



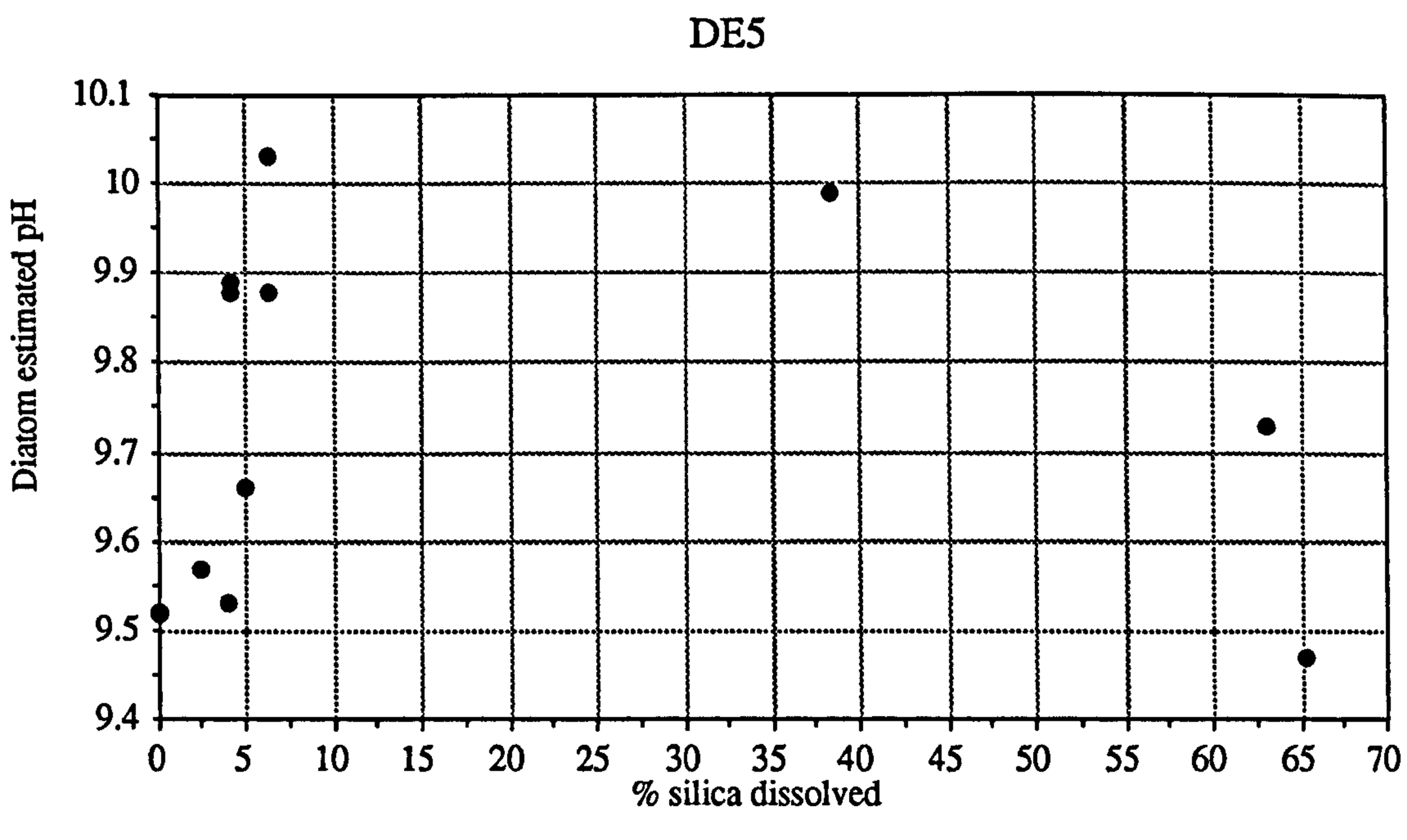


Figure 5.9. The effect of dissolution on diatom derived pH estimates.

might be expected in addition to those that remain. Clues to former assemblage composition may be found in other parts of cores or sections where dissolution is thought not to be as great a problem, or more generally from the results of synecological studies. The results of these experiments will be applied to the interpretation of the fossil diatom assemblages from Magadi and Manyara in order to reduce errors introduced by assemblage diagenesis.

CHAPTER SIX: DISCUSSION

Diatom analysis of the cores from lakes Magadi and Manyara has revealed profound fluctuations in the dominant species during the Late Pleistocene and early Holocene. Using modern diatom assemblages as analogues with which to interpret the life-form and ecological requirements of the fossil diatom taxa, changes in the diatom assemblages can be related to fluctuations in the palaeoenvironment. Quantitative techniques are used wherever possible to estimate former chemical parameters by application of the methods discussed in chapter 2.

Palaeoenvironmental reconstruction from the fossil diatom assemblages cannot be undertaken directly because of the intervention of taphonomic processes. The formation of the final fossil assemblage is the sum of the forces controlling the preservation of frustules, and the processes responsible for the mixing of diatom assemblages. These can operate both at the time of death and after deposition, and can upset the balance that diatom analysis assumes between palaeo-communities and ambient environmental conditions. Understanding the representivity of the fossil assemblages contained within the cores is paramount in providing accurate palaeoenvironmental interpretation from diatom-based palaeoecology. Therefore, the reconstruction of past environments as indicated by the fossil diatom sequences is preceded by a discussion of possible taphonomic processes that have contributed to the formation of the taphocoenoses.

Section A of this chapter considers the implication of changes in the diatom assemblages from Magadi, by comparing these data to that arising from the other palaeoenvironmental studies of the EQUARIFT programme. Section B is concerned with the studies from Lake Manyara, and how this new data is to be interpreted following the earlier palaeolimnological work of Holdship (1976), the stromatolite investigations of Casanova (1986a) and importantly the dissolution experiments described in the preceding chapter.

A: Lake Magadi.

Three diatom bearing cores were described in chapter 3, two of *c.* 9m from Flamingo Nursery, and one of approximately 3m from the Northern Lagoon. A preliminary diatom survey of NF2 has shown that it holds the same stratigraphical sequence as NF1, although full diatom counts have been restricted to selected core

portions. The study of NF2 is important as it provides additional information on the nature of the transitions between the major diatom zones, and for the missing sections of NF1. The discussion of these cores from Flamingo Nursery will focus primarily on NF1, but with reference made to NF2 where appropriate. The third core NL1, is much shorter than those from Flamingo Nursery, but also shows interesting variations in its diatom record. The wider significance of changes occurring amongst the diatom assemblages within each core, and in particular their relation to other stratigraphical and shoreline studies from Magadi will be examined in the final chapter.

Taphonomy of diatom assemblages at Flamingo Nursery (NF1 and NF2).

Taphonomic and diagenetic processes have undoubtedly contributed greatly to the formation of the diatom assemblages within the Flamingo Nursery cores. This is most clearly manifested in two ways; firstly by the highly diverse mixture of apparently incompatible diatom taxa found in zone 2 and sub-zone 3B, and secondly by the evidence in sub-zone 3A for valve destruction and possible diagenesis into various silicate minerals.

a) Mixing processes

The diatom taphocoenose of zones 2 and 3B has no **single** modern analogue. Instead, it combines two contrasting diatom communities. One has species typically associated with fresh- or oligosaline water, for example *Aulacoseira granulata, Fragilaria brevistriata,* and *Epithemia sorex.* The other assemblage includes species such as *Navicula elkab*, and *Thalassiosira faurii*, which are highly characteristic of hypersaline waters. This apparent paradox can only be reconciled if mixing processes are invoked.

Multiple working hypotheses can be suggested to explain this unusual conjunction of assemblages, involving either the spatial mixing of contemporaneous diatoms from disparate habitats, or the bringing together of non-contemporaneous assemblages that were living under different environmental regimes. Three hypotheses are proposed, each will be considered separately, although a combination of any of these is equally possible.

Hypothesis 1. One explanation is that the lake was seasonally stratified and supported different diatom communities at different times of the year. This has been observed elsewhere in the tropics where extreme seasonality has brought together apparently incompatible diatom species in bottom mud and core samples, for example in the Guidimouni salt pond, Niger (Gasse 1987), and in the Cuenca de México, (Bradbury 1989). Periodic stratification at Magadi occurs under the present highly contrasting climatic system with a relatively dilute lens developing above the concentrated brines (Eugster 1986). However, despite this marked seasonality the modern diatom assemblages do not contain such completely contrasting diatom species as are found in these fossil samples. Instead the modern diatom flora is typical of meso-hypersaline environments which casts doubt upon this hypothesis. Other arguments against this explanation can be envisaged. If the periodic development of a freshwater lens did allow the development of a freshwater diatom community, then these would be largely confined to an open water habitat. The diatom taphocoenoses would consequently be expected to be comprised of freshwater planktonic species and saline benthic forms. In fact 30-40% of fresh-oligosaline diatoms in these samples are littoral or benthic, whilst several euplanktonic saline species are also present (figure 6.1).

Hypothesis 2. The reworking of much older deposits and therefore the mixing of non-contemporaneous diatom assemblages offers a second hypothesis by which to explain this situation. It is possible that the entire section is comprised of reworked material, or alternatively - and more feasibly - derived material may only be a partial contributor to the sediments. The most likely cause of the latter is if older freshwater assemblages were deposited into an existing saline lake. For hypothesis 2 to be accepted it is necessary to find both a source for the reworked material and a means by which it has been transported.

The erosion of older lake deposits within the Magadi basin could offer a potential source of reworked material. Palaeolakes have filled the Magadi trough on many occasions and their deposits could well have contained diatoms, although none have been reported in the detailed studies of the Oloronga beds of the Early-Middle Pleistocene conducted by Baker (1958), and Surdam and Eugster (1976). The apparent dearth of diatoms in these deposits might be explained by the abundance of diagenetic silicate minerals, indicating the dissolution and re-precipitation of silica, which may have largely destroyed any diatom frustules once contained in these deposits. Although absence of evidence does not necessarily give evidence of absence, the failure to find

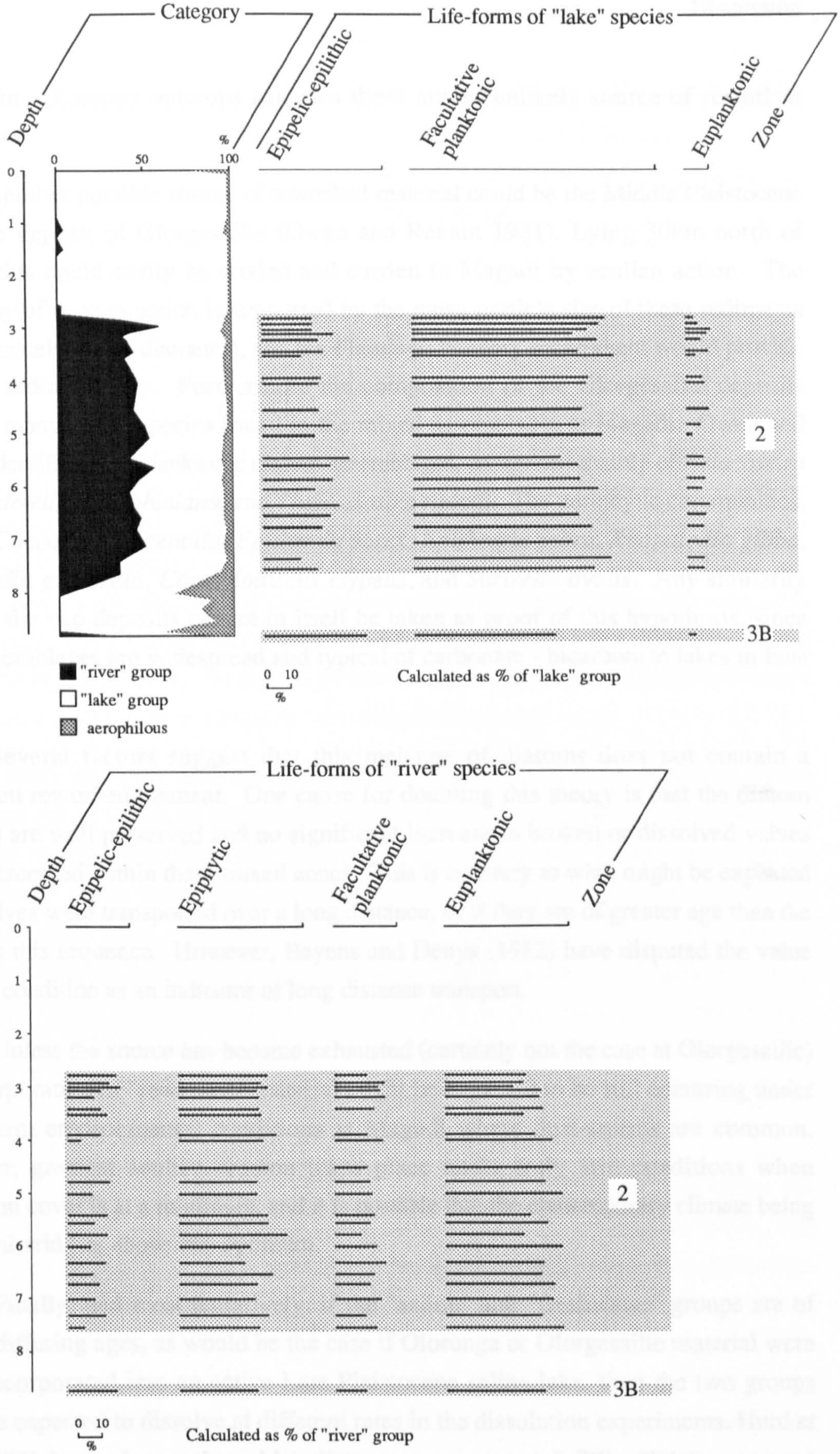


Figure 6.1. Life-forms of "river" and "lake" groups for zone 2 and sub-zone 3B of core NF1.

diatoms in Oloronga outcrops suggests these are an unlikely source of reworked sediments.

Another possible source of reworked material could be the Middle Pleistocene diatomite deposit of Olorgesailie (Owen and Renaut 1981). Lying 30km north of Magadi this could easily be eroded and carried to Magadi by aeolian action. The possibility of aeolian action is supported by the mean particle size of these sediments (approximately 39μm diameter), and the Flamingo Nursery escarpment would provide an ideal sediment trap. Furthermore the composition of the Olorgesailie deposits includes many of the species found in the mixed assemblages at Magadi. Owen and Renaut identified four planktonic diatom assemblages, comprised mainly of *Aulacoseira* spp., *Cyclotella meneghiniana,* and *Thalassiosira rudolfi.* The periphytic communities, include *Cocconeis placentula, Epithemia sorex, Epithemia zebra, Rhopalodia gibba, Rhopalodia gibberula, Campylodiscus clypeus*, and *Surirella ovalis.* Any similarity between the two deposits cannot in itself be taken as proof of this hypothesis, since these assemblages are widespread and typical of carbonate - bicarbonate lakes in East Africa.

Several factors suggest that this melange of diatoms does not contain a significant reworked element. One cause for doubting this theory is that the diatom frustules are well preserved and no significant increase in broken or dissolved valves can be discerned within these mixed zones. This is contrary to what might be expected if the valves were transported over a long distance, or if they are of greater age than the others in this sequence. However, Beyens and Denys (1982) have disputed the value of valve condition as an indicator of long distance transport.

Unless the source has become exhausted (certainly not the case at Olorgesailie) the incorporation of "reworked" material might be expected to be still occurring under the present environmental conditions at Magadi where dust-storms are common. However, greatest aeolian erosion takes place under truly arid conditions when vegetation cover is at a minimum, and it is possible that the contemporary climate being only semi-arid lies above this optimum.

Finally, and most tentatively, if the "saline" and "freshwater" groups are of greatly differing ages, as would be the case if Oloronga or Olorgesailie material were being incorporated into an active Late Pleistocene saline lake, then the two groups might be expected to dissolve at different rates in the dissolution experiments. Hurd *et al.* (1981) have shown that older diatomaceous material (Plio-Pleistocene age) dissolves more slowly than Holocene diatomite, as its specific surface area is greatly reduced by increased crystallinity. Dissolving material from zone 2 suggested no

appreciable difference in the dissolution rate of the "freshwater" or "saline" groups. Therefore, it can be cautiously suggested from this that no great difference exists in the ages of the saline and freshwater diatom frustules. Whilst the aeolian hypothesis cannot be ruled out entirely, obvious supporting evidence is lacking.

Hypothesis 3. Hypotheses 1 and 2 have assumed that the conjunction of contrasting species is a result of temporal change on various scales, an alternative hypothesis is that the two communities were contemporaneous, but spatially separate. This explanation envisages a relatively saline lake into which rivers or streams discharge bringing with them freshwater diatoms. The Ewaso Ngiro river system is one potential source except that at present its tectonically controlled course prohibits its entry into Magadi and large scale tectonic movements would have to be postulated to divert its course directly into Magadi. A more plausible source of freshwater comes from small channels to the north of Flamingo Nursery especially if they were enhanced in the past. However, direct geomorphological evidence for a small palaeochannel is unlikely to be preserved as this event occurred before the most recent Lake Magadi highstand.

Unlike the suggestion regarding the development of a freshwater lens, where freshwater species with planktonic life-forms would be anticipated, this hypothesis allows for the presence of the full range of life-forms within the freshwater group. A wide range of niches would have been available for periphytic taxa, including those in the river channel itself, and those from within the riparian zone. Moreover, the extra energy provided by a fluvial input could help to explain the unusual degree of mixing which gives little up/down variation in the proportion of particular species through almost 4.5m of sediment in zone 2. It might also help to explain the considerable degree of oxidation shown by the sediments of zone 2, in contrast to the highly reduced materials of zones 1 and 3.

A stream-borne input could also be periodic, only occurring when the groundwater supplying the lake has risen sufficiently to allow surface flows, and thereby overcoming an intrinsic threshold in the system. Under present conditions the water-table is too low and surface water disappears below ground. However, if the groundwater reservoir were to rise by only a few metres this could instigate surface flows from the channels to the north of Flamingo Nursery. If the water table was higher than today the lake would also be deeper. Support for this is found amongst the saline "lake" group of diatoms which contains more facultative planktonic (*e.g. Nitzschia* sp. af. *fonticola* and *Nitzschia subrostrata*) and euplanktonic forms (*e.g. Thalassiosira rudolfi* and *Thalassiosira faurii*) than in the present Magadi diatom

communities which are comprised in the main of littoral benthic species (*e.g.* *Anomoeoneis sphaerophora* and *Rhopalodia gibberula*) (figure 6.1).

The evidence supporting hypothesis 3 by no means conclusive, but falsification is equally difficult from the data available. It overcomes many of the difficulties associated with either of the other avenues explored above, notably the distribution of life-forms (hypothesis 1), and the lack of evidence for the poor preservation of reworked valves (hypothesis 2). A problem remains with the small average grain size of these well sorted sediments, making them more characteristic of aeolian rather than fluvial transport. However, this may be partly explained by the nature of the sediment source which is rich in fine volcanic glasses. Therefore, this scenario of distinct but spatially contemporaneous habitats, combined fluvially by freshwater discharging into a more saline lake is adopted as a working hypothesis in the following palaeoenvironmental interpretation.

It is unrealistic to attempt to apply the quantitative methods of diatom palaeoecology to a fossil assemblage which represents more than one set of environmental parameters. Under these circumstances it is necessary to split the taphocoenose into a fresh-oligosaline "river" group and a relatively saline "lacustrine" group. Table 6.1 shows the chemical classification (pH and conductivity) of the species found in zone 2 as indicated by Gasse (1986a) and the division made between "lake" and "river" groups. Salinity tolerance and preference is the major criterion in distinguishing the two groups (*cf.* Beyens and Denys 1982), although other factors such as habitat preference have been considered. The "lake" group is restricted to species which tolerate conductivities in excess of 10,000μScm^{-1}. Several species are only found in such concentrated waters including *Achnanthes brevipes, Anomoeoneis sphaerophora, Navicula elkab, Navicula gawaniensis* and *Nitzschia subrostrata* (Gasse 1986a). Other species listed in the "lake" group have broader salinity requirements but were found in concentrated waters of more than 10,000μScm^{-1} by Gasse (*ibid.*). An exception is *Mastogloia smithi* but this species does tolerate moderate salinities and is typically associated with lake marginal habitats (Gasse *ibid.*). Eurysaline species such as *Nitzschia* sp. af. *fonticola, Caloneis bacillium, Cymbella affinis, Cymbella cistula, Cymbella turgida, Fragilaria pinnata, Gomphonema gracile, Nitzschia amphibia, Stephanodiscus minutus* and *Surirella ovalis* are more difficult to classify. They are found across the full range of salinity categories and could be placed in either "lake" or "river" groups. However, *Nitzschia* sp. af. *fonticola* and *Stephanodiscus minutus* are placed here in the "lake" group as they are usually associated with lacustrine habitats (Gasse *ibid.*) the other eurysaline species are assigned to the"river" group.

(Saline) "Lake" group

Species	max%	pH group	Cond. group
A. brevipes	0.2	5	5
A. coffaeformis	0.6	2-3	3-5
A. costata	0.2	4-5	3-5
A. sphaerophora	0.6	5	5
C. clypeus	0.8	3-5	4-5
C. iris	0.4	3-5	3-5
C. meneghiniana	10.6	3-5	2-5
C. ocellata	3.8	3-5	3-5
M. elliptica	2.2	3-5	3-5
M. smithi	2.8	2-3	1-4
N. elkab	10.1	5	5
N. gawaniensis	0.6	5	5
N. halophila	1.35	3-5	2-5
N. pseudohalophila	1.4	4-5	2-5
N. "group latens"	22.9	4-5	4-5
N. frustulum	2.8	4-5	3-5
N sp. af. *fonticola*	30.9	2-5	1-5
N. subrostrata	25.5	5	5
R. gibberula	5.4	4-5	3-5
S. minutus	4.0	3-5	1-5
T. faurii	5.9	5	4-5
T. rudolfi	1.2	4-5	3-5

(Fresh-oligosaline) "River" group

Species	max%	pH group	Cond. group	Species	max%	pH group	Cond. group
A. engelbrechtii	0.4	1	1	*F. pinnata*	3.5	3	1-5
A. exilis	0.8	1-3	1	*F. ulna* +v. *acus*	5.7	2-3	1-2
A. ovalis	0.8	2-3	1-2	*G. clevei*	2.4	2	1-3
A. veneta	0.4	2-4	1-3	*G. gracile*	1.3	3	1-5
A. granulata	10.7	2-3	1-2	*G. intricatum*	0.6	2-3	1-2
A. granulata v. *angustissima*	4.8	3-4	1-3	*G. lanceolatum*	0.4	2-3	1-2
C. bacillium	0.6	2-5	1-5	*G. parvulum*	0.4	2-3	1-4
C. ventricosa	0.2	-	-	*N. cryptocephala*	0.6	2-3	1-4
C. placentula	2.1	1-4	1-3	*N. damasii*	0.6	3-4	1-3
C. thumensis	0.2	2	1	*N. elephantis*	0.4	2-3	1-4
C. comta	0.4	3	2	*N. exiguiformis*	0.4	2-5	1-3
C. stelligera	0.8	2-3	1	*N. gastrum*	0.2	1-3	1-2
C. affinis	1.8	2-5	1-5	*N. grimmei*	0.4	2-3	1-4
C. cistula	1.0	2-5	1-5	*N. hassiaca*	0.2	1-2	1
C. microcephala	2.1	2-3	1-2	*N. pupula*	1.4	2-4	1-4
C. muellerii	0.8	2-5	2-5	*N. radiosa*	1.2	3	2
C. perpusilla	0.4	2-3	1	*N. amphibia*	2.9	2-5	1-5
C. ruttneri	0.2	2	1	*N. lancettula*	1.5	2-4	2
C. turgida	0.8	2-4	1-5	*N. palea*	1.2	2-4	1-3
D. elliptica	1.6	2	1	*N. paleacea*	2.6	2-3	1-2
D. ovalis	0.4	-	-	*N. recta*	0.2	1-3	1-2
E. sorex	5.4	2-4	2-3	*N. thermalis*	0.2	2-3	1
E. zebra	4.2	3-4	1-3	*R. curvata*	0.2	2-4	1-2
F. brevistriata	6.8	2-3	1-2	*R. gibba*	3.0	3-4	1-3
F. construens	1.3	3-4	1-3	*S. ovalis*	0.2	2-5	1-5
F. leptostauron	1.0	2-3	1				

Table 6.1. The division of diatom species from the mixed assemblages of NF1 and NF2. Showing (a) maximum % achieved in zone 2; (b) pH classification of species from Gasse (1986a). (1: pH<6. 2: pH 6-7. 3: pH 7-8.5. 4: pH 8.5-9.5. 5: pH >9.5.); (c) conductivity classification of species from Gasse (1986a) (in μScm^{-1}. 1: <300. 2: 300-1,000. 3: 1,000-3,000. 4: 3,000-10,000. 5: >10,000.).

b) Dissolution of diatom valves.

Equally important factors are those governing the preservation and/or destruction of the assemblages. Chapter five highlighted the consequences of dissolution and the ways by which it can be identified in controlled laboratory experiments. These characteristics are often ambiguous, arising from factors other than dissolution, and their interpretation must be treated with caution.

TABLE 6.2. Indicators of dissolution in diatom assemblages.

Characteristic	*Comments*
Appearance of valves	Direct evidence of dissolution provides the most reliable indicator
Sterile levels and low abundance	Suggests dissolution, but can arise from other factors
Low diversity and assemblage composition	Differential dissolution reduces diversity, and can lead to enrichment of robust taxa, but can arise from other factors
Diagenetic silicate minerals	Indicates dissolution and re-precipitation of amorphous silica

Of the characteristics listed in table 6.2 only the appearance of the valves is a direct and incontrovertible sign of dissolution, all the others are circumstantial and two are based on negative evidence. For example, in the Flamingo Nursery core the lowest diversity is found in zones 1B and 1C, rich in *Nitzschia* "group latens" and *Nitzschia* sp. af. *fonticola* respectively. However, dissolution is not considered a major factor in shaping these assemblages since valve abundance is high and the general condition of the valves is good. Moreover, the taxa occupying these zones are relatively small and are not particularly well preserved in the dissolution experiments performed here.

Dissolution can be diagnosed with greater confidence when several of the characteristics listed in table 6.2 are found together, as is the case for sub-zone 3A. This sub-zone has all the hallmarks of dissolution. It is dominated by the large robust species *Anomoeoneis sphaerophora*, diversity is low, and many valves are in a poor state of preservation. Valve abundance is also low and diatoms are completely missing at several levels. More positively, the mineralogy supports this hypothesis in containing

zeolites including erionite, and other diagenetic silicates such as magadiite. These minerals form following the dissolution of amorphous silica (including biogenic silica) and are therefore good indicators of the modification of diatom assemblages.

From the species composition of diatom valves surviving in sub-zone 3A, and using modern assemblages as analogues, it is possible to suggest how the fossil assemblages have been altered. Certain taxa are likely to have been proportionally increased by being relatively resistant to dissolution, and these include *Anomoeoneis sphaerophora, Rhopalodia gibberula* and *Hantzschia amphioxys*. It is more difficult to suggest which species are under-represented or have been removed from the record. However, the modern assemblages from Flamingo Nursery which otherwise provide a close analogue for this sub-zone are rich in the small, delicate species *Navicula jakhalsensis*. This is restricted to a single sample of NF1 at 791cm and to part of NF2, which could result from differential dissolution as well as ecological factors. Other taxa that could be under-represented in this zone are *Nitzschia frustulum* and *Nitzschia* "group latens"; being small and weakly silicified they have a high propensity for dissolution.

The experiments described in chapter 5 have shown how quantitative reconstructions can be greatly affected by differential dissolution, and that the direction of the change is unpredictable. Dissolution will bias the value of environmental parameters estimated from the transfer functions toward the values favoured by the most robust taxa in the calibration data set. For sub-zone 3A the most robust species is *Anomoeoneis sphaerophora* which is associated with a mean pH of 10.4 and a mean conductivity of 21,200μScm^{-1} in the East African diatom database (EADD). Therefore, the quantitative estimates of pH conductivity and life-form from sub-zone 3A must be interpreted cautiously.

Palaeoenvironmental reconstruction of the Flamingo Nursery cores.

The reconstruction is based primarily upon the modern ecological relationships of individual diatom taxa to particular environmental variables (pH and conductivity) through the use of transfer functions to estimate the values of these parameters. The limitations of the transfer function approach have been expressed in general terms in chapter 2. More specifically a problem is encountered where species present in cores are not found in the calibration data set, or they fall below the statistical cut-off by being present in insufficient numbers in too few samples. For Magadi the proportion of the assemblage not found in the calibration data was small for pH, but much greater for

conductivity, thereby reducing the accuracy of this estimate. The pH estimate was based on over 90% of the assemblage for all but two samples, at 791cm (74%) and at the surface (69%), since these have a large proportion of *Navicula jakhalsensis* which has few analogues in the EADD. For conductivity fewer coefficients are available and the mean proportion of the assemblage included in the calculation was only 84%, with 5 samples based on less than 70% (280cm, 64%; 302cm, 62%; 600cm, 66%; 791cm, 62%; and 861cm, 63%). The most important species with no coefficient for conductivity in the Flamingo Nursery cores is the meso-hypersaline *Nitzschia subrostrata*, and a qualitative correction for this is made in the interpretation given below. As can be seen from figure 6.2 a very close relationship is shown between conductivity and pH which results from their correlation in the EADD from which the transfer functions are derived. In sodium carbonate systems these two variables are highly correlated and it is not possible to ascertain whether changes in salinity or alkalinity are responsible for the variations found amongst the diatom assemblages.

Sub-zone 3B is represented by a single sample at the base of core NF1. Its designation as a separate unit from the remainder of zone 3 rests on the unusual diversity which has brought together diatoms from opposite ends of the salinity spectrum as discussed above. Following hypothesis 3 that this situation has come about due to a river or stream entering the lake close to the coring site, it is possible to reconstruct both the "lacustrine" and "fluvial" environments (figure 6.2). The division of the diatom taxa into these two groups is based on the assumption that the most halophilous species were found in the lake, whereas freshwater and oligosaline species were members of the river community. Therefore, since chemical preference was used to separate the assemblages, the transfer function estimates of pH and conductivity for the lake and river groups represent maximum and minimum values respectively.

Diatom estimated conductivity for the "lake" group is high (16,600μScm^{-1}) and is matched by an equally high pH (10.3). The comparable figures from the "river" group are 2,200μScm^{-1} and 7.3. The estimate for pH is broadly in line with the actual measurements made on the Ewaso Ngiro by Jones *et al.* (1977).

The presence of littoral species such as *Anomoeoneis sphaerophora* and *Rhopalodia gibberula* in the "lake" group, suggests that the lake was not only saline but also relatively shallow. However, a number of facultative planktonic species included in the "lake" group such as *Nitzschia* sp. af. *fonticola*, *Nitzschia subrostrata*, and *Nitzschia* "group latens", could indicate deeper conditions than found in the remainder of zone 3. It compares favourably to assemblage IVc of the classification proposed by Gasse *et al.* (1983) in their synecological survey of East African diatoms. They suggest that this group could be either periphytic or planktonic, and is found in

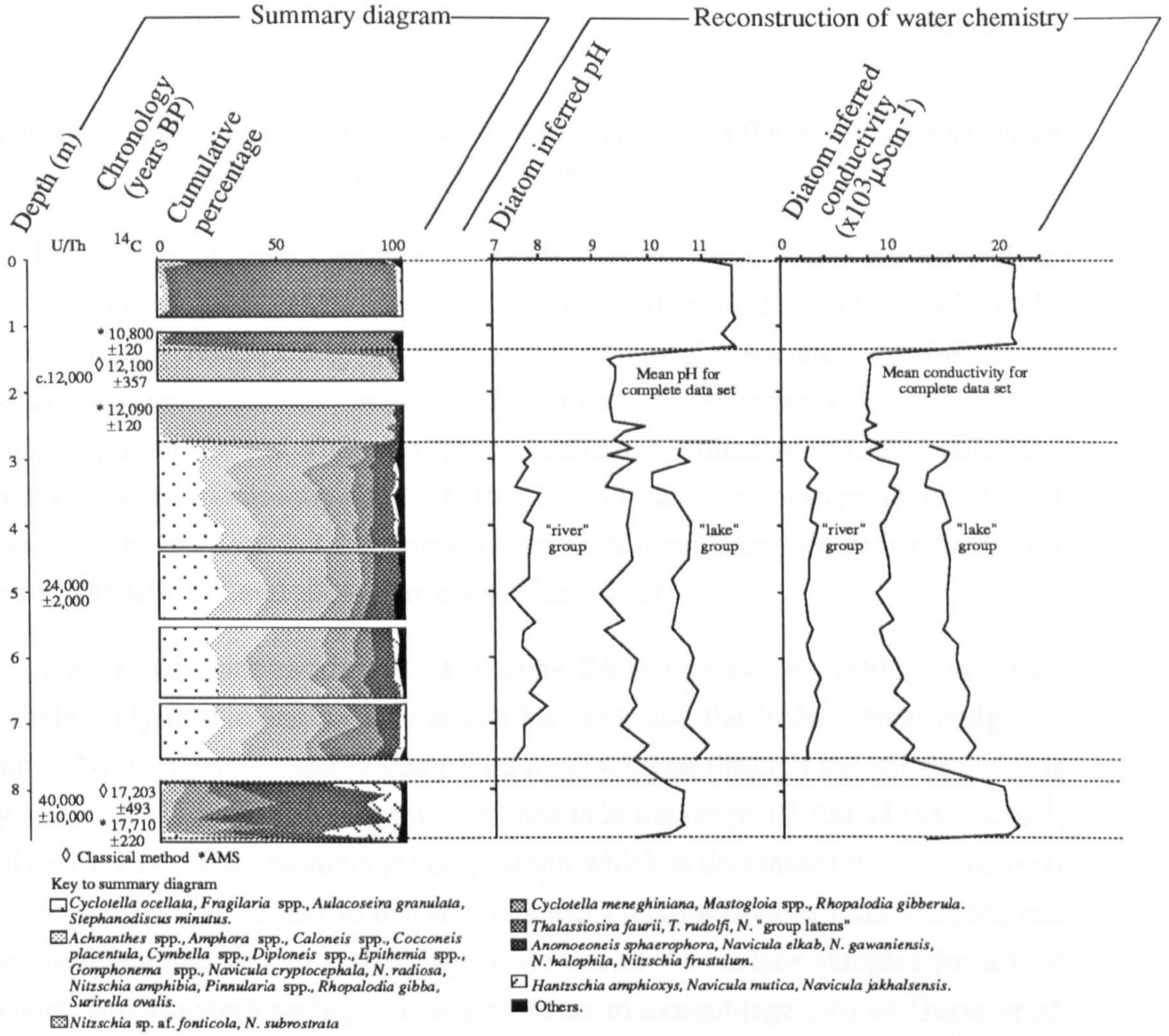


Figure 6.2. Diatom life-forms and palaeoenvironmental reconstruction from core NF1.

lakes as well as hot springs where conductivity exceeds 6,000μScm^{-1}, pH is above 9.1, and water temperatures are in the range 19-55 °C.

Estimated values of chemical parameters from this sub-zone are difficult to assess as a wide range of values are suggested even within the diatom taxa assigned to the "lake" group. *Nitzschia* sp. af. *fonticola* is normally associated with relatively dilute oligosaline-mesosaline waters. In contrast, *Anomoeoneis sphaerophora*, *Rhopalodia gibberula*, and *Nitzschia* "group latens" are indicative of higher salinities, and form a diatom community similar to that found in the present hypersaline Magadi springs. This assemblage is also common in other African lakes where conductivities exceed 10,000μScm^{-1} and pH is above 9.4 (Gasse 1986a).

The "river" species are absent in zone 3A where the assemblage becomes overwhelmingly dominated by littoral-benthic taxa, and the hydrological budget of Flamingo Nursery was probably controlled by discharge through the springs as it is today. Estimated conductivity for this sub-zone is in the range 19,700-21,000μScm^{-1}, and pH 10.1-10.4. The assemblage composition which is dominated by *Anomoeoneis sphaerophora*, is very similar to that of the modern diatom flora of Lake Magadi, and shows most resemblance to assemblage 2 present in the surface samples from Bird Rock and Southwestern springs. It is also close to assemblage IVd of Gasse *et al.* (1983) which is regarded as periphytic and is found in Lake Lgarya and Lake Gidamur, Tanzania. The sample at 791cm in which *Navicula jakhalsensis* is abundant is more akin to modern assemblage 1 from Flamingo Nursery. If the modern Magadi environment is a useful analogue (pH 8.9-9.6) then it is likely that the estimated pH from the transfer function is slightly too high. Moreover, these estimates may be unreliable since differential dissolution could have preferentially enriched the samples from this zone with *Anomoeoneis sphaerophora*. Valve preservation is poor and a range of diagenetic silicate minerals are present.

Magadiite is frequent at several levels in sub-zone 3A. The specific mechanism for its formation is unknown, but at least two routes have been suggested. The first was proposed by Eugster (1967), and imagines a seasonally stratified lake with an underlying saline water body containing a large store of dissolved silica. Flooding by freshwater lowers the alkalinity and allows lake-wide precipitation of magadiite. This hypothesis was originally developed to explain the layers of magadiite amongst the High Magadi beds when a deeper lake than that envisaged for sub-zone 3A was thought to have filled the basin. A second theory to explain the formation of magadiite was generated following its discovery at Kanem, an interdunal depression close to Lake Chad (Maglione 1970). Here diatom evidence indicates only a shallow lake and the formation of magadiite is thought to result from the interaction of saline groundwaters

with silica rich diatomaceous deposits. Therefore, of these two hypotheses Maglione's is more consistent with the diatom evidence for the lakes hydrological status at this time, whereas that of Eugster requires a much deeper lake than the diatoms indicate. Furthermore, Maglione's hypothesis would also account for the dissolution of valves within this sub-zone.

Sub-zone 3A terminates through the complex assemblages found in 3A' of NF2. Importantly, this includes several levels in which aerophilous species (*e.g. Navicula mutica* and *Hantzschia amphioxys*) are abundant, signifying merely moist conditions close to the coring site, drier than those at present. Both are common in a range of sub-aerial habitats including soils (Patrick 1977).

Considerably different habitat conditions are suggested by *Nitzschia* "group latens" which rises to dominate the assemblage toward the transition with zone 2 reaching 92%. *Nitzschia* "group latens" can be either periphytic or facultative planktonic in life-form but is always found in meso-hypersaline conditions (Gasse 1986). This level of dominance probably indicates a planktonic assemblage, directly comparable to that found in sub-zone 1B (a more complete discussion of this interpretation is given below). The transition to zone 2 receives a "false-start", with the diverse assemblages typical of this zone appearing first at 728cm, only to be replaced once more by *Nitzschia* "group latens" at 726cm, before the commencement of zone 2 *sensu stricto* 2cm stratigraphically above this. However, it is possible that is stratigraphically inverted this due to vertical sedimentary mixing.

The taphonomic processes responsible for shaping zone 3B returned to produce the unusual amalgam of diatom communities found in zone 2. If a river or stream entered close to the coring site to deposit zone 3B, then the remarkable similarity of zone 2 to 3B suggests the same explanation is applicable. However, whereas sub-zone 3B is represented by only a single sample which could be considered anomalous, conditions responsible for the formation of zone 2 persisted during the deposition of over 4.5m of sediment. Throughout this time the diatom assemblages show little variability suggesting either a considerable degree of environmental stability and/or extensive vertical mixing of sediments. The stratigraphical homogeneity might also point to the rapid deposition of zone 2, although the sedimentation rate cannot be adequately estimated because of the difficulties of dating this section of the core.

As for sub-zone 3B the fossil diatom taphocoenose has been tentatively split into "lake" and "river" components. The lake group is dominated by *Nitzschia* sp. af. *fonticola, Nitzschia subrostrata, Nitzschia* "group latens", and *Nitzschia frustulum*, which alongside *Cyclotella meneghiniana*, and *Thalassiosira faurii*, probably formed a

planktonic community. Also present are a number of species including *Rhopalodia gibberula*, and *Navicula elkab* which have been found as opportunistic elements in the plankton of lakes but are more typically members of the periphyton. High salinities are indicated by this "lacustrine" assemblage and the conductivity is estimated to be within the range 12,600-17,000μScm^{-1}, and pH 9.8-10.8.

In contrast to these high salinities amongst the "lake" species the "river" assemblage produced an estimated conductivity of only 2,100-3,500μScm^{-1} with pH in the range 7.3-7.9. Characteristic species include *Aulacoseira granulata*, *Epithemia sorex, Epithemia zebra, Fragilaria brevistriata, Fragilaria pinnata, Fragilaria construens*, and numerous members of the genera *Cymbella, Gomphonema, Navicula*, and *Achnanthes*, together producing an highly diverse assemblage. Little is known of the modern diatom populations of minor African rivers as envisaged here, although Gasse *et al.* (1989a) reported *Aulacoseira granulata* as abundant in the highly turbid waters of the Niger and Congo.

The majority of taxa included in this group (with the notable exception of *Aulacoseira granulata*) are epipelic-epilithic, or epiphytic. The number of epiphytic taxa is of particular interest as epiphytes are rare in other sections of NF1, probably due to the lack of niches available to aquatic macrophytes. When water levels are low enough to allow fringing vegetation to develop, the high salinities would be prohibitive to most species, and during more dilute episodes water-levels would rise vertically due to the control exerted by the Flamingo Nursery escarpment again limiting the prospects for attached vegetation. Hence, this variety of diatom life-forms would favour the incorporation of diatoms from other habitats (*cf.* hypothesis 3).

Diatom analysis from core NF2 identifies the abrupt nature of the transition from zone 2 to sub-zone 1C, which probably results from an hiatus. The length of the break in sedimentation is uncertain, but accumulation at Flamingo Nursery resumed at *c.* 12,500 BP. The change in the diatom flora between these two zones is complete, changing from one of extremely high diversity to being virtually monospecific. *Nitzschia* sp. af. *fonticola* dominates sub-zone 1C (69-96%) with *Nitzschia subrostrata*, and *Nitzschia frustulum* also present.

The taxonomy and ecology of *Nitzschia* sp. af. *fonticola* is not well known and environmental interpretation is accordingly difficult. The taxon *Nitzschia* sp. af. *fonticola* incorporates several morphological forms ranging from elliptical to lanceolate which may have different ecological distributions (Gasse 1986a). The most similar morphotype to those from sub-zone 1C is *Nitzschia* sp. af. *fonticola* "type 1" synonymous to *Nitzschia lacuum* of Lange-Bertalot (1980).

Gasse (1986a) reports this from very diverse habitats, ranging from the plankton of large freshwater lakes to hot saline springs. Examples of these include Sonachi Crater lake (conductivity 5,100 μScm^{-1}, pH 9.9), and Lake Abiyata (conductivity 8,600-30,000μScm^{-1}, and pH 9.3-9.5). However, in these samples *Nitzschia* sp. af.*fonticola* was not dominant and their use as analogues is limited. The most abundant occurrence of this taxon in the EADD is from Lake Mwamba, Uganda, where it comprised 90% of a bottom mud sample. This is a rather dilute lake having a conductivity of only 387 μScm^{-1} and a pH of 8.7 (Melack 1976). Direct comparison of the slides from Lake Mwamba to those from Magadi shows that the valves from the former are narrower and so again this does not provide an ideal analogue.

Transfer functions (based on all morphological forms) indicate that this is the most dilute of the strictly lacustrine diatom assemblages at Flamingo Nursery. Conductivity falls to 7,100-8,300μScm^{-1} and pH to 9-9.8. The estimated degree of dilution and the contrast to other assemblages found in the core could become even greater if a narrower definition of *Nitzschia* sp. af.*fonticola* had been adopted.

The life-form of *Nitzschia* sp. af.*fonticola* is also difficult to categorize as it has been reported from both the periphyton and plankton of lakes. However, its complete dominance of these assemblages, resulting in the exceptionally low diversity of sub-zone 1C, suggests that a planktonic life-form is most probable, where fewer niches are available to its competitors than would be the case in the periphyton.

Eco-physiological studies show *Nitzschia* sp. af.*fonticola* is an obligate nitrogen heterotroph, it requires the presence of nitrogen fixing hosts, notably cyanophytes like *Microcystis* to supply this nutrient (Kilham *et al.* 1986). Therefore, from the presence of *Nitzschia* sp. af.*fonticola* it could be inferred that cyanophytes were important at this time. Interestingly, the presence of cyanophytes is also shown by the formation of stromatolites, as the radiocarbon dating of the stromatolite belt *c.* 50m above the present lake level corresponds well to the age of this sub-zone. Thus, at this time the lake was not only dilute as indicated by the diatom flora, but also deep.

Sub-zone 1B has much in common with 1C in being dominated by a single taxon, except that here *Nitzschia* sp. af.*fonticola* is replaced by *Nitzschia* "group latens" (83-97%). Analogues for this sub-zone are also difficult to find, not least because of the morphological variation associated with the dominant taxon. The definition used here follows that of Gasse (1986a) who incorporates *Nitzschia latens s.s.*, *Nitzschia estohensis*, *Nitzschia elliptica*, and *Nitzschia* sp. af. *pura*, into a single taxon of *Nitzschia* "group latens" as these are only separated by valve shape which is

unreliable as a taxonomic distinction. Furthermore, in intermediate forms between the various morphotypes are found which supports their combination within a single taxon.

All these taxa are to be found within similar hypersaline environments with pH above 10 and conductivities greater than 10,000μScm^{-1}. However, as discussed in chapter 3 different levels are dominated by particular morphotypes and these might warrant slightly different palaeoenvironmental interpretations. The lowest section of sub-zone 1B is dominated by the elongate rhombic form which compares favourably to *Nitzschia* sp. af. *pura*. This is abundant (66%) in a bottom mud sample from Lake Elmenteita, Kenya which has a conductivity of 43,750μScm^{-1} and a pH between 10.4 and 10.9. The next form to dominate in sub-zone 1B resembles *Nitzschia latens sensu stricto*. This taxa reaches its greatest abundance (75%) in the EADD in Lake Gidamur, Tanzania, which is less concentrated than Elmenteita having a pH of 9.4 and conductivity of only 7,920μScm^{-1}. Finally, the uppermost samples from this sub-zone contain a more elliptical morphotype (*cf. Nitzschia elliptica*) which is best developed in a rock scraping from Lake Shala, Ethiopia (conductivity 16,770-29,500μScm^{-1}, pH 9.7-10.1).

Transfer functions are based on the assumption that the autecology of *Nitzschia latens sensu stricto* is representative of *Nitzschia* "group latens", and suggest that conductivity lies between 19,700 and 21,200μScm^{-1}, whereas pH is between 11.0 and 11.3. These values would seem to be too high, especially that for pH given the high solubility of silica at these levels. Several reasons could explain these high values, not least the problem of assigning analogues to this ill-defined taxon. Furthermore, mean chemical values derived from the EADD are inflated by the occurrence of this taxon in samples from hot springs in which ionic concentrations are invariably higher than in lakes.

Nitzschia "group latens" is another taxon which has been encountered in several life-forms. In the modern samples from Magadi it is found amongst littoral and benthic species, but the abundance with which it is present in sub-zone 1B suggests an explanation similar to that advanced for *Nitzschia* sp. af. *fonticola* in sub-zone 1C. If it were living in the periphyton then a much more diverse assemblage would be anticipated as in the modern samples.

The uppermost sample of NF1 is placed within a separate sub-zone 1A as the diatom flora changes strikingly at this point. This abrupt change supported by sandy horizons shown in the sediments, indicates that an hiatus divides these sub-zones. *Nitzschia* "group latens" is greatly reduced in abundance and is joined by *Anomoeoneis*

sphaerophora, *Navicula jakhalsensis*, and *Rhopalodia gibberula*, forming a similar epipelic-epilithic assemblage to that found in the modern samples from Magadi.

Lake-level interpretation derived from the diatom sequence of Flamingo Nursery.

The dating of NF1 and NF2 has proved problematical with U/Th and ^{14}C giving different ages for the lower section of the cores, although both agree for zone 1. Zone 3, dated to 17-18,000 BP by ^{14}C and 30-50,000 BP by U/Th, contains a series of diatom assemblages suggesting low water-levels (figure 6.3). The lake-level declined between sub-zone 3B and 3A, cutting off the supply of freshwater to Flamingo Nursery if the taphonomic explanation expressed in hypothesis 3 is accepted. Chemical conditions in sub-zone 3A became highly concentrated and unconducive to frustule preservation, a situation for which the present Magadi environment offers a useful analogue. Flamingo Nursery became slightly drier than the present situation within parts of sub-zone 3A and 3A' when aerophilous taxa became abundant.

A short-lived deepening of the lake is reflected in the diatom assemblages at the top of sub-zone 3A' with a rise to dominance of *Nitzschia* "group latens". This took water-levels above those of both 3A and 3B, and took the edge of the lake further from the Flamingo Nursery core site. The depth of the lake at this time cannot be accurately discerned. However, the water level or the turbidity must have been sufficient to prevent light penetrating to the lake bed as no benthic species are present. This need not be a great depth as the photic zone in many East African saline lakes is confined to only a few centimetres (Melack and Kilham 1974). A possible hiatus separates zones 3 from zone 2, although this is not as clear as that which divides zone 2 from zone 1.

Zone 2 indicates a recession following the relatively high episode at the end of 3A', when hydrological conditions returned to those responsible for the formation of sub-zone 3B. The water table rose crossing the threshold that enables surface flows close to the coring site, but the lake was insufficiently high to support a wholly planktonic diatom flora. This zone has not been dated by ^{14}C due to the low level of organic matter in this section, although U/Th gives it an age of 24,000±2,000 BP.

An hiatus followed the deposition of zone 2, persisting until *c.* 12,700 BP when lake-level rose sharply to at least 50m deep. The waters were dilute, as deduced from diatom ecology, and also stratified allowing the precipitation of magadiite and the formation of laminae (plates 6.1-6.3). A single lake filled both the Magadi and Natron basins, which was in existence for at least 1500 years. However, chemical conditions

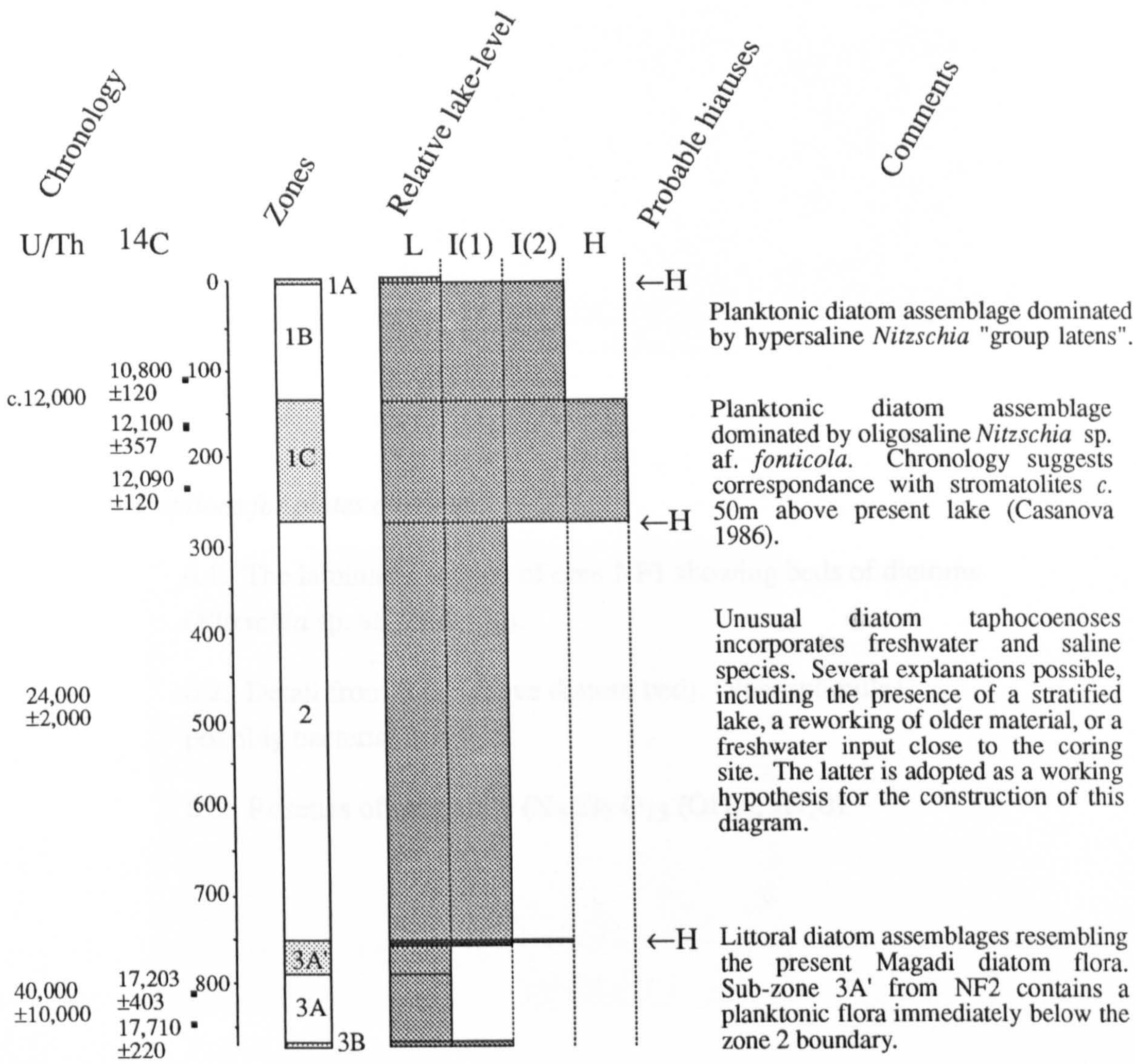


Figure 6.3. Schematic representation of lake-level changes as deduced from the diatom analysis of NF1 and NF2, Lake Magadi

Captions for plates overleaf.

6.1. The laminated section of core NF1 showing beds of diatoms (*Nitzschia* sp. af. *fonticola*).

6.2. Detail from 6.1. (above diatom bed). Nanospherules, possibly bacterial in origin.

6.3. Rosettes of magadiite ($Na\ Si_7\ O_{13}\ (OH)_3,\ 3H_20$).

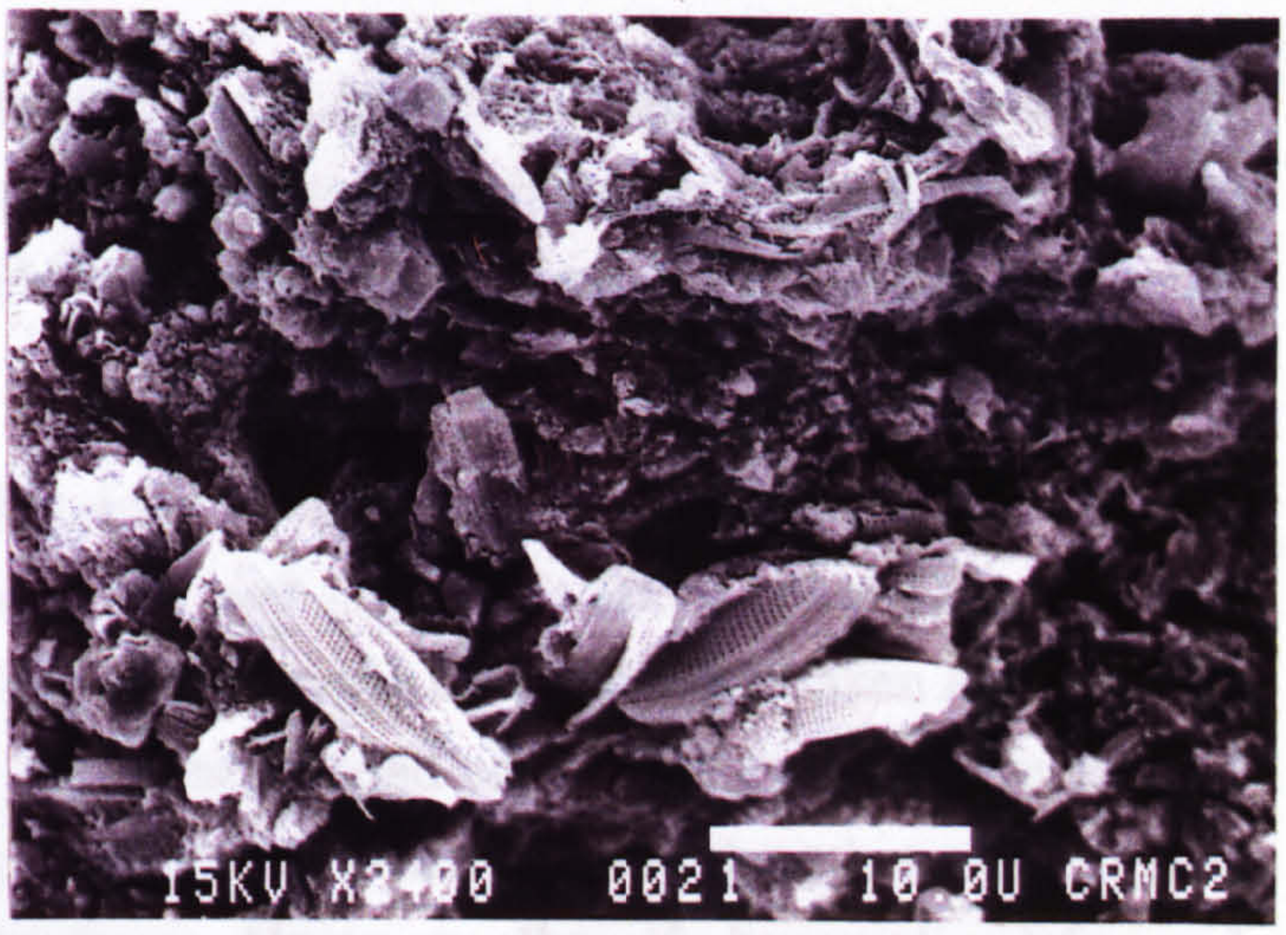


Plate 6.1

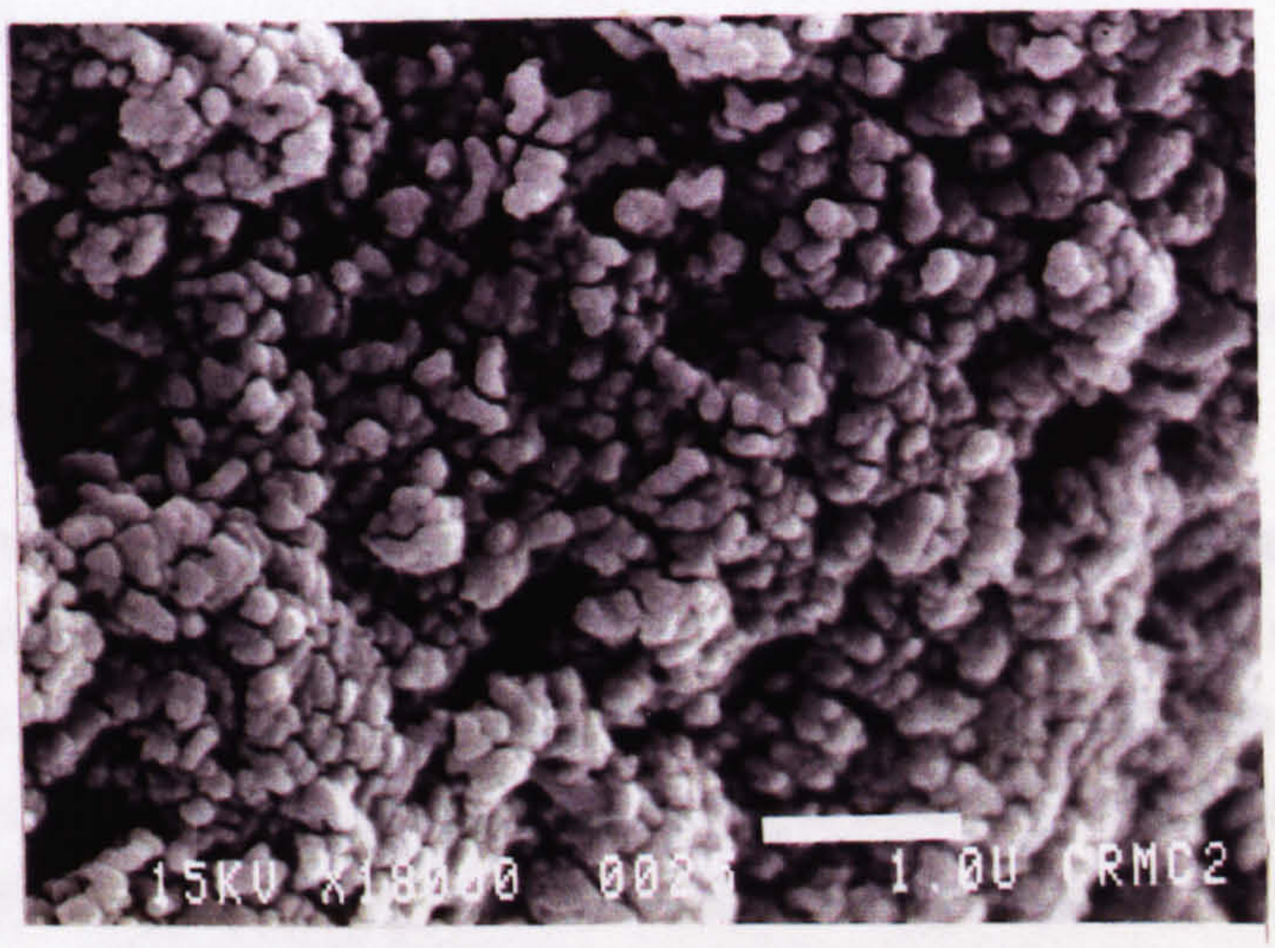


Plate 6.2

Plate 6.3

became abruptly concentrated once again at *c.*11,000 BP probably associated with a fall in water-level. Alternatively, it could signify the separation of Magadi from Natron which would need lake-level to fall 26m from the high level of 1C as discussed in the final chapter.

Sub-zone 1B could be subdivided further into the different morphotypes of *Nitzschia* "group latens" (*Nitzschia* sp. af. *pura* - *Nitzschia latens* - *Nitzschia elliptica*). If the modern analogues in which this species reach dominance are taken literally, this succession could signify slightly less concentrated conditions during the period of dominance of *Nitzschia latens sensu stricto* than when either of the other morphotypes within *Nitzschia* "group latens" dominate. However, all typify hypersaline lakes and any dilution can only have been marginal. The top of zone 1B is undated but it seems certain that a hiatus divides this from the modern assemblages of sub-zone 1A, and that much of the Holocene sediments are missing due to deflation under the arid regime of the last few millennia.

Differential dissolution and palaeoenvironmental interpretation of the Northern lagoon core.

The short core from the Northern lagoon (NL1) contains a sequence of diatom assemblages which closely resemble those found in the modern samples from the various springs at Magadi (figure 6.4). Indeed differences between these springs can provide spatial analogues for the temporal changes evident in the cores. As in the cores studied from Flamingo Nursery the role of taphonomy (and for NL1 of dissolution in particular) has to be subtracted from possible environmental changes in shaping the diatom assemblages.

Transfer functions are not used because two important species in this section *Navicula jakhalsensis* and *Stauroneis* sp. af. *wislouchii* do not have sufficient analogues in the EADD to be assigned coefficients. The modern samples from Magadi offer more appropriate analogues for the reconstruction of palaeoenvironments from these samples. They contain each of the four most abundant and ubiquitous taxa, *Nitzschia* "group latens", *Navicula jakhalsensis*, *Stauroneis* sp. af. *wislouchii*, and *Anomoeoneis sphaerophora*. However, some differences exist , notably the absence from the modern samples of *Cyclotella meneghiniana* which is common in the core, and the presence of *Rhopalodia gibberula* in the modern samples in far greater proportion than it is found in NL1.

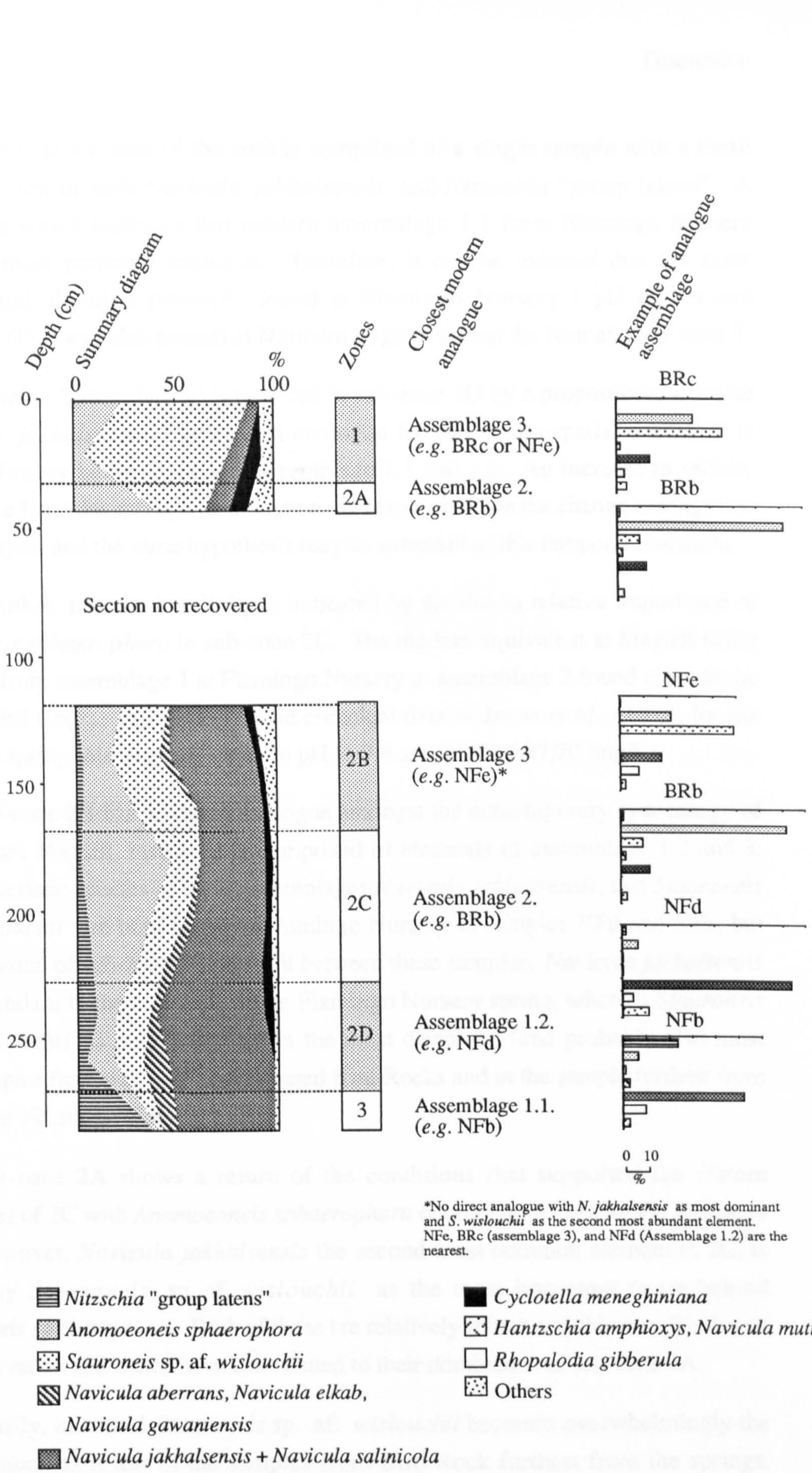


Figure 6.4. Suggested modern analogues from Magadi for the Northern Lagoon core (NL1).

Zone 3, at the base of the core is comprised of a single sample with a fossil assemblage rich in both *Navicula jakhalsensis* and *Nitzschia* "group latens". A combination which indicates that modern assemblage 1.1 from Flamingo Nursery provides a most pertinent analogue. Therefore, it can be inferred that the same environmental situation presently found at Flamingo Nursery (pH of 8.9 and 20,000mg/l TDS) was also present at Northern Lagoon during the formation of zone 3.

Nitzschia "group latens" is replaced in sub-zone 2D by a proportional increase in *Navicula jakhalsensis*. The closest analogue for this is the spatial transition at Flamingo Nursery between modern assemblage 1.1 and 1.2. An increase in salinity with distance from the spring was thought to be responsible for the change amongst the modern samples and the same hypothesis may be extended to this temporal transition.

A further increase in salinity is indicated by the rise in relative importance of *Anomoeoneis sphaerophora* in sub-zone 2C. The modern equivalent at Magadi being the change from assemblage 1 at Flamingo Nursery to assemblage 2 found close to the spring at Bird Rocks. According to the chemical data of Jones *et al.* (1977) for the Bird Rocks spring this suggests a rise in pH to 9.8 and TDS of 37,700mg/l.

Sub-zone 2B has no direct analogue amongst the contemporary synecology of diatoms from Magadi, instead it is comprised of elements of assemblage 1.2 and 3. The characteristic species of these assemblages *Navicula jakhalsensis*, and *Stauroneis* sp. af. *wislouchii* are both found at Flamingo Nursery in samples NFd and NFe, but the composition of sub-zone 2B places it between these samples. *Navicula jakhalsensis* is most abundant in the relatively dilute Flamingo Nursery spring, whereas *Stauroneis* sp. af. *wislouchii* is only dominant in the most dissolved (and probably also most saline) samples from the more concentrated Bird Rocks and in the sample furthest from the spring at Flamingo Nursery (NFe).

Sub-zone 2A shows a return of the conditions that supported the diatom assemblages of 2C with *Anomoeoneis sphaerophora* once again becoming the dominant taxon. However, *Navicula jakhalsensis* the second most common element in 2C, is replaced by *Stauroneis* sp. af. *wislouchii* as the most important taxon behind *Anomoeoneis sphaerophora*. Both of these are relatively robust and this may facilitated their preservation and hence have contributed to their dominance of sub-zone 2A.

Finally, in zone 1 *Stauroneis* sp. af. *wislouchii* becomes overwhelmingly the dominant taxa, as it has in the samples from Bird Rock furthest from the springs. Again this may reflect differential dissolution, which could have substantially modified the fossil assemblages. Species such as *Navicula jakhalsensis* would be poorly

preserved under such conditions, and the dissolution of samples such as those from sub-zone 2B could produce the taphocoenoses found in zone 1. Support for this hypothesis is given by the abundant analcime crystals found within these samples, which signifies silica diagenesis.

Therefore, the small spatial changes in the habitat characteristics of the Magadi springs can be seen reflected over time in the recent changes in the diatom assemblages at the Northern Lagoon spring. To what extent do these result from changes in the environment and what is the role of dissolution? In several respects these would operate in the same direction since either differential dissolution or a rise in salinity could produce a change from *Navicula jakhalsensis* and *Nitzschia* "group latens" to *Anomoeoneis sphaerophora* and *Stauroneis* sp. af. *wislouchii*. However, the state of frustule preservation and the presence of zeolites suggests the greatest alteration has occurred amongst the samples of zone 1, whilst elsewhere environmental changes have been more important.

No radiometric dates are available for core NL1 and so it is impossible to put any palaeoenvironmental changes in a temporal context. All of the diatom communities reflect a shallow hot spring environment and no major lacustrine phase is represented. However, the variation in the diatom assemblages would seem to represent the changing discharge of the Northern lagoon spring. The environmental progression is one of increasing salinity/dissolution (assuming no post-depositional dissolution, from zone 3 through to sub-zone 2C. The trend may have been reversed briefly in sub-zone 2B, but then once again became increasingly concentrated in sub-zone 2A and zone 1 eventually leading to frustule dissolution.

B: Lake Manyara

Diatom taphonomy at Manyara.

The sporadic preservation of diatom frustules encountered by Holdship (1976) and also in core MANE-87 has been a major hindrance to palaeoenvironmental reconstruction at Manyara. The experimental studies of chapter 5 allow the prediction of those assemblages most likely to have suffered from dissolution, and the major sources of evidence for this have been summarized in table 6.1. The most extreme consequence of dissolution is when the entire diatom assemblage is dissolved, as appears to have occurred in the lower 7m of the MANE-87 core. More insidious than

this is the modification of assemblages by differential dissolution which can substantially alter the reconstruction reached. Therefore, identifying samples in which differential dissolution may have determined the diatom assemblage composition is important if errors are to be avoided.

The most direct evidence for dissolution is given by the state of valve preservation. In order to assess this quantitatively it is necessary to to select a single species, since different species dissolve at various rates and in different ways. For MANE-87 *Cyclotella meneghiniana* provides a useful indicator of dissolution. Firstly it is present in abundance throughout the core, secondly the experiments have shown that dissolution proceeds in a predictable manner with the marginal areolae being lost first, and thirdly the surviving parts of the valves remain identifiable even after protracted dissolution. The "dissolution index" (DI) of figure 6.5 shows the percentage of *Cyclotella meneghiniana* valves that are without areolae for each sample where this species was sufficiently abundant (*i.e.* more than 100 valves counted). This excludes 6 samples at 3cm, 210cm, 261cm, 528cm, 538cm, and 547cm.

However, the results of DE1-4 also suggest that the loss of the marginal areolae in *Cyclotella meneghiniana* may be a relatively late stage in the dissolution process and several species could have disappeared entirely before this occurs. Therefore, this is only a coarse measure of sample dissolution and it may underestimate the degree of alteration that has modified the fossil assemblages.

Alternatively, dissolution can be identified by reference to the preservation potential of individual taxa within an assemblage as identified in the dissolution experiments which are listed in table 6.3. Those samples in which species from the "high" category of preservation potential are common and few from the "low" category occur may be suspected of differential dissolution. Species composition is not a direct indicator, and ecological factors are more often responsible for this than taphonomy. Nevertheless, if supported by other evidence it can provide a useful indicator.

TABLE 6.3. Preservation potential for selected diatom taxa found in MANE-87.

Low	Intermediate	High
Achnanthes spp.	*Rhopalodia gibberula*	*Aulacoseira* spp.
Fragilaria spp.	*Thalassiosira rudolfi*	*Anomoeoneis sphaerophora*
Nitzschia "group latens"	*Stephanodiscus minutus*	*Cyclotella meneghiniana*
Nitzschia paleacea		*Thalassiosira faurii*
Nitzschia sp. af. *fonticola*		*Campylodiscus clypeus*
		Surirella ovalis

Using both direct evidence from the state of frustule preservation, and indirect indication from the assemblage composition, it is possible to suggest which zones from MANE-87 are most likely to contain samples that have been partially dissolved. Sub-zone 5C positioned immediately above the sterile section might be anticipated to be a likely candidate for differential dissolution. It is rich in diagenetic silicate minerals suggesting the dissolution and re-precipitation of amorphous silica (of which biogenic silica is a part). However, the species composition indicates otherwise, since *Nitzschia* sp. af. *fonticola* is abundant in this zone, and it has low preservation potential. Furthermore, the DI is not particularly high suggesting that dissolution has not advanced as far as might have been expected given the stratigraphical position of sub-zone 5C.

Evidence for differential dissolution in sub-zone 5B is ambiguous. Zeolites are common, valve abundance is low and the assemblage is almost monospecific, factors typically associated with dissolution. It is dominated by the robust *Cyclotella meneghiniana* (>87%) which was consistently well preserved in the dissolution experiments. However, the proportion of dissolved *Cyclotella meneghiniana* is very variable between samples. In the lowest level of this sub-zone (604cm) nearly 90% of *Cyclotella meneghiniana* have lost their areolae (*i.e.* the DI is high), whereas in the samples above this the DI declines markedly. Interpretation of this sub-zone might therefore anticipate that the diatom death assemblage was less dominated by this species than appears from the taphocoenoses. Other less well preserved species common in the neighbouring sub-zones 5A and 5C, such as *Nitzschia* sp. af. *fonticola* and *Thalassiosira rudolfi* may have formerly been more abundant, particularly at 604cm.

For the same reasons advanced for sub-zone 5B, differential dissolution is likely to have modified the diatom assemblages found in sub-zones 5A, 3A, 3B, and

3C. All the samples in these sub-zones are dominated by *Cyclotella meneghiniana*, although 5A and 3B also have significant amounts of *Thalassiosira rudolfi* and *Thalassiosira faurii*. It is likely that the high proportions of these relatively robust species with low surface area : volume ratios are a consequence of dissolution. The dissolution index is high for the majority of samples and very high at certain levels (figure 6.5) lending further support to this assertion.

Zone 2 is another candidate for differential dissolution, despite its high diversity. All the species which are abundant are robust, *e.g. Cyclotella meneghiniana, Campylodiscus clypeus*, and *Rhopalodia gibberula*. The DI is high for each sample of zone 2. Zone 4 is the least likely to have been greatly modified as it is both diverse and has an abundance of species with low propensity for preservation *e.g. Nitzschia* "group latens".

Zone 1 may have been influenced by dissolution but a different taphonomic process been more important in shaping its composition. It contains a diverse range of species with very different ecological requirements. For example, the most abundant species is the freshwater *Stephanodiscus rotula*, but it is joined in the taphocoenoses by hypersaline taxa such as *Nitzschia* "group latens" *Anomoeoneis sphaerophora*, and *Thalassiosira faurii*. This situation is similar to that encountered at Flamingo Nursery where apparently incompatible taxa are found within the same taphocoenoses. Several hypotheses can again be envisaged to explain this unusual conjunction of species, but here additional information is provided by the core studied by Holdship (1976) in which this section of the core is better developed. An examination of Holdship's data shows the presence of these saline species immediately before, and then again after, the rise to dominance of *Stephanodiscus minutus* and *Stephanodiscus rotula*. Therefore, rather than being contemporary but spatially disparate assemblages as was concluded to explain the mixed assemblages at Flamingo Nursery, here it seems that the assemblages were temporally separate, only to be brought together by vertical sedimentary mixing processes and deflation.

Palaeoenvironmental reconstruction of core MANE-87.

Sub-zone 5C, the lowest diatom bearing zone, is dominated by two species, *Nitzschia* sp. af. *fonticola* and *Cyclotella meneghiniana*. The difficulty in finding suitable analogues for *Nitzschia* sp. af. *fonticola* has been discussed above for the Flamingo Nursery core. The same problems are faced at Manyara where a similar morphotype to that from Magadi was found, although here the valves were narrower

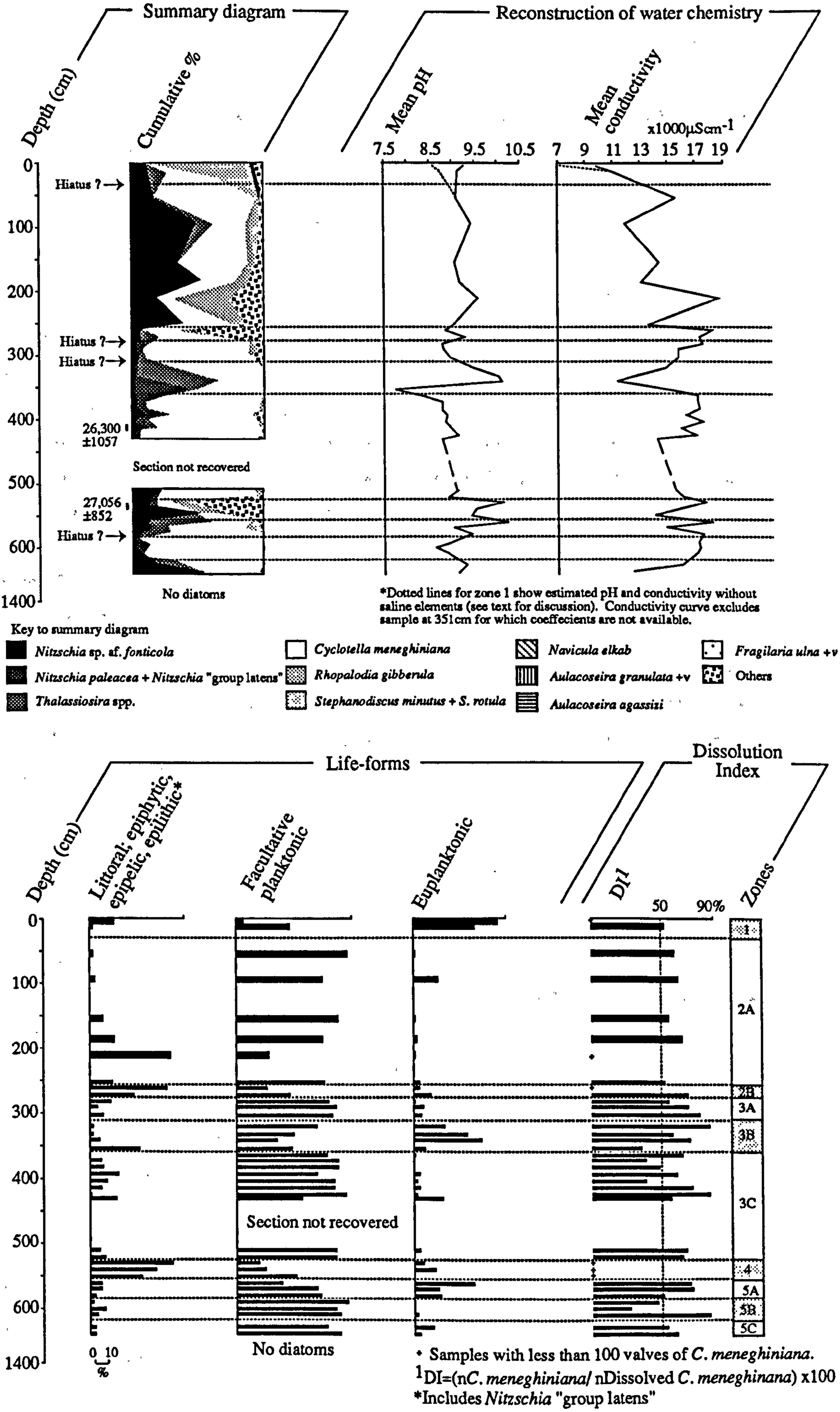


Figure 6.5. Diatom life-forms and palaeoenvironmental reconstruction from core MANE-87, Lake Manyara.

and often had protracted apices. *Cyclotella meneghiniana* was also found at Magadi but not in the abundance in which it occurs at Manyara, where it is present in almost every sample and dominant in most. This species is both alkaliphilous and halophilous, although it has also been found in less concentrated conditions (Tuchman *et al.* 1984, Gasse 1986a). Hecky and Kilham (1973) found it to be the dominant species in the less concentrated East African lakes within their survey (see chapter 2).

Both *Nitzschia* sp. af. *fonticola* and *Cyclotella meneghiniana* are common in the plankton and the periphyton of lakes, but are classified in these samples as facultative planktonic since few littoral competitors are present (figure 6.5). Cholnoky (1968) considers them to be nitrogen heterotrophs and this may suggest an association with nitrogen fixing cyanophytes (Kilham *et al.* 1986). Few littoral species are found in this sub-zone, and a small proportion of the planktonic taxa *Thalassiosira rudolfi* is present. The planktonic or facultative planktonic life-forms of these taxa and the absence of definitive periphytic species suggests relatively deepwater conditions during the formation of this sub-zone.

As is shown by figure 6.5, transfer functions estimate this assemblage to represent waters of moderate-high conductivity (12-16,000μScm^{-1}) and a pH between 9.1-9.4. However, both dominant taxa exhibit considerable flexibility in their modern environmental distribution and so these "mean" conditions could mask considerable variance.

Environmental reconstruction of sub-zone 5B is dependent on the autecology of *Cyclotella meneghiniana* which dominates the assemblage almost entirely. Moreover, this sub-zone has been identified as one in which differential dissolution is suspected and so the values calculated by the transfer functions must be treated with caution. Conductivity may have risen above 17,000μScm^{-1} with pH tentatively estimated between 8.6 and 9.0. If delicate species such as *Nitzschia* sp. af. *fonticola* were once present, then the transfer functions may overestimate the degree of chemical concentration. Even allowing for differential dissolution of some unknown species, the complete absence of littoral species suggests that this was a moderately deep episode, comparable to sub-zone 5C.

A peak in the euplanktonic species *Thalassiosira rudolfi* is found in sub-zone 5A. However, conductivity remains high lying within the range 15-17,000μScm^{-1} and pH between 9 and 10. A small increase in *Stephanodiscus minutus* explains the slight reduction in both pH and conductivity during this zone which may suggest a small and perhaps short-lived dilution of the lake at this time. Magnetic susceptibility is also high

during this zone which would be consistent with a phase of increased run-off eroding minerogenic material, and perhaps initiating a deepening of the lake.

Nitzschia "group latens" dominates zone 4 within a diverse assemblage. The habitat preference of *Nitzschia* "group latens" is unclear as it has been classified as either littoral or facultative planktonic (see the discussion of sub-zone 1B of the Flamingo Nursery core above). Here it is associated with a much more diverse group of species than in Flamingo Nursery, including littoral elements and so it is considered to have been living in the periphyton. Other species within this zone include the euplanktonic *Stephanodiscus minutus*, and the facultative planktonic species *Nitzschia* sp. af. *fonticola* and *Cyclotella meneghiniana*. Conversely *Nitzschia paleacea, Nitzschia frustulum* and *Rhopalodia gibberula* are characteristic littoral taxa, and a small amount of aerophilous species (2%) is also present suggesting very shallow or merely moist conditions close to the coring site. Organic carbon peaks in this zone which could suggest an encroachment of the fringing vegetation, thereby providing suitable habitat conditions for the epiphytic diatoms.

Mean conductivity is estimated as 14-18,000μScm^{-1} (excluding *Nitzschia paleacea* for which there is no coefficient for conductivity in the EADD as it occurs in too few samples) and mean pH is within the range 9.5 and 10 for these samples. However, the species present are indicative of a still wider range of water chemistry, for example *Nitzschia paleacea* and *Stephanodiscus minutus* suggest fresh-oligosaline water, whilst *Nitzschia* "group latens" and *Rhopalodia gibberula* are typically saline alkaliphilous taxa. Therefore, zone 4 probably corresponds to a period when the coring site lay close to the edge of the lake.

A return to conditions similar to those of zone 5 is found in zone 3. Sub-zone 3C is dominated by the facultative planktonic *Cyclotella meneghiniana* but significant amounts of the littoral *Nitzschia paleacea* are also present. Whilst this suggests a generally deeper lake than in zone 4 the lake margin cannot have been far from the coring site on the account of the periphytic *Nitzschia paleacea*, unless this species was occupying a similar niche to the facultative planktonic heterotroph *Nitzschia* sp. af. *fonticola*. Conductivity is estimated to be in the range 14-18,000μScm^{-1} with mean pH between 8.8 and 9.2 except for the sample at the top of this sub-zone in which pH falls to 8.2 due to an increase in *Nitzschia paleacea*.

Sub-zone 3B begins with a continuation of the peak in *Nitzschia paleacea* which results in estimated pH falling to 7.8; the lowest value calculated for this sequence. No estimate of conductivity is possible for this sample (351cm) as this would have to be based on only 57% of the assemblage as a result of the abundance of *Nitzschia paleacea*

which has no coefficient for conductivity. A peak in organic carbon coincides with the high proportion of littoral species at the foot of this zone which might suggest an encroachment of the fringing vegetation close to the coring site as in zone 4. The assemblage then became dominated by *Thalassiosira faurii* which indicates a rapid rise in pH to in excess of 10, however, conductivity is estimated to be relatively low at only 12-15,000μScm^{-1}. This species reaches its greatest abundance in the EADD of 65% in Lake Kirongoro, Uganda in which conductivity is 16,300μScm^{-1}, and pH is 9.3 (Gasse 1986a).

The composition of the diatom samples in sub-zone 3A shows great similarity to those from 3C and 5B, in being dominated almost completely by *Cyclotella meneghiniana.* Again the possibility of differential dissolution is suggested by the preponderance of robust taxa and as a result environmental conditions are difficult to estimate. A similar scenario to that from the other zones dominated entirely by *Cyclotella meneghiniana* can be proposed with transfer functions estimating a mean pH of 8.8 and conductivity of 15,500-17,500μScm^{-1}. However, these values become meaningless if dissolution has substantially altered the assemblage as is suspected.

Species diversity increases in sub-zone 2B with a rise in the proportion of littoral epilithic taxa such as *Campylodiscus clypeus.* This represents a period when shallow water conditions persisted close to the coring site, as in zone 4. However, conditions were more chemically concentrated than in zone 4 with pH rising above 9 and conductivity passing 17,000μScm^{-1}. *Campylodiscus clypeus* is often found in chloride rich waters and it is possible that Manyara became relatively enriched in this anion at this time. A mechanism for this could be the precipitation of salts of carbonate and bicarbonate leaving the more soluble chloride salts in solution as occurs in the final brines at Magadi.

The suggestion of shallow water is also found in the lower section of sub-zone 2A which has significant proportions of the littoral species *Rhopalodia gibberula* and *Campylodiscus clypeus.* These are replaced by facultative planktonic taxa elsewhere in this sub-zone. Conductivity reaches its maximum value anywhere in MANE-87 of almost 19,000μScm^{-1} in the lower part of this zone, but declines greatly to a minimum of 12,000μScm^{-1} in its upper section. In contrast, pH changes only marginally, lying within the range 8.5-9 throughout this sub-zone.

Zone 1 represents the most dilute phase of this core with conductivity falling below 10,000μScm^{-1}. This value would have been even lower had it not been for the presence of small but significant amounts of saline species such as *Thalassiosira faurii*, *Anomoeoneis sphaerophora* and *Nitzschia* "group latens" alongside the freshwater

species that dominate the zone. This suggests some mixing of the assemblages, either during sampling from these augered samples or by the taphonomic processes responsible for bringing together the assemblages as discussed above. The transfer functions were re-calculated excluding the saline elements from the sum. This resulted in a conductivity of 7-11,000μScm^{-1} and a pH of 8.7-8.8, as shown by figure 6.5.

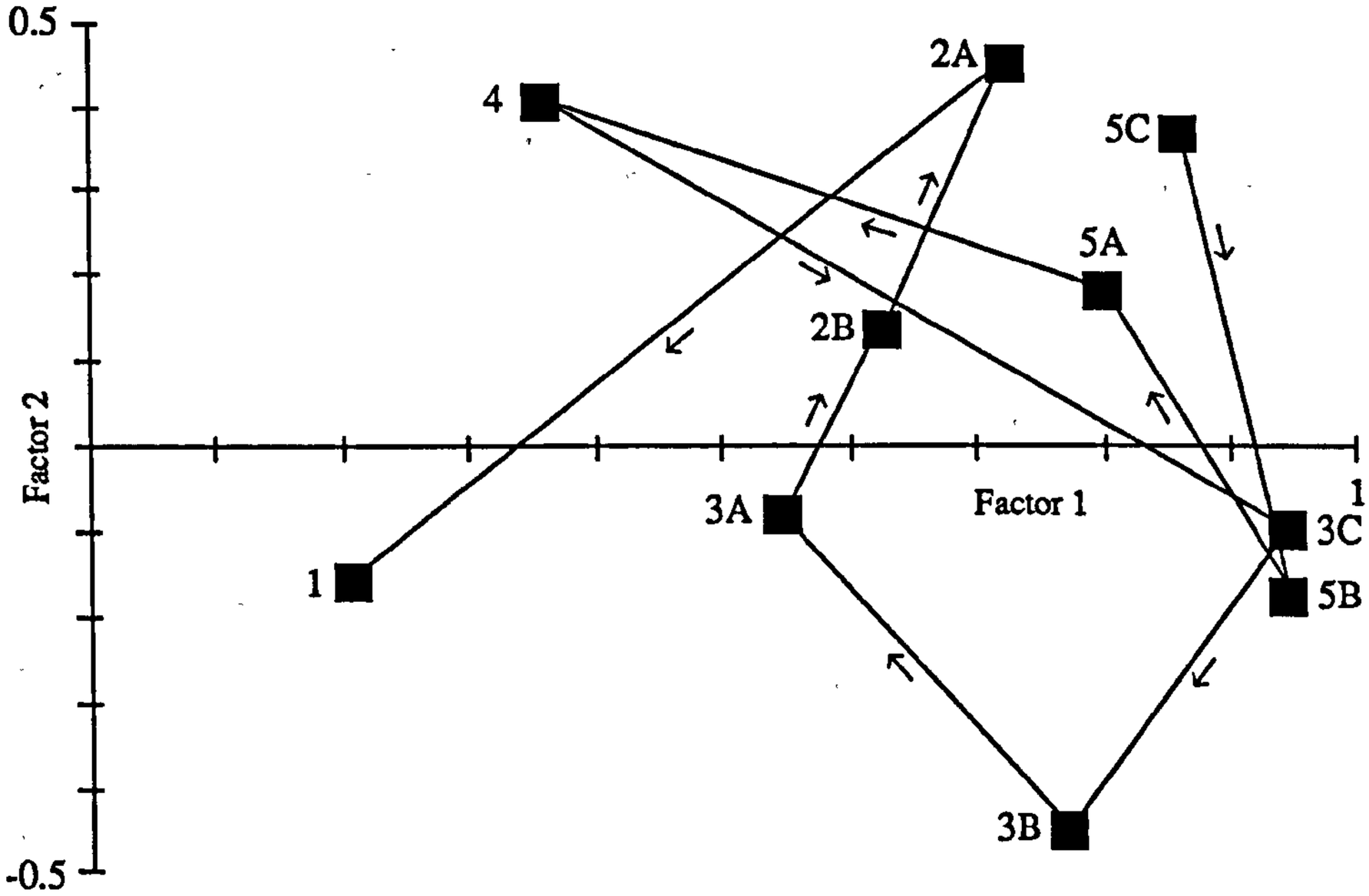
Lake-level fluctuations at Manyara.

Correlation of MANE-87 to the core of Holdship (1976) has allowed several hiatuses in deposition to be identified and the complex chronology of MANE-87 to be more fully understood. The punctuation of the stratigraphy by hiatuses is a consequence of its location at the lake margin and the lake-level falling below this point on numerous occasions during the Late Pleistocene and Holocene. From the opposite perspective, this study aids the interpretation of Holdship's core, and especially of his zone B which is more complete in MANE-87.

A feature of MANE-87 is the pronounced similarity in diatom species composition found amongst zones 2, 3 and 5. This results from the dominance of *Cyclotella meneghiniana* in each of these zones. Figure 6.6 shows the relationship existing between these zones statistically, as defined by their principle components. Factor 1 is *Cyclotella meneghiniana* and factor two is *Nitzschia* sp. af. *fonticola*. The closest similarity is found between sub-zones 3C and 5B where *Cyclotella meneghiniana* is virtually monospecific. A second cluster incorporates 5A, 5B, 2A, and 2B which score highly for both of the principle components.

A consequence of this meta-stable equilibrium situation is that estimated pH and conductivity from these assemblages show little variation for much of the core, and it seems that these zones represent the same palaeoenvironmental situation. However, this apparent similarity might in part be artificially engendered by differential dissolution. Initially diverse and dissimilar assemblages may have become dissolved, leaving only the most robust species such as *Cyclotella meneghiniana* and producing an unfounded correspondence. A combination of these two explanations is probably most likely. Interestingly, pollen analysis of these sections of the MANE-87 core show little variation in the relative abundance of different species through these levels (Vincens pers. comm.), indicating that the terrestrial vegetation was relatively stable even though these samples are separated by several hiatuses.

The recurrent appearance of similar aquatic palaeoenvironments could stem from the asymmetrical morphology of the basin. The western edge is clearly delimited



*Arrows show stratigraphical sequence

Figure 6.6. Ordination of diatom zones from Lake Manyara using PCA scaling.

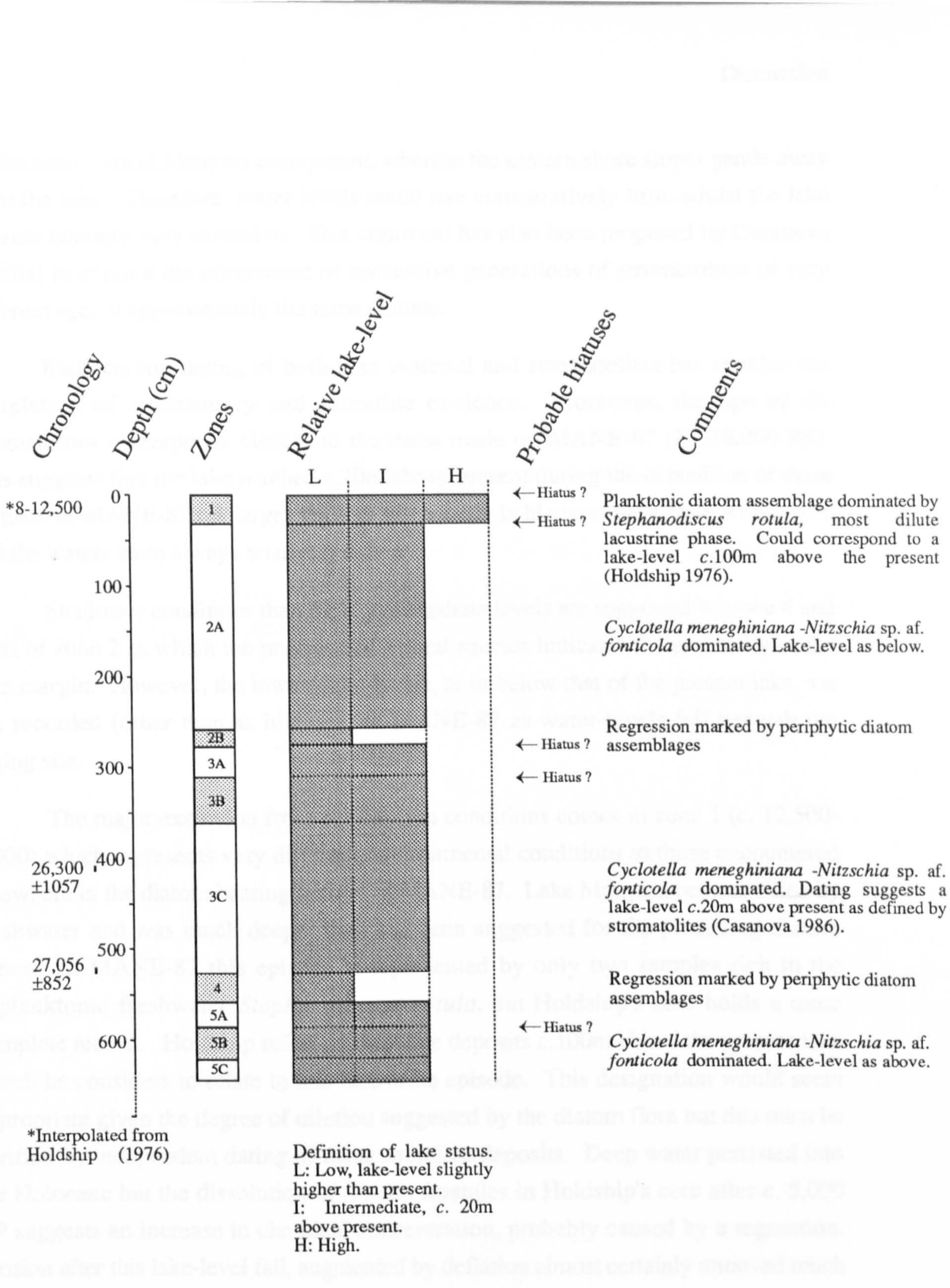


Figure 6.7. Schematic representation of lake-level changes as deduced from diatom analysis of MANE-87.

by the near-vertical Manyara escarpment, whereas the eastern shore slopes gentle away from the lake. Therefore, water levels could rise comparatively little whilst the lake became laterally very extensive. This argument has also been proposed by Casanova (1986a) to explain the occurrence of successive generations of stromatolites of very different ages at approximately the same altitude.

Radiocarbon dating of both core material and stromatolites has enabled the correlation of sedimentary and shoreline evidence. Moreover, the age of the stromatolites corresponds closely to the dates made on MANE-87 (27-26,000 BP). This suggests that the lake reached *c*.20m above present during the deposition of these sections of MANE-87. A large, shallow water body is likely to have been well mixed and the waters were always relatively saline.

Shallower conditions than these intermediate levels are suggested by zone 4 and parts of zone 2 in which the presence of littoral species indicates the proximity of the lake margin. However, the lowest lake-levels, at or below that of the present lake, are not recorded (other than as hiatuses) in MANE-87 as water-levels fell beneath the coring site.

The major excursion from equilibrium conditions comes in zone 1 (c. 12,500-8,000) which represents very different environmental conditions to those encountered elsewhere in the diatom bearing section of MANE-87. Lake Manyara became filled by freshwater and was much deeper than has been suggested for the preceding diatom zones. In MANE-87 this episode is represented by only two samples rich in the euplanktonic freshwater *Stephanodiscus rotula*, but Holdship's core holds a more complete record. Holdship refers to shoreline deposits *c*.100m above the present lake which he considers to relate to this lacustrine episode. This designation would seem appropriate given the degree of dilution suggested by the diatom flora but this must be verified by independent dating of these shoreline deposits. Deep water persisted into the Holocene but the dissolution of diatom frustules in Holdship's core after *c*. 5,000 BP suggests an increase in chemical concentration, probably caused by a regression. Erosion after this lake-level fall, augmented by deflation almost certainly removed much of the Holocene material at the MANE-87 site.

Conclusion.

Diatom analysis of the three cores from Magadi and one from Manyara has facilitated the reconstruction of palaeoenvironmental change during the Late Pleistocene and Early Holocene. A recurring problem has been the separation of taphonomic and

sedimentological change from ecological factors explaining the composition of the diatom assemblages. The relative importance of these factors in shaping the composition of the diatom assemblages from the three cores studied is considered in the final chapter.

The palaeolimnological evidence from the principal cores NF1 and MANE-87 falls upon two periods. The Manyara sequence demonstrates most completely limnological changes between 30,000 and 20,000 BP, whereas the last 20,000 is less well marked and indeed the majority of the Holocene is absent. At Magadi chronology is difficult to resolve prior to 12,700 BP, although the U/Th dates do suggest correspondences with the MANE-87 core. Therefore, the clearest part of NF1 is the Late Pleistocene -Holocene transition *c.* 12,700-9,500 BP which is well dated and contains evidence of abrupt environmental change. The concluding chapter will focus on the significance of these palaeolimnological events to regional palaeoclimate.

CHAPTER SEVEN: CONCLUSION

Two aims were specified in the introduction. The first of these was methodological and concerned the role of taphonomy in diatom-based palaeoecological studies from saline lakes. Dissolving diatomaceous sediments from Magadi and Manyara has helped to interpret the poorly preserved assemblages found in several sections of the cores. Moreover, the experiments have enabled some more general conclusions regarding the differential dissolution of diatom frustules, the recognition of dissolution, and the influence dissolution can have on palaeoenvironmental reconstruction to be made. Another distortion to palaeoenvironmental reconstructions arises from the spatial and vertical mixing of assemblages within sediments. Multiple working hypotheses were evaluated to explain unusually mixed assemblages found in Magadi. A further problem has been the interpretation of cores which are punctuated by hiatuses. Can these sharp changes in diatom biostratigraphy be distinguished from the effects of abrupt environmental change?

The second aim was to reconstruct the palaeolimnology of these lakes from the record of fossil diatoms in conjunction with results of the other investigations of the EQUARIFT programme. Schematic models of lake-level change for Magadi and Manyara have been proposed in the preceding chapter. The principal cores from each lake show close agreement in the periods they cover. Both have good records for the Late Pleistocene, in particular of the period before 20,000 BP and also of the Pleistocene-Holocene transition (especially so in the case of Magadi). What are the implications of these palaeolimnological records for climatic change in this region during these two critical periods, and to what extent are they a result of local hydrogeological factors?

Methodological considerations.

a) Diatom dissolution.

The dissolution experiments of chapter 5 have in many respects raised as many new issues as they have answered. Silica dissolution in natural waters is poorly understood, although temperature, pH, silica concentration, particle size and shape are all known to be important. Equally important to diatom solubility are those factors

which retard dissolution such as organic matter and/or inorganic metal ions (*cf.* Lewin 1961). The removal of these agents can have considerable influence on the rate of silica solution. This has been demonstrated by the varying degrees of dissolution evident after different pre-treatments. Strong acids (*e.g.* HCl) provided a greater stimulus to dissolution than oxidizing agents such as H_2O_2. For example sediment which showed little sign of dissolution after 36 hours of exposure to highly saline solution, was dissolved within minutes after acid cleaning. This supports Lewin's conclusion that inorganic materials supercede their inorganic counterparts in controlling the rate of dissolution. However, the mechanism of the dissolution process and its role in silica cycling in the natural context is poorly understood, and it is worthy of further analysis.

The experiments have focussed on the palaeoecological implications of diatom dissolution, specifically upon how dissolution effects different species, to what extent dissolution introduces bias into palaeoenvironmental reconstructions, and how dissolution can be diagnosed in fossil assemblages. Previous work has suggested that the absence of certain diatom species from sediments which are commonly found in living communities is a result of differential dissolution. This hypothesis has rarely been tested except for a few marine species (Mikkelsen 1980, Shemesh *et al.* 1989). In order to interpret the sedimentary records from Magadi and Manyara in which dissolution was suspected, it was necessary to investigate the relative solubility of the range of species encountered.

The experiments have shown conclusively that dissolution proceeds differentially, subtly altering the composition of the assemblage by the selective removal of certain taxa. In the samples dissolved in the experiments of chapter 5 species such as *Cyclotella ocellata, Cymbella microcephala,* and *Nitzschia* sp. af. *fonticola*, were amongst the most easily removed. Moreover, these species are lost in the early stages of dissolution and DE5 showed that when only 10% of the silica from the assemblage had been dissolved many of these species were already absent. Conversely, *Cyclotella meneghiniana, Epithemia sorex, Aulacoseira granulata*, and *Campylodiscus clypeus* became relatively more important as dissolution progressed. Valve morphometry in part explains these patterns of differential dissolution and a weak correlation has been established between the surface area : volume ratio and dissolution propensity. However, other factors including the degree of silicification, the intricacy of the sculpturing, and the ability to recognize a species when highly dissolved are also important considerations.

Dissolution reduces the absolute abundance of valves in samples and can introduce uncertainty into the counting statistics if the sample size has to be reduced to below 350 valves (*cf.* figure 2.2). For certain levels of core NF1 the count had to

reduced to 150 valves because of low diatom abundance in the sediment as a consequence of dissolution and hence the reliability of the reconstructions reached is weakened. The extent that bias can be introduced into quantitative palaeoenvironmental reconstruction by differential changes has also been investigated in chapter 5. Dissolution of mixed *Cyclotella meneghiniana* - *Nitzschia* sp. af. *fonticola* samples from Manyara produced a virtually monospecific *Cyclotella meneghiniana* assemblage. The result was to increase the diatom estimated pH by 0.5 pH units. A similar experiment from Magadi reduced a sample containing over 60 species to one with less than 40. Diatom estimated pH showed an erratic response, first rising by 0.5 units with less than 10% of the total silica dissolved, and then declining back to the initial level when 65% of the silica had dissolved. Therefore, the general direction of dissolution-induced change in a particular environmental variable is unpredictable and is entirely dependent upon the assemblage composition. The estimate of pH or conductivity becomes skewed toward the optimum levels in the calibration data-set favoured by the most robust species.

The correct identification of dissolution in a fossil diatom assemblage is essential in any attempt to account for its influence in palaeoenvironmental reconstruction. All the experiments resulted in the progressive loss of species and consequently a reduction in diversity. It could be inferred from this that low diversity assemblages are often a product of dissolution, but as the diatom record from Flamingo Nursery has demonstrated this can also be attributed to ecological rather than taphonomic change. Diatom concentration was also greatly reduced as dissolution progressed but again this cannot be positively attributed to dissolution. A more useful indication is the type of species remaining in the assemblage. If the diatom flora is dominated by a few robust species then dissolution must be suspected.

The most direct means of recognizing dissolution is from the condition of the diatom frustules themselves. The experiments have allowed the progressive dissolution of particular species to be followed. *Cyclotella meneghiniana* decays by first losing its marginal areolae, leaving behind only the ribs, until finally just a featureless disc of silica remains. *Anomoeoneis sphaerophora* is reduced to only its central area and raphe as it becomes increasingly dissolved. Elongate spicular taxa such as certain *Nitzschia* spp. are especially prone to dissolution and this begins first with the apices. This selective dissolution of parts of the diatom frustule can lead to taxa becoming unidentifiable at different points in the progression, and it creates fragments which have to be accommodated in the counting strategy to avoid bias.

Dissolved biogenic silica can be re-precipitated in mineral form and the presence of certain minerals in sediments can be diagnostic of dissolution. At Magadi zeolites

(erionite, analcime) are common in deposits from which diatoms are absent and a diatom precursor may be suspected. The presence of magadiite in the cores may signal the dissolution of diatom silica as suggested at lake Chad by Maglione (1970), especially in the lower section of the Flamingo Nursery core where the assemblages are dominated by robust diatom species which show signs of poor preservation. Magadiite is also common in the upper section of the Flamingo Nursery core associated with the delicate and easily soluble *Nitzschia* sp. af. *fonticola*, which might intimate that biogenic silica has not been a major contribution to the formation of this mineral in this section.

The experiments DE1-5 have highlighted many of the problems that need to be addressed if the dissolution of diatom frustules is to be thoroughly understood. Several refinements could be made to these experiments and some suggestions for further work made.

-Tentative relationships between valve volume/surface area and dissolution potential have been identified. For the strength of this relationship to be adequately measured the range of species investigated needs to be increased and the morphometric measurements made with greater precision. The estimates of volume and surface area used here were rather imprecise, being based on light microscopy and an approximation to the nearest geometric shape. The accuracy of these measurements could be greatly improved by using the thin-section approach of Sicko-Goad *et al.* (1983) made via electron microscopy.

-A more complete measurement of a species dissolution potential requires the quantification of more enigmatic factors such as the degree of frustule sculpturing and silicification.

-Errors could have arisen from the sediments used, which were already at the tail-end of the dissolution process. Whilst these sediments were appropriate for understanding the role of dissolution at Magadi and Manyara, for experiments designed only to test for dissolution modern sediments or cultured material should be used.

-The behaviour of diatom silica has only been examined here in sodium carbonate solutions. This may not be representative of other limnologically important salts such as sodium chloride and magnesium carbonate and further investigation of these is required. Moreover, the concentration of the salt used here was held constant and solubility at different concentrations could be tested.

-The process of dissolution requires much greater attention. An examination of the ultrastructure of diatom frustules by electron microscope and microprobe analysis may be illuminating in this respect, especially if the presence of metal cations can be confirmed. This may help explain the resistance to dissolution of species such as *Nitzschia subrostrata* whose size and shape would suggest otherwise.

b) The nature of the diatom records.

A recent debate amongst Quaternary scientists has concerned the non-linear response of the climate system to astronomical forcing. Strong evidence for a two-stage deglaciation has been found from ocean cores and sea level studies (Jansen *et al.* 1990, Fairbanks 1989), and this may have produced step-wise transitions in terrestrial environmental systems (Street-Perrott and Perrott 1990, Gasse *et al.* 1990). However, abrupt changes in sedimentary records can arise from several sources other than climate change. Some of the problems of identifying abrupt events are demonstrated by the cores examined here.

A feature of the diatom analysis from the three cores (NF1, NL1 and MANE-87) is that each includes long sections where between-sample variation is slight followed by abrupt changes in the diatom stratigraphy. For example, the diatom bearing section of MANE-87 is for the most part dominated by a limited array of taxa comprising *Cyclotella meneghiniana, Nitzschia* spp., and *Thalassiosira* spp.. With the exceptions of zones 1 and 4 where the diatom flora changes markedly, fluctuations amongst the assemblages are small variations in the proportions of these principal taxa. Zone 2 of NF1 extends throughout over 4m of sediment and yet differences amongst the samples are minimal. However, its boundaries with zones 1 and 3 are contrastingly abrupt. Moreover, zone 1 of NF1 is dominated by first *Nitzschia* sp. af. *fonticola* and then *Nitzschia* "group latens"; inter-sample variability is limited although the changes between the sub-zones are abrupt. A similar situation is found in the Northern Lagoon core NL1 with a largely unchanging central section (zone 2) occupying the majority of the 285cm core.

Three explanations for these periods of apparent stability accompanied by abrupt transitions can be proposed. The first is that environmental change was step-wise, being minimal during the periods of little variation in the diatom communities, and then shifting dramatically to another level of equilibrium. Secondly, local hydrogeological and sedimentological factors may be invoked producing periods of

stasis interupted by abrupt transitions as internal thresholds are crossed. Thirdly, the role of taphonomy must be considered. All of these factors are interrelated and have been important in producing the diatom taphocoenoses encountered in the three cores. However, their relative importance has varied between different sections of the cores and this has had to be reconciled in the interpretations reached. The interaction of taphonomy, environmental change, and internal thresholds, in forming the distinctive diatom assemblages will now be considered.

Taphonomy has had a profound influence on the diatom records from the three sites studied, either through differential frustule preservation or from mixing processes which have incorporated fossils of different periods and provenance. The impact of taphonomy in the Magadi and Manyara cores has been to mask changes amongst the diatom assemblages and to reduce variability between samples, thus artificially engineering homogeneity. For example, progressive dissolution of samples which were once more diverse could result in the formation of the same taphocoenose. The diatom sequence from MANE-87 exemplifies the role of dissolution in reducing variability, with the dominance of *Cyclotella meneghiniana* being exaggerated by its ability to resist dissolution. The changes which do occur are relatively minor and could result from either differences in the degree of dissolution, or subtle changes in environment. The Northern Lagoon core from Magadi also demonstrates the difficulty of separating ecological from taphonomic change. The up-core changes in the diatom assemblages could be interpreted as a progressive shift to higher salinity. However, the samples also show a trend to contain increasingly robust taxa at the surface, indicating potential dissolution. Further evidence for dissolution is given by authigenic silicate minerals and poor frustule preservation in the uppermost samples. Either explanation is possible and in fact it is likely both occurred simultaneously since the effect of higher salinity is to exacerbate dissolution assuming other factors constant.

In marked contrast to the relatively small changes or even homogenization caused by taphonomic processes, local hydrogeological factors and changes in the sedimentary regime can create exaggerated changes in the diatom biostratigraphy. Intrinsic thresholds within the system may dampen the limnological response to environmental forcing until a threshold is breached when an abrupt change may be registered by the biota. For example zone 1 of NF1 includes two periods of very different, but apparently stable limnological conditions. Sub-zone 1C contains a diatom flora indicative of oligosaline conditions, whereas 1B indicates a return to higher salinities. The transition between the two is extremely abrupt and an hiatus might potentially be inferred. However, the sediments here are laminated and do not suggest a break in sedimentation. Furthermore, this boundary is bracketed by conformable ^{14}C

dates. This rapid shift from one planktonic diatom assemblage to another is probably a consequence of the local hydrogeological situation switching from one state of equilibrium to another. An explanation for this comes from Magadi's connection during high levels with Lake Natron. When the lake reached its high level 56m above present they held a surficial connection, and importantly Magadi became directly linked with the major Ewaso Ngiro drainage network. The ratio between runoff and groundwater inputs to Magadi would increase and the lake would become less concentrated. However, a regression of more than 26m from this highstand would have caused the lake to fall below the 630m contour and sever links with Natron. The consequence of this would be a rapid increase in salinity as groundwater again dominated the inputs to Magadi and freshwater supplies were diminished. Tectonic disturbance or increased local volcanic activity could also be considered as contributing to this abrupt shift in salinity. The Magadi region is highly tectonically active and this could have a profound effect on the lake hydrochemistry especially if surficial inputs were diverted. No evidence for disturbance of this magnitude is apparent in the Late Pleistocene-Early Holocene deposits at Magadi although minor faulting has been reported. Volcanic activity could also influence water chemistry either directly through ash-falls or from from local changes in climate. The latter explanation is unlikely to result in a lake regression as the effect of atmospheric dust is to supress evaporation. The Magadi sediments are rich in volcanic tuffs and these could have had important effects on the water chemistry. However, no sudden increase in these materials which might have initiated an abrupt change is found at *c.* 11,000 BP.

Another important local factor controlling the composition of diatom samples and the preservation of frustules is groundwater. At Magadi this acts to maintain a steady state over a long time-scale and allows quasi-continuous sedimentation in the vicinity of the springs. In preserving relatively constant habitat conditions, groundwater may prevent minor changes in environment being recorded by the diatom communities. This could help explain the limited changes found in the Northern lagoon diatom assemblages. However, groundwater has also served to maintain a chemical environment at Flamingo Nursery and the Northern lagoon conducive to the preservation of diatom frustules. Without the silica-laden, relatively dilute spring discharge, the lagoons would soon concentrate, thereby rendering biogenic silica soluble. Groundwater has had less of a moderating influence at Manyara and here low water levels are recorded by periods of diatom dissolution as found by Holdship (1976).

Elsewhere in the cores equally sharp transitions are shown by the diatom assemblages but these may be due to changes in sedimentation rather than abrupt

changes in lake-level. MANE-87 is punctuated by abrupt changes in the diatom record which probably reflect changing centres of deposition rather than abrupt environmental change. In this core the transition from intermediate to low water levels is recorded by a step-wise shift in the diatom assemblages, as the lake fell below the coring site and a hiatus occurred. Without reference to the more continuous sequence of Holdship (1976) these transitions might have been misinterpreted as abrupt changes in environment rather than sedimentation. The Flamingo Nursery core also contains evidence of hiatuses at several levels, which produce sharp changes amongst successive diatom samples. An example is the zone 2/ sub-zone 1C transition. Not only are the diatom assemblages of zone 2 truncated, but critically the sedimentology shows a change at the same point as the diatoms and a sandy horizon is present.

However, evidence for abrupt environmental change can also be derived from sub-zone 1C of core NF1. The lake became oligosaline-fresh with little evidence of a transitive phase. Although preceded by an hiatus which may have eroded the climax of zone 2, it is likely that the onset of this transgressional episode would be preserved within the sediments.

The collusion of taphonomic, environmental and internal thresholds has helped to produce the distinctive diatom taphocoenoses found in NL1, NF1 and MANE-87. A steady-state is maintained by the effects of strong groundwater flows and artificially engineered by mixing and dissolution processes. Changes in sediment distribution cause an abrupt shift in the diatom record as does the crossing of a geomorphological threshold. Distinguishing between the two requires an understanding of the local sedimentary and hydrological context. However, at *c.* 12,700 BP lake Magadi registered a sudden rise which can be less ambiguously assigned to an abrupt shift in the regional climatic situation.

Palaeoclimatic implication of the lake-level records from Magadi and Manyara.

a) 30,000-20,000 BP

A convergence of palaeoenvironmental evidence for the last 20,000 years has revealed the salient shifts in African climate (Street-Perrott and Roberts 1983). Much less is known of the period between 30,000 and 20,000 BP owing to the relative paucity of records and the difficulties associated with establishing chronologies for this

period (Perrott and Street-Perrott 1981). Desiccation and deflation during the Late Pleistocene arid phase were probably responsible for removing much of the older sedimentary evidence. Furthermore radiocarbon dating, which underpins the chronostratigraphy established for the last 20,000 years, becomes an increasingly unreliable method for dating older sediments. This problem has been exemplified in the recent reassessment of lake sediments from North Africa which were originally thought to be in the order of 20,000-40,000 BP by the ^{14}C method, but the U/Th method has produced ages in excess of 90,000 BP (Causse *et al.* 1988).

Chronological difficulties are greatly diminished if continuous sequences are found and the core of Holdship (1976) from Manyara represents one of the most complete records extending before 20,000 BP yet found in Africa. The ^{14}C chronology of this core is also relatively secure as re-evaluation by U/Th has shown generally good agreement with the original ages, except for a section dated to *c.* 16,000 by ^{14}C which U/Th suggests is several thousand years older (Goetz 1990). Moreover, this broad concurrence between the two methods lends credence to the validity of the radiocarbon dates from MANE-87, and the estimated ages suggested by biostratigraphical correlation between the diatom assemblages. The Flamingo Nursery core from Magadi has revealed a considerable discrepancy between the U/Th and ^{14}C chronologies. The age of the lowest diatom bearing section (zone 3) was established at 17-18,000 BP by ^{14}C, whereas the U/Th method estimates a much older age of 30,000-50,000 BP. U/Th has also provided an age for the intermediate diatom zone from NF1 (zone 2) of 24,000 ± 2,000. Assuming the U/Th age of diatom zone 2 is reliable comparisons may be drawn between the hydrological status of the two lakes at this time.

The palaeoenvironmental record from Manyara is particularly rich for the period 20,000-30,000 BP. Shoreline data is provided by stromatolites 20m above the present lake which have ^{14}C ages between 23,000 and 27,000 BP, with a modal frequency of dates at *c.* 25,500 BP (Casanova 1986). These ages compare favourably with those interpolated by Holdship (1976) for diatom zone B (26,500-27,000). MANE-87 contains a more complete representation of this episode including sub-zones 5A to 3B. The correlation has been established biostratigraphically and radiometrically with ^{14}C dates placing this section between *c.* 27,500 and 26,000. The diatom assemblages are comprised principally of *Cyclotella meneghiniana, Thalassiosira* spp., and *Nitzschia* spp. These are largely planktonic or facultative planktonic species, and indicate moderate to high chemical concentrations. For example conductivity is estimated in the range 12-18,000µS and pH 8.8-10. The most saline conditions are found within diatom zone 4 which is dominated by *Nitzschia* "group latens". This zone suggests a

minor regressional phase at *c.* 27,000 BP. Therefore, both shoreline and sedimentary evidence points to the existence of a lake intermediate between the highly concentrated shallow water body of today and the dilute, possibly overflowing lake of the Late Pleistocene-Early Holocene. However, at least one regression is suggested, and others marked by hiatuses in the MANE-87 core are also possible.

Diatom evidence from Magadi (core NF1) is ambiguous for this period due to the operation of taphonomic processes. Whilst several competing hypotheses are possible to explain the formation of the diatom assemblages as discussed in the preceding chapter, the one adopted as most likely suggests a relatively shallow saline lake into which freshwater discharged. A freshwater "river" group of diatoms has been distinguished from a saline "lake" group. The latter includes several planktonic forms suggesting a lake intermediate between that of today and the late Pleistocene high lacustrine phase. Furthermore, if freshwater inputs from surface flows to the Flamingo Nursery site were initiated, then this would tend to suggest the general raising of the water-table.

Lakes elsewhere in the region also register this event. Between Magadi and Manyara is Ngorogoro crater which contains a soda lake also known as Magadi or Magad. Hay (1976) has obtained two ^{14}C dates from ostracod rich deposits of 27,900 and 24,400 indicating a lake transgression at this point. Although based on carbonates which tend not to be as reliable as ^{14}C dates on organic matter, this corresponds well to the intermediate lacustrine phases present in Magadi and Manyara. North of Magadi is lake Nakuru which may again have risen at this period as determined by ostracod palaeoecological evidence. However, the diatom record of the same core is at odds with this interpretation (Richardson and Dussinger 1986). Nevertheless, the convergence of evidence from these hydrologically disparate sites would seem to suggest a positive shift in the regional P:E ratio causing the rise of lake-levels.

The status of this event is critically dependent upon the strength of the dating from each site. Inevitably the radiocarbon ages have large error margins upon them and this severely limits the precision with which correlations can be made. Moreover, these chronologies need to be re-affirmed independently by other methods such as U/Th which appear to overcome many of the errors associated with ^{14}C. However, these data indicate a marked limnological transgression beginning in the equatorial lakes after *c.*27,500 and lasting until perhaps *c.*22,000. Whilst this was greatly inferior to the Late Pleistocene -Early Holocene rise in lake levels many lakes achieved at least intermediate levels. The onset of lake-level rise was therefore slightly earlier than that of *c.*25,000 proposed by Perrott and Street-Perrott (1981).

b) 12,700-9,000

In common with the majority of African lakes, Magadi and Manyara experienced their maximum levels during this period. However, when the detail of this event is studied differences in the timing and the geographical extent of lake-level fluctuations during this period become evident. The pattern becomes even more complex when local hydrological factors are considered. Many lakes were overflowing and so regressions are unlikely to produce changes in lake-level indicators unless they were to fall beneath their sill and salinity began to rise. The response time of other lakes is such that events on the scale of 10^2-10^3 may not be recorded.

Important abrupt shifts are found in the diatom record from Magadi (core NF1) and these may offer a useful insight into the fine structure of this period. The timing of these major events in the diatom record from Flamingo Nursery are summarized in table 7.1. The dates are extrapolated from the two AMS radiocarbon dates of 12,080 ±357 and 10,800 ± 120 from 115cm and 225cm respectively. The assumption is made that the rate of sedimentation between these two dates is equivalent to that of the remainder of this section. Current work on the laminations from this part of the core will enable a more precise chronology to be established (Damnati pers. comm.). The equivalent period in MANE-87 is represented by only the uppermost two samples but a more substantial representation is given by the core of Holdship (1976). Unfortunately this section of Holdship's core is poorly dated (no ^{14}C date falls within this period) and the resolution of fine stratigraphical events cannot be adequately achieved.

TABLE 7.1. Chronology of the major changes in diatom assemblages for zone 1 of NF1.

Depth	Transition	Age
3cm	1B/1A	*c.*9,500
115cm	Change in dominant morpho-type of *Nitzschia* "group latens"	*c.*10,800
135cm	1C/1B	*c.*11,000
275cm	2/1C	*c.*12,700

The diatom biostratigraphy suggests a single high-level phase beginning at *c.*12,700 BP followed by an abrupt fall to intermediate levels at *c.*11,000. A transitional phase lasting perhaps 200 years could be logically inferred from the changes within the taxon *Nitzschia* "group latens", although the ecological significance of this change in valve morphology is uncertain. This reconstruction shows only partial agreement with the three phases of high lake-levels proposed by the stromatolite record at 11,500, 10,300, and 9,000 years BP (Hillaire-Marcel and Casanova 1987). The earliest group of dates could coincide with high lake-level suggested by diatom sub-zone 1B and the youngest period represented by the stromatolites may well be missing from the NF1 core. It is more difficult to explain the cluster of dates centred on 10,300 BP. Since the different ages of stromatolites are all at the same altitude it would be necessary to infer that the lake-level was equivalent for both zones 1B and 1C. This is unlikely as the diatom assemblages of zone 1C represent much more dilute conditions than those of 1B and it is difficult to imagine this transition without a fall in lake-level. Errors could have been incorporated into the ^{14}C chronology of either the core or the stromatolites. The stromatolite ^{14}C ages are from carbonate which are generally considered less reliable than those made on organic matter although these have been corrected with reference to the present isotopic equilibria. Dates from the core are made on total organic matter which includes aquatic plant remains that could have acquired an apparent age if the water in which the plants were living was not in equilibrium with the atmosphere, although Hillaire-Marcel and Casanova (1987) consider that equilibrium was achieved by the palaeolake waters. A further explanation for this lack of correspondence with the shoreline evidence is that the time period occupied by zone 1B was shorter than suggested by extrapolation. This would require a considerable expansion of the sedimentation rate from 0.89mm/yr between 12,000 and 10,800 to in excess of 2.2mm/yr if the sub-zone were to terminate prior to 10,300. A series of radiocarbon dates from this section of the core and further examination of the laminae are necessary to test this hypothesis. However, stratigraphical records are considered more reliable than the statistical distribution of ages from isolated samples.

The early high lake-level (12,700-11,000) suggested by the stromatolites and supported by the diatom record of sub-zone 1C indicates a single water body filling both the Magadi and Natron basins. The lake was *c.*50m deep with an area of 1959km^2 and a volume of 83km^3 (Hillaire-Marcel and Casanova 1987). Lakes immediately north and south of Magadi showed also expanded at this time. Lake Nakuru showed a similarly early rise in lake level beginning at *c.*12,800 BP (Richardson and Dussinger 1986), while water levels in lake Manyara began to rise at approximately 12,500 BP (calculated by extrapolation, Holdship 1976) as did Naivasha

(Richardson and Dussinger 1986). Given the errors associated with dating the onset of this transgression and the varying response times of the different lakes this event may be considered virtually simultaneous.

This high level phase was short lived at Magadi and at *c.* 11,000 BP the diatoms indicate a pronounced limnological change with a marked rise in salinity. This is of a magnitude unlikely to have occurred without a fall in lake level although the rise in salinity may have been amplified by the crossing of an intrinsic hydro-geomorphological threshold as outlined above. The cause of this regression could be either tectonic or climatic. The former is given support by the proposed displacement of shorelines to the west of Magadi by the rejuvenation of the Nguruman fault between *c.*11,500 and 9,800 BP (Casanova 1986a). If this diverted the Ewaso Ngiro system into Natron then water levels in Magadi would fall and salinity increase very rapidly indeed. However, the evidence suggests the movement was much more modest and would have been unlikely to have caused a permanent fall in lake-level at Magadi.

If climate were responsible for this regression at *c.* 11,000 BP then other lakes in the region may be expected to respond similarly if their local hydrogeological situation allows. Little change in the diatom record from Manyara can be deduced at this time but this could be a result of the lake overflowing and salinity would only begin to rise if the lake became closed. Moreover, the dating of this section from Holdship's core is poor. Naivasha was also overflowing during this episode and consequently the diatom assemblages record no fluctuation in salinity. Furthermore, no register of this event is found in records from Victoria or from Tanganyika. However, these great lakes would be unlikely to respond sharply to short-lived climatic events.

The lakes most likely to record this event are those of the amplifier type which were not overflowing. A regression is found in lake Nakuru, although this is dated earlier than that at Magadi, from 12,000-11,000 BP. Lake Bogoria supports Magadi more closely and experienced a regression at *c.* 11,000 BP (Tiercelin and Vincens 1987). The chronology at Bogoria is poorly defined and more conclusive evidence comes from the better dated sequence from Ziway-Shala (Gillespie *et al.* 1983). The Ziway-Shala lakes regressed from an intermediate level beginning at *c.* 11,000 BP and culminating at 10,400 BP before the onset of a major transgression at *c.* 10,000 BP. Therefore, the convergence of evidence from geographically diverse sites suggests a climatic explanation for this regressional event although local thresholds probably amplified this event at Magadi.

Street (1980) classified the responsiveness of lakes to climatic shifts according to their hydrological balance. Groundwater fed lakes were thought to be relatively poor

indicators of abrupt changes as they would have a lagged response. Magadi is the archetypal groundwater fed lake having only a negligible contribution from runoff to its water balance at present. However, the results have shown that it rose early relative to many of its neighbours after the Late Pleistocene arid phase at *c.*12,700 BP and registered an abrupt limnological change at *c.* 11,000 BP that probably had regional significance. Two explanations for this rapid rate of response can be suggested. Firstly, much of the groundwater entering Magadi is of shallow origin and from an unconfined aquifer enabling surface flows to be instigated once the water table rose relatively slightly. Secondly, when Magadi rises it becomes directly connected to a very large catchment and will respond more like an amplifier lake until a regression causes direct runoff to decline.

Conclusion.

The Late Pleistocene limnological history at lakes Magadi and Manyara has been been revealed by diatom analysis. This has proved to a sensitive tool in reconstructing palaeoenvironments once the role of taphonomy and the impact of local factors has been established. Problems with taphonomy have resulted in some of the conclusions reached being tentative and further work is necessary to choose between competing hypotheses for the central section of the Flamingo Nursery cores. Diatom dissolution has hindered previous investigations at Manyara but the laboratory experiments conducted here have helped to reinterpret this work and to make the diatom based reconstructions more secure. However, the importance of dissolution in saline lakes demands further investigation if the full quantitative potential of diatom analysis is to be realised.

The palaeoecology of salt lakes offers an important insight into limnological and climatic change. In Africa this has enabled the broad pattern of palaeoclimates since the last global ice-volume maximum to be firmly established. Attention is now being focussed on earlier periods which will offer the chance to test models of long-term climatic change. However, equally important are the abrupt shifts in climate being increasingly recognised from responsive lakes with high resolution records, and it is these which will show how the environment responds to external forcing on a more human time-scale.

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Appendices

Appendix 1: Species list.

Achnanthes brevipes (Kütz.) Cleve.
Achnanthes engelbrechtii Choln.
Achnanthes exigua Grun.
Achnanthes exilis Kütz.
Achnanthes minutissima Kütz.
Amphora coffaeformis Agardh.
Amphora ovalis Kütz.
Amphora pediculus (Kütz.) Hust.
Amphora veneta Kütz.
Anomoeoneis costata (Kütz.) Hust.
Anomoeoneis sphaerophora (Kütz.) Pfitzer.
Aulacoseira agassizii (Öst.) Crawford.
Aulacoseira distans (Ehr.) Crawford.
Aulacoseira granulata (Ehr.) Crawford.
Aulacoseira granulata v. *angustissima* (O.Müller) Crawford.
Caloneis bacillium (Grun.) Mereschkowsky.
Caloneis ventricosa (Ehr.) Meister.
Campylodiscus clypeus Ehr.
Cocconeis placentula Ehr.
Cocconeis thumensis Mayer.
Cyclotella comta (Ehr.) Kütz.
Cyclotella iris Brun and Héribaud.
Cyclotella meneghiniana Kütz.
Cyclotella ocellata Pant.
Cyclotella stelligera Cleve and Grun.
Cymbella affinis Kütz.
Cymbella cistula (Grun.) Hemprich.
Cymbella fonticola Hust.
Cymbella leptoceros (Ehr.) Grun.
Cymbella microcephala Grun.
Cymbella muelleri Hust..
Cymbella perpusilla Cleve
Cymbella ruttneri Hust.
Cymbella tumidula Grun.
Cymbella turgida Greg.
Cymbella ventricosa Agardh.
Diatoma vulgare Bory.
Diploneis elliptica (Kütz.) Cleve
Diploneis ovalis (Hilse) Cleve.
Diploneis subovalis Cleve
Epithemia sorex Kütz.
Epithemia zebra (Ehr.) Kütz.
Eunotia pectinalis (Kütz.) Rab.
Fragilaria brevistriata Grun.
Fragilaria capucina v.*vaucheriae* (Kütz.) L.-B.
Fragilaria construens (Ehr.) Grun.
Fragilaria leptostauron (Ehr.) Hust.
Fragilaria pinnata Ehr.
Fragilaria ulna (Kütz.) L.-B.
Fragilaria ulna v. *acus* (Nitzsch) L.-B.
Gomphonema clevei Fricke
Gomphonema constrictum Ehr.
Gomphonema gracile Ehr.
Gomphonema intricatum Kütz.
Gomphonema lanceolatum Ehr.
Gomphonema parvulum (Kütz.) Ehr.
Hantzschia amphioxys (Ehr.) Grun.
Mastogloia elliptica (Ag.) Cleve
Mastogloia smithii Thwaites
Navicula aberrans Simonsen
Navicula agulhasica Choln.
Navicula cryptocephala Kütz.
Navicula damasii Hust.
Navicula decussis Östrup.
Navicula elephantis Choln.
Navicula elkab O. Müller
Navicula exiguaformis Hust.
Navicula fossalis Krasske.

Navicula gastrum (Ehr.) Kutz.
Navicula gawaniensis Gasse.
Navicula grimmei Krasske.
Navicula halophila (Grun.) Cleve.
Navicula hassiaca Krasske.
Navicula jakhalsensis Van Land.
Navicula minima Grun.
Navicula minisculoides Hust.
Navicula monoculata Hust.
Navicula mutica Kutz.
Navicula platycephala Muller.
Navicula pseudohalophila Choln.
Navicula pupula Kütz.
Navicula radiosa Kütz.
Navicula salinicola Hust.
Navicula tenella Bréb.
Nitzschia amphibia Grun.
Nitzschia denticula Grun.
Nitzschia frustulum (Kütz.) Grun. *sensu* Gasse.
Nitzschia "group latens" including *Nitzschia elliptica* Hust., *Nitzschia estohensis* Choln., *Nitzschia latens* Hust.,*Nitzschia pura* Hust.
Nitzschia hungarica
Nitzschia lancettula O. Müller
Nitzschia palea (Kütz.) W. Smith.
Nitzschia paleacea Grun.
Nitzschia recta Hantzsch.
Nitzschia rostellata Hust.
Nitzschia sigma (Kütz) W. Smith.
Nitzschia sp. af. *fonticola* Grun. *sensu* Gasse.
Nitzschia subrostrata Hust.
Nitzschia thermalis (Ehr.) Averswald.
Pinnularia appendiculata (Ag.) Cleve
Pinnularia borealis Ehr.
Pinnularia microstauron (Ehr.) Cleve.
Rhoicosphena curvata (Kütz.) Grun.
Rhopalodia gibba (Ehr.) O. Müller
Rhopalodia gibberula (Ehr.) O. Müller
Stauroneis phoenicentron (Nitzsch.) Ehr.
Stauroneis salina W.Smith
Stauroneis wislouchii Poret and Anisimowa.
Stephanodiscus minutus Grun.
Stephanodiscus rotula (Kütz) Hendey.
Surirella ovalis Bréb.
Terpsinoë mutica Ehr.
Thalassiosira faurii (Gasse) Hasle.
Thalassiosira rudolfi Bach.

Recent synonyms

Several new genera and combinations have been proposed by Round *et al.* (1990) based on observations made with the scanning electron microscope. The synonyms they propose for the names of the species found in this study are listed below.

Cymbella muelleri Hust. = *Encyonema muelleri* (Hust.) D.G. Mann.

Cymbella perpusilla Cleve = *Encyonema perpusila* (Cleve) D.G. Mann.

Navicula monoculata Hust. = *Fallacia monoculata* (Hust.) D.G. Mann.

Navicula mutica Kütz. = *Luticola mutica* (Kütz) D.G. Mann.

Stauroneis salina W. Smith = *Staurophora salina* (Smith) Mereschkowsky.

Stauroneis wislouchii Poret and Anisimowa. = *Staurophora wislouchii* (Poret and Anisimowa) D.G. Mann.

Abbreviations.

Ag. = Agardh.

Bach. = Bachmann.

Bréb. = Brébisson.

Choln. = Cholnocky.

Ehr. = Ehrenberg.

Grun. = Grunow.

Hust. = Hustedt.

Kütz = Kützing.

L. -B. =Lange-Bertalot.

Öst. = Östrup.

Pant. = Pantocsek.

Rab. = Rabenhorst.

Van Lan. = Van Landingham.

Appendix 2: Diatom Counts.

Diatom counts NF1

Species A-N. c/Depth 0-85cm	0cm	6cm	11cm	20cm	40cm	80cm	85cm
Achnanthes brevipes					1		
Achnanthes engelbrechtii							
Achnanthes exigua			1		1	8	
Achnanthes exilis							
Amphora coffaeformis							
Amphora ovalis							
Amphora veneta							
Anomoeoneis costata							
Anomoeoneis sphaerophora	58	2	1			2	
Aulacoseira granulata	3	1					
Aulacoseira granulata v. angustissima							
Caloneis bacillium							
Caloneis ventricosa							
Campylodiscus clypeus							
Cocconeis placentula		1	1				
Cocconeis thumensis							
Cyclotella comta							
Cyclotella iris							
Cyclotella meneghiniana	1	1					
Cyclotella ocellata							
Cyclotella stelligera							
Cymbella affinis			1				
Cymbella cistula							
Cymbella fonticola							
Cymbella leptoceros							
Cymbella microcephala							
Cymbella muellerii							
Cymbella perpusilla							
Cymbella ruttneri							
Cymbella turgida							
Diploneis elliptica							
Diploneis ovalis							
Epithemia sorex							
Epithemia zebra	1						
Eunotia pectinalis							
Fragilaria brevistriata						1	1
Fragilaria construens							
Fragilaria leptostauron							
Fragilaria pinnata	1						
Fragilaria ulna + v. acus						2	
Gomphonema clevei							
Gomphonema constrictum							
Gomphonema gracile					1		
Gomphonema intricatum							
Gomphonema lanceolatum							
Gomphonema parvulum							
Hantzschia amphioxys	4						
Mastogloia elliptica							
Mastogloia smithii			1				
Navicula agulhasica	16						
Navicula cryptocephala							

Diatom counts NF1

Species A-N. c/Depth 110-160	110cm	120cm	130cm	139cm	145cm	148cm	160cm
A. brevipes							
A. engelbrechtii			1			2	
A. exigua	4			1			
A. exilis		1	2				
A. coffaeformis							
A. ovalis							
A. veneta			1				
A. costata	1						
A. sphaerophora				1		2	1
A. granulata		2		1		2	
A. granulata v. angustissima		2		1			
C. bacillium							
C. ventricosa							
C. clypeus							
C. placentula		1		3		5	2
C. thumensis							
C. comta							
C. iris							
C. meneghiniana				1		1	1
C. ocellata							
C. stelligera	1						
C. affinis							
C. cistula							
C. fonticola							
C. leptoceros							
C. microcephala							
C. muellerii							
C. perpusilla							
C. ruttneri							
C. turgida							
D. elliptica	1						
D. ovalis							
E. sorex							
E. zebra							
E. pectinalis							
F. brevistriata			1			1	1
F. construens							
F. leptostauron							
F. pinnata					1		
F. ulna + v. acus	1	1		1	3	3	1
G. clevei							
G. constrictum						2	
G. gracile							
G. intricatum							
G. lanceolatum							
G. parvulum							
H. amphioxys	2						
M. elliptica							
M. smithii					1		
N. agulhasica							
N. cryptocephala							1

Diatom counts NF1

Species A-N. c/Depth 178-270	178cm	221cm	230cm	242cm	250cm	259cm	270cm
A. brevipes		2					
A. engelbrechtii							
A. exigua							
A. exilis						1	
A. coffaeformis							
A. ovalis							
A. veneta							
A. costata							
A. sphaerophora						1	
A. granulata				2		2	
A. granulata v. angustissima							
C. bacillium							
C. ventricosa							
C. clypeus					1		
C. placentula	1			1			
C. thumensis							
C. comta							
C. iris							
C. meneghiniana				1	1	5	2
C. ocellata							1
C. stelligera							
C. affinis							
C. cistula					1		
C. fonticola							
C. leptoceros							
C. microcephala						1	
C. muellerii							4
C. perpusilla							
C. ruttneri							
C. turgida							
D. elliptica						1	
D. ovalis							
E. sorex					1		2
E. zebra							
E. pectinalis							
F. brevistriata				2	1	3	1
F. construens							
F. leptostauron							
F. pinnata					1		
F. ulna + v. acus		4	2	1	1	4	1
G. clevei							
G. constrictum							
G. gracile	2						
G. intricatum							
G. lanceolatum						2	
G. parvulum							
H. amphioxys				1	3	1	1
M. elliptica							
M. smithii							
N. agulhasica							
N. cryptocephala							

Diatom counts NF1

Species A-N. c/Depth 280-350	280cm	291cm	302cm	309cm	320cm	341cm	350cm
A. brevipes							
A. engelbrechtii			1	2			
A. exigua	3				2	1	2
A. exilis	1	3	4				
A. coffaeformis				1		2	
A. ovalis		4	2				1
A. veneta		2					
A. costata							1
A. sphaerophora	3			2		1	
A. granulata	23	45	36	21	31	35	18
A. granulata v. angustissima	1	13	9	7	10	5	8
C. bacillium	1	1		2	3	3	2
C. ventricosa							
C. clypeus		2	2	3		4	
C. placentula	7	6	4	1	6	10	3
C. thumensis				1			
C. comta	2		2				
C. iris		2				1	
C. meneghiniana	32	48	45	37	63	45	49
C. ocellata	2	5	4	4	10	1	8
C. stelligera		2					2
C. affinis	1	3	7	4	8	4	
C. cistula	1	3	7	1	5	4	3
C. fonticola							
C. leptoceros							
C. microcephala	11	3	4	7	3	3	6
C. muellerii		4					2
C. perpusilla							
C. ruttneri							
C. turgida					1		4
D. elliptica	4	8	4		1	2	1
D. ovalis							
E. sorex	10	23	17	13	10	13	10
E. zebra	6	18	10	8	6	12	9
E. pectinalis		2			2		1
F. brevistriata	15	34	20	22	21	23	18
F. construens	2	6	3	1	3	2	4
F. leptostauron							
F. pinnata	10	3	4	8	4	2	7
F. ulna + v. acus	15	10		9	17	13	20
G. clevei				3	2	6	1
G. constrictum							
G. gracile	6	4	1	1	3		2
G. intricatum		1					
G. lanceolatum	1		2				
G. parvulum							
H. amphioxys	1		4		2	3	2
M. elliptica	2		8	11	2	2	1
M. smithii	10	9	5			2	6
N. agulhasica							
N. cryptocephala							

Diatom counts NF1

Species A-N. c/Depth 391-555	391cm	400cm	450cm	479cm	500cm	540cm	555cm
A. brevipes			1				
A. engelbrechtii							
A. exigua		1	4	2	4		1
A. exilis				1		2	
A. coffaeformis					1	1	1
A. ovalis					1		2
A. veneta		2					
A. costata		1					
A. sphaerophora		1	1	1			1
A. granulata	44	49	27	48	54	26	39
A. granulata v. angustissima	4	8	17	10	13	9	13
C. bacillium			1	1		1	1
C. ventricosa				1			
C. clypeus	1		2	1	1		1
C. placentula	9	7	4	6	2	7	11
C. thumensis				1			
C. comta	1					2	
C. iris				1			
C. meneghiniana	39	31	46	51	39	26	49
C. ocellata	6	20	6	5	8	5	11
C. stelligera	2	2			1		6
C. affinis	3	5	5	3	6	3	7
C. cistula	3			2		1	
C. fonticola							
C. leptoceros							
C. microcephala	4	6	2	2	7	10	6
C. muellerii		1	1		1		1
C. perpusilla							
C. ruttneri							1
C. turgida	3		1	3	2	1	1
D. elliptica	3		2	2	2		3
D. ovalis				2		2	
E. sorex	15	18	10	21	19	20	11
E. zebra	11	15	18	11	8	11	14
E. pectinalis	1						
F. brevistriata	16	17	12	23	18	17	16
F. construens	1	1	7	1		4	1
F. leptostauron					5		
F. pinnata	14	13	8	9	7	6	18
F. ulna + v. acus	10	27	27	11	27	13	30
G. clevei	6		1	4	3	5	4
G. constrictum							
G. gracile	4	1	7		6		
G. intricatum							3
G. lanceolatum	1				2	2	
G. parvulum		2					
H. amphioxys		4	1	1	8	4	5
M. elliptica			1			1	
M. smithii	9	5	6	5	3	14	6
N. agulhasica							
N. cryptocephala						2	

Diatom counts NF1

Species A-N. c/Depth 579-731	579cm	600cm	629cm	650cm	671cm	701cm	731cm
A. brevipes						1	
A. engelbrechtii	1	2	1				
A. exigua		2	1	1	2	7	2
A. exilis	1						
A. coffaeformis			3				
A. ovalis			4	3			
A. veneta							
A. costata						2	
A. sphaerophora		1		2			1
A. granulata	30	27	38	40	33	41	27
A. granulata v. angustissima	18	24	6	8	13	18	8
C. bacillium	2		1			1	1
C. ventricosa							
C. clypeus	1	2		1	1	1	1
C. placentula	10	3	2	7	5	6	8
C. thumensis		2					
C. comta							
C. iris							
C. meneghiniana	32	34	37	36	43	47	16
C. ocellata	6	7	15	9	17	12	3
C. stelligera		2	2		1	2	
C. affinis	9	1	7		2	8	2
C. cistula	3	1	3	2	1		3
C. fonticola							
C. leptoceros				3			
C. microcephala	2	7	1	5	3	3	2
C. muellerii		1					
C. perpusilla				2			
C. ruttneri							
C. turgida				1			
D. elliptica		1	1	2	2	3	
D. ovalis				1			
E. sorex	23	16	13	12	20	6	29
E. zebra	17	5	9	17	17	21	11
E. pectinalis			2				1
F. brevistriata	15	17	19	21	5	20	18
F. construens	1	3	1	2	2	2	
F. leptostauron							
F. pinnata	13	12	8	18	6	6	2
F. ulna + v. acus	9	14	15	18	14	22	19
G. clevei	12		2	8	5	4	4
G. constrictum							
G. gracile							
G. intricatum							
G. lanceolatum							
G. parvulum							
H. amphioxys	7	4	4	5	3	1	3
M. elliptica	2						
M. smithii	7	5	7	4	5	9	5
N. agulhasica							
N. cryptocephala							3

Diatom counts NF1

Species A-N. c/Depth 750-869	750cm	791cm	800cm	820cm	842cm	850cm	861cm	869cm
A. brevipes					1	2	1	
A. engelbrechtii						1		5
A. exigua	3							1
A. exilis								
A. coffaeformis								
A. ovalis								
A. veneta					3			
A. costata		4	16		4		2	1
A. sphaerophora	1	183	223	37	325	40	44	54
A. granulata	31			1	1	1		21
A. granulata v. angustissima	19	1						5
C. bacillium	1	2	1					3
C. ventricosa								
C. clypeus								1
C. placentula	3							2
C. thumensis								
C. comta								
C. iris								
C. meneghiniana	13		1					34
C. ocellata	5	1						2
C. stelligera	4					1		2
C. affinis	4							
C. cistula	5							
C. fonticola		9						
C. leptoceros								
C. microcephala	3							1
C. muellerii								3
C. perpusilla		1						
C. ruttneri								
C. turgida								
D. elliptica	3							
D. ovalis								
E. sorex	13							18
E. zebra	11							1
E. pectinalis	2							
F. brevistriata	11							8
F. construens	3							1
F. leptostauron								
F. pinnata	11							8
F. ulna + v. acus	16							13
G. clevei								
G. constrictum								
G. gracile								
G. intricatum								
G. lanceolatum								
G. parvulum								
H. amphioxys	4	16	17	7	22	14	34	5
M. elliptica				1				
M. smithii	6		2					7
N. agulhasica								
N. cryptocephala								

Diatom counts NF1

Species N. d-Total/Depth 0-85	0cm	6cm	11cm	20cm	40cm	80cm	85cm
Navicula damasii							
Navicula elephantis							
Navicula elkab	5	4	3				
Navicula exiguaformis							
Navicula gastrum							
Navicula gawaniensis	19	2			2	1	
Navicula grimmei							
Navicula halophila	6	1					
Navicula hassiaca							
Navicula jakhalsensis	33						
Navicula minima	3						
Navicula monoculata							
Navicula mutica	3						
Navicula pseudohalophila							
Navicula pupula	3						
Navicula radiosa							
Navicula tenella	18	1		2	4		
Nitzschia 'group latens' (N. elliptica)		51	29		19		3
Nitzschia 'group latens' (N. latens)	86	306	245	469	1358	839	481
Nitzschia 'group latens' (N. pura)		58	208	10	46	60	15
Nitzschia amphibia		1	1				
Nitzschia frustulum	19		3	7	2		4
Nitzschia lancetulla							
Nitzschia palea							
Nitzschia paleacea							
Nitzschia recta							
Nitzschia sp. af. fonticola		49	5	6	45	18	1
Nitzschia subrostrata							
Nitzschia thermalis							
Pinnularia borealis							
Pinnularia microstauron							
Rhoicosphena curvata							
Rhopalodia gibba					1		
Rhopalodia gibberula	27	12	5	8	13	11	2
Stephanodiscus minutus						2	
Surirella ovalis							
Thalassiosira faurii	2						
Thalassiosira rudolfi							
Unidentified	13	10				1	
Total	321	500	504	502	1493	945	507

Diatom counts NF1

Species N. d-Tot/Depth 110-16(	110cm	120cm	130cm	139cm	145cm	148cm	160cm
N. damasii							
N. elephantis							
N. elkab					2		
N. exiguaformis							
N. gastrum							
N. gawaniensis		1					
N. grimmei							
N. halophila							
N. hassiaca							
N. jakhalsensis					1		
N. minima		5			1		
N. monoculata							
N. mutica						3	
N. pseudohalophila							
N. pupula							
N. radiosa							
N. tenella		3			1		
N. 'group latens' (N. elliptica)	5		11		10		
N. 'group latens' (N. latens)	324	12	2		34		
N. 'group latens' (N. pura)	180	455	536	7	3		16
N. amphibia							1
N. frustulum	4	8		12	1	16	
N. lancetulla					1		
N. palea				2			
N. paleacea	13				6	2	
N. recta							
N. sp. af. fonticola	15	2	2	463	654	475	488
N. subrostrata		1		5			
N. thermalis							
P. borealis					1		
P. microstauron							
R. curvata							
R. gibba					1		
R. gibberula	12	12	5	1		2	6
S. minutus		3			1		
S. ovalis							
T. faurii	1						
T. rudolfi	2						
Unidentified		1	1	1	4	3	
Total	566	510	562	500	726	519	518

Diatom counts NF1

Species N. d-Tot/Depth 178-270	178cm	221cm	230cm	242cm	250cm	259cm	270cm
N. damasii							
N. elephantis							
N. elkab					3	1	1
N. exiguaformis							
N. gastrum							
N. gawaniensis					1		
N. grimmei						1	
N. halophila					1		
N. hassiaca							
N. jakhalsensis							
N. minima		1			1		
N. monoculata							
N. mutica			1	2			1
N. pseudohalophila							
N. pupula							
N. radiosa							1
N. tenella			1	1			1
N. 'group latens' (N. elliptica)							
N. 'group latens' (N. latens)	2	6	2		29		
N. 'group latens' (N. pura)	12		1				2
N. amphibia							
N. frustulum			21	8	11	1	2
N. lancetulla							
N. palea		3				3	
N. paleacea		1	2				
N. recta							
N. sp. af. fonticola	487	570	507	477	500	418	479
N. subrostrata				6	167	66	3
N. thermalis							
P. borealis							
P. microstauron		1					
R. curvata							
R. gibba				1			2
R. gibberula	2				3		1
S. minutus			1				
S. ovalis							
T. faurii							1
T. rudolfi		3					
Unidentified	1	1		1		3	3
Total	507	592	538	504	726	514	509

Diatom counts NF1

Species N. d-Tot/Depth 280-350	280cm	291cm	302cm	309cm	320cm	341cm	350cm
N. damasii		3					
N. elephantis							2
N. elkab	35	18	26	38	60	38	27
N. exiguaformis			2				
N. gastrum				1			
N. gawaniensis	3	3			2	1	1
N. grimmei	2						
N. halophila	7			2	1		
N. hassiaca							
N. jakhalsensis		1	3				5
N. minima	1	1	4	1	3	1	5
N. monoculata							
N. mutica	1			5	3	2	
N. pseudohalophila	5	7					
N. pupula	1	1	7		2		
N. radiosa	5	6	5	1	1		
N. tenella	7	6	7	3	3	3	6
N. 'group latens' (N. elliptica)	3	2					
N. 'group latens' (N. latens)	9					2	4
N. 'group latens' (N. pura)	5	2		11	23	9	33
N. amphibia	5	1	7	2	2	4	2
N. frustulum		4	2	9	7	4	3
N. lancetulla	8	1		2	5	1	1
N. palea	2	6	2		8	1	
N. paleacea	8	2		5		3	1
N. recta							
N. sp. af. fonticola	84	30	26	87	183	130	100
N. subrostrata	132	95	144	80	25	24	84
N. thermalis							
P. borealis	3	1	2	2			
P. microstauron		1					
R. curvata							
R. gibba	5	14	12	6	12	10	15
R. gibberula	1	4	12	27	14	21	14
S. minutus	5	6	1	20	4	13	1
S. ovalis				1			
T. faurii	6	9	30	25	20	27	10
T. rudolfi	1	2		1			1
Unidentified	4	10	11	5		7	4
Total	518	500	508	503	593	500	510

Diatom counts NF1

Species N. d-Tot/Depth 391-555	391cm	400cm	450cm	479cm	500cm	540cm	555cm
N. damasii							
N. elephantis						1	
N. elkab	40	37	33	45	33	46	43
N. exiguaformis	1			1			
N. gastrum							
N. gawaniensis		1					
N. grimmei							
N. halophila	3	3					
N. hassiaca							
N. jakhalsensis		5	1		5		
N. minima		2	1		4	2	6
N. monoculata					1		
N. mutica	3			5		6	1
N. pseudohalophila							
N. pupula	2				1	1	
N. radiosa	1			6		3	
N. tenella	2	2	6	3	4	9	1
N. 'group latens' (N. elliptica)							
N. 'group latens' (N. latens)						2	
N. 'group latens' (N. pura)	18	14	8	9	21	11	7
N. amphibia	7	3	1	5	1	4	4
N. frustulum	4	14	9	9	11	14	7
N. lancetulla	3	1	1	1		3	1
N. palea	6	3	5	1			4
N. paleacea		3	2	6	13	6	
N. recta							
N. sp. af. fonticola	41	49	48	68	67	64	58
N. subrostrata	123	113	119	65	70	72	64
N. thermalis							
P. borealis	3	1	1				
P. microstauron							
R. curvata							
R. gibba	14	4	10	9	3	7	16
R. gibberula	13	6	22	19	4	25	12
S. minutus	11	6	7	14	8	12	15
S. ovalis				1			
T. faurii	17	19	24	15	5	18	16
T. rudolfi	1	2	2				2
Unidentified	7	6	4	6	5	5	10
Total	530	531	522	517	504	506	530

Diatom counts NF1

Species N. d-Tot/Depth 579-73	579cm	600cm	629cm	650cm	671cm	701cm	731cm
N. damasii			1				
N. elephantis							
N. elkab	28	26	44	40	36	41	28
N. exiguaformis							
N. gastrum							
N. gawaniensis							
N. grimmei							
N. halophila	1		4		1	1	
N. hassiaca		1					
N. jakhalsensis	2						
N. minima	2	2	1	4	2		5
N. monoculata	2					1	
N. mutica	4	2	7	4	4	2	2
N. pseudohalophila							
N. pupula			4	1		1	
N. radiosa	5	1	3		1	3	1
N. tenella	10	2	6	4	3	1	
N. 'group latens' (N. elliptica)							
N. 'group latens' (N. latens)	5	4	10		25		17
N. 'group latens' (N. pura)	17	19	17	19	31	9	106
N. amphibia	10	1	7	6	15		7
N. frustulum	9	9	11	12	13	6	8
N. lancetulla	1	1	2	3	4		
N. palea						1	
N. paleacea		2					
N. recta						1	
N. sp. af. fonticola	29	49	40	25	44	37	41
N. subrostrata	100	119	79	110	80	83	93
N. thermalis			1				
P. borealis					1	3	1
P. microstauron							
R. curvata				1			
R. gibba	10	7	13	9	5	11	13
R. gibberula	26	20	16	18	19	18	10
S. minutus	6	13	14	11	20	5	12
S. ovalis			1				
T. faurii	18	14	22	14	16	15	21
T. rudolfi		2	3	5	1	6	
Unidentified	4	13	4	6	4	12	4
Total	510	500	512	520	525	500	538

Diatom counts NF1

Species N. d-Tot/Depth 750-869	750cm	791cm	800cm	820cm	842cm	850cm	861cm	869cm
N. damasii								
N. elephantis								
N. elkab	24	2	2		2			27
N. exiguaformis								
N. gastrum								
N. gawaniensis			9		5		1	
N. grimmei								
N. halophila	3	11	5	2	2			5
N. hassiaca								
N. jakhalsensis	3	123				1		1
N. minima	5		8		3		3	15
N. monoculata								
N. mutica	1	19	15	17	13	17	13	3
N. pseudohalophila								
N. pupula				3				
N. radiosa								
N. tenella	7		16	2	6	2	1	22
N. 'group latens' (N. elliptica)			1					
N. 'group latens' (N. latens)	1	26	43	26	15	16	6	14
N. 'group latens' (N. pura)	68	3	31			2	3	23
N. amphibia	1						2	6
N. frustulum	10	13	14	10	34	4	8	8
N. lancetulla								
N. palea								
N. paleacea								
N. recta								
N. sp. af. fonticola	56	12	24	1	1			65
N. subrostrata	79	16	16	5	10		1	59
N. thermalis								
P. borealis	3	2						
P. microstauron								
R. curvata								
R. gibba	4	1						6
R. gibberula	21	49	46	35	50	49	26	34
S. minutus	12							4
S. ovalis								
T. faurii	11		2	2				8
T. rudolfi	5		1			3		
Unidentified	14	6	7	1	4	2	6	6
Total	500	500	500	150	501	155	151	502

Diatom counts NF2 (zone 2/ sub-zone 1C boundary)

Species A-N. a/Depth 275.5-280.5	275.5cm	276.5cm	277.5cm	278.5cm	279.5cm	280.5cm
Achnanthes engelbrechtii						2
Achnanthes exigua				3		1
Achnanthes exilis					2	
Achnanthes minutissima			1	2		
Amphora ovalis				2		5
Anomoeoneis sphaerophora		1			2	
Aulacoseira granulata	2		3	13	22	14
A. granulata v. angustissima			1	11	10	12
Caloneis bacillium					1	
Campylodiscus clypeus				2	2	
Cocconeis placentula	1		3	3	4	2
Cocconeis thumensis				1	1	2
Cyclotella iris			2	1	1	1
Cyclotella meneghiniana	2		12	47	32	68
Cyclotella ocellata			2	5	9	4
Cyclotella stelligera				1	3	
Cymbella affinis				4	7	7
Cymbella cistula				2	1	5
Cymbella microcephala				14	9	11
Cymbella muellerii			3	4	2	1
Diploneis elliptica						1
Epithemia sorex		1	4	30	21	13
Epithemia zebra			1	4	3	1
Eunotia pectinalis				1		
Fragilaria brevistriata			2	16	23	18
Fragilaria construens				3	3	5
Fragilaria leptostauron						2
Fragilaria pinnata				11	9	7
Fragilaria ulna +v. acus		1	3	10	11	8
Fragilaria vaucheriae						3
Gomphonema clevei				1	2	
Gomphonema gracile			7	4	7	10
Gomphonema lanceolatum						5
Gomphonema parvulum						5
Hantzschia amphioxys			3	1	4	2
Mastogloia elliptica			1		1	3
Mastogloia smithii				6	6	8
Navicula decussis					3	
Navicula elephantis	1					
Navicula elkab			1	38	60	73
Navicula gawaniensis			1			
Navicula grimmei				2		
Navicula jakhalsensis			2			
Navicula minima				3	3	1
Navicula mutica	7		5		1	1
Navicula pseudohalophila	1					
Navicula pupula				1		
Navicula radiosa				2		3
Navicula salinicola						
Navicula tenella				3	5	6
Nitzschia 'group latens' (N. latens)		1				
Nitzschia amphibia				6	8	6

Diatom counts NF2 (zone 2/ sub-zone 1C boundary)

Species N.d-Tot/Depth 275.5-280.5	275.5cm	276.5cm	277.5cm	278.5cm	279.5cm	280.5cm
Nitzschia denticula	1			4	2	3
Nitzschia frustulum	5	3	4	31	19	16
Nitzschia hungarica				2		
Nitzschia lancettula	1			5	3	2
Nitzschia palea	9	10	31	2		
Nitzschia paleacea				8	7	6
Nitzschia sigma						8
Nitzschia sp. af. fonticola	457	450	345	67	17	9
Nitzschia subrostrata	19	33	57	119	133	130
Rhopalodia gibba			4	6	7	9
Rhopalodia gibberula	3		4	3	7	3
Stephanodiscus minutus			3	4	6	5
Thalassiosira faurii	3		3	12	16	21
Thalassiosira rudolfi			2	1	3	
Unidentified	3	1	3	8	7	8
Total	515	501	513	529	505	536

Diatom counts NF2 (sub-zone 3A/ zone 2 boundary)

Species A-N. f/Depth 721.5-729.5	721.5cm	723.5cm	725.5cm	727.5cm	729.5cm
Achnanthes engelbrechtii		2			
Achnanthes exigua	2				
Achnanthes exilis		1			
Achnanthes minutissima	3				
Amphora ovalis	5	4			
Amphora pediculus					
Anomoeoneis sphaerophora				1	1
Aulacoseira distans					
Aulacoseira granulata	30	26	1	16	3
Aulacoseira granulata v. angustissima	8	10		7	
Caloneis bacillium		3		1	
Campylodiscus clypeus		1		1	
Cocconeis placentula	11	4	1		
Cyclotella iris	2	1			
Cyclotella meneghiniana	27	27	1	29	3
Cyclotella ocellata	5	3		1	
Cyclotella stelligera	2				
Cymbella affinis	3	1			
Cymbella cistula				1	
Cymbella leptoceros	1	1			
Cymbella microcephala	4	2			
Cymbella muellerii	6	3		3	
Diploneis elliptica	2	1			
Diploneis ovalis	1				
Epithemia sorex	13	19			1
Epithemia zebra	5	8		3	
Eunotia pectinalis				1	
Fragilaria brevistriata	9	3		1	
Fragilaria construens	6	3	1	5	3
Fragilaria pinnata	4	6		3	
Fragilaria ulna +v. acus	6	3		7	1
Gomphonema gracile	5	2			
Gomphonema lanceolatum	2	3			
Gomphonema parvulum	3				
Hantzschia amphioxys	9	3	2	7	2
Mastogloia elliptica					
Mastogloia smithii	4	7			
Navicula elkab	38	31	1	4	3
Navicula fossalis	1				
Navicula jakhalsensis					
Navicula minima	1	2	1	2	
Navicula mutica	7	7		11	16
Navicula pupula					
Navicula radiosa		1			
Navicula salinicola					
Navicula tenella	4	1			1
Nitzschia 'group latens' (N. elliptica)	2			10	3
Nitzschia 'group latens' (N. latens)	18	31	38	59	56
Nitzschia 'group latens' (N. pura)	95	108	426	130	9
Nitzschia amphibia	3	3		3	1
Nitzschia denticula	3	1	2		
Nitzschia frustulum	26	31	28	29	34

Diatom counts NF2 (sub-zone 3A/ zone 2 boundary)

Species A-N. f/Depth 731.5-769.6	731.5cm	736.9cm	744.8cm	750cm	769.6cm
Achnanthes engelbrechtii					
Achnanthes exigua					
Achnanthes exilis					
Achnanthes minutissima					
Amphora ovalis					
Amphora pediculus	1				
Anomoeoneis sphaerophora			6	7	9
Aulacoseira distans				3	
Aulacoseira granulata		8		2	
Aulacoseira granulata v. angustissima					
Caloneis bacillium		1	2		
Campylodiscus clypeus					
Cocconeis placentula	1				
Cyclotella iris					
Cyclotella meneghiniana	20	9	9		
Cyclotella ocellata					
Cyclotella stelligera					
Cymbella affinis					
Cymbella cistula					
Cymbella leptoceros					
Cymbella microcephala					
Cymbella muellerii		2			
Diploneis elliptica					
Diploneis ovalis					
Epithemia sorex	1				
Epithemia zebra	1	5			
Eunotia pectinalis					
Fragilaria brevistriata					
Fragilaria construens		3			
Fragilaria pinnata		1		1	
Fragilaria ulna +v. acus	1				
Gomphonema gracile					
Gomphonema lanceolatum					
Gomphonema parvulum					
Hantzschia amphioxys	2	9	26	32	8
Mastogloia elliptica					
Mastogloia smithii					
Navicula elkab	6			1	1
Navicula fossalis					
Navicula jakhalsensis	4			37	51
Navicula minima					
Navicula mutica	12	13	42	84	9
Navicula pupula	1			1	
Navicula radiosa					
Navicula salinicola			1		
Navicula tenella	1				2
Nitzschia 'group latens' (N. elliptica)	6		3	13	23
Nitzschia 'group latens' (N. latens)	354	215	17	198	24
Nitzschia 'group latens' (N. pura)	55	22		50	3
Nitzschia amphibia		1			1
Nitzschia denticula		2			
Nitzschia frustulum	41	40	20	51	19

Diatom counts NF2 (sub-zone 3A/ zone 2 boundary)

Species A-N. f/Depth 780.3-789.1	780.3cm	789.1cm
Achnanthes engelbrechtii		
Achnanthes exigua		2
Achnanthes exilis		
Achnanthes minutissima		
Amphora ovalis	2	
Amphora pediculus		
Anomoeoneis sphaerophora	86	32
Aulacoseira distans		
Aulacoseira granulata	1	1
Aulacoseira granulata v. angustissima		
Caloneis bacillium		
Campylodiscus clypeus		
Cocconeis placentula	1	
Cyclotella iris		
Cyclotella meneghiniana	2	2
Cyclotella ocellata		
Cyclotella stelligera		1
Cymbella affinis		
Cymbella cistula		
Cymbella leptoceros		
Cymbella microcephala		
Cymbella muellerii		
Diploneis elliptica		
Diploneis ovalis		
Epithemia sorex		
Epithemia zebra		
Eunotia pectinalis		
Fragilaria brevistriata		
Fragilaria construens		
Fragilaria pinnata		
Fragilaria ulna +v. acus		
Gomphonema gracile		
Gomphonema lanceolatum		
Gomphonema parvulum		
Hantzschia amphioxys	9	7
Mastogloia elliptica		
Mastogloia smithii		
Navicula elkab	8	1
Navicula fossalis		
Navicula jakhalsensis	242	58
Navicula minima		
Navicula mutica	12	8
Navicula pupula		
Navicula radiosa		
Navicula salinicola	3	
Navicula tenella	3	
Nitzschia 'group latens' (N. elliptica)	13	6
Nitzschia 'group latens' (N. latens)	10	5
Nitzschia 'group latens' (N. pura)	2	
Nitzschia amphibia		
Nitzschia denticula		
Nitzschia frustulum	38	15

Diatom counts NF2 (sub-zone 3A/ zone 2 boundary)

Species N. h-Total/Depth 721.5-729.5	721.5cm	723.5cm	725.5cm	727.5cm	729.5cm
Nitzschia hungarica		2			
Nitzschia paleacea	13	3			
Nitzschia recta	2				
Nitzschia sigma	1			3	
Nitzschia sp. af. fonticola	20	11	1	4	
Nitzschia subrostrata	90	80		4	2
Pinnularia borealis	1	2			
Rhopalodia gibba	10	19		5	2
Rhopalodia gibberula	16	25	8	20	11
Stauroneis phoenicentron					
Stauroneis sp. af. wislouchii					2
Stephanodiscus minutus		1		5	
Thalassiosira faurii	20	21		3	2
Thalassiosira rudolfi		2		1	1
Unidentified	10	7	2	5	1
Total	559	536	513	385	158

Diatom counts NF2 (sub-zone 3A/ zone 2 boundary)

Species N. h-Total/Depth 731.5-769.6	731.5cm	736.9cm	744.8cm	750cm	769.6cm
Nitzschia hungarica					
Nitzschia paleacea	3	2	2	1	2
Nitzschia recta					
Nitzschia sigma					
Nitzschia sp. af. fonticola	2	18	2	5	4
Nitzschia subrostrata	3	5		3	3
Pinnularia borealis	1			4	
Rhopalodia gibba		3			
Rhopalodia gibberula	18	16	19	7	26
Stauroneis phoenicentron		1			
Stauroneis sp. af. wislouchii			1	1	
Stephanodiscus minutus					
Thalassiosira faurii	1				
Thalassiosira rudolfi	1	3	1		
Unidentified	4	3	2	4	6
Total	540	382	153	505	191

Diatom counts NF2 (sub-zone 3A/ zone 2 boundary)

Species N. h-Total/Depth 780.3-789.1	780.3cm	789.1cm
Nitzschia hungarica		
Nitzschia paleacea	2	
Nitzschia recta		
Nitzschia sigma	2	
Nitzschia sp. af. fonticola	4	2
Nitzschia subrostrata	9	
Pinnularia borealis	2	
Rhopalodia gibba		
Rhopalodia gibberula	30	39
Stauroneis phoenicentron		
Stauroneis sp. af. wislouchii	22	4
Stephanodiscus minutus		
Thalassiosira faurii		1
Thalassiosira rudolfi		
Unidentified	4	1
Total	507	185

Diatom counts NL1

Depth 3.2-138cm	3.2cm	21.5cm	42.2cm	117.5cm	138cm
Achnanthes exigua	1				
Anomoeoneis costata			15		12
Anomoeoneis sphaerophora	106	22	205	106	75
Aulacoseira distans	2	2	4		
Aulacoseira granulata		1		1	1
Cocconeis placentula			4	4	
Cyclotella meneghiniana	14	22	45	31	12
Cyclotella ocellata			1		
Cymbella muellerii	1				
Cymbella tumidula					
Epithemia sorex					
Epithemia zebra				1	
Fragilaria pinnata			1		
Fragilaria ulna +v. acus		1	1		
Gomphonema clevei		2		1	3
Hantzschia amphioxys	7	2	14	10	2
Navicula aberrans	1		2		14
Navicula cryptocephala			2		
Navicula elkab	4	5	3	12	6
Navicula fossalis					
Navicula gawaniensis			9	1	5
Navicula grimmeii					
Navicula halophila	3	8	5	2	4
Navicula jakhalsensis	28	56	53	148	219
Navicula minisculoides					
Navicula mutica	4	9	13	14	3
Navicula platycephala					
Navicula pseudohalophila	6	18		2	6
Navicula pupula				1	
Navicula salinicola	1		6	11	14
Navicula tenella					2
Nitzschia "group latens" (N. elliptica)	3	3	2	2	6
Nitzschia "group latens" (N. estohensis)					
Nitzschia "group latens" (N. latens)				2	5
Nitzschia "group latens" (N. pura)	1				
Nitzschia amphibia		1	3	3	2
Nitzschia frustulum	3	5	8	6	
Nitzschia sp. af. fonticola					1
Pinnularia appendiculata					
Rhopalodia gibberula			1	3	
Stauroneis salina		1		1	
Stauroneis wislouchii	337	380	108	116	122
Stephanodiscus minutus					2
Thalassiosira faurii			1		
Unidentified	8	1	2	6	4
TOTAL	521	538	491	478	504

Diatom counts NL1

Depth 158.8-238.2cm	158.8cm	179.2cm	200.7cm	217.5cm	238.2cm
Achnanthes exigua				2	
Anomoeoneis costata					
Anomoeoneis sphaerophora	130	226	164	120	57
Aulacoseira distans					
Aulacoseira granulata					1
Cocconeis placentula	2		2	1	
Cyclotella meneghiniana	15	12	20	18	17
Cyclotella ocellata					
Cymbella muellerii		2	3	1	
Cymbella tumidula				1	
Epithemia sorex					1
Epithemia zebra					
Fragilaria pinnata					
Fragilaria ulna +v. acus	2				
Gomphonema clevei					
Hantzschia amphioxys	2	5	1	3	1
Navicula aberrans			6	13	10
Navicula cryptocephala					
Navicula elkab	5		15	16	5
Navicula fossalis				1	
Navicula gawaniensis					2
Navicula grimmeii					1
Navicula halophila				1	1
Navicula jakhalsensis	141	117	152	200	269
Navicula minisculoides		3			1
Navicula mutica	7		2	4	2
Navicula platycephala					
Navicula pseudohalophila		1	4	2	1
Navicula pupula				2	
Navicula salinicola	27	52	26	12	6
Navicula tenella					
Nitzschia "group latens" (N. elliptica)	5	2	17	20	19
Nitzschia "group latens" (N. estohensis)				4	
Nitzschia "group latens" (N. latens)	4	3	3	5	19
Nitzschia "group latens" (N. pura)				3	1
Nitzschia amphibia	2	1		1	
Nitzschia frustulum	1	1		1	3
Nitzschia sp. af. fonticola					
Pinnularia appendiculata		1			
Rhopalodia gibberula		1	1		2
Stauroneis salina					
Stauroneis wislouchii	156	79	84	71	79
Stephanodiscus minutus					
Thalassiosira faurii			2		
Unidentified	4	3	2	3	4
TOTAL	499	506	502	500	498

Diatom counts NL1

Depth 257.6-285cm	257.6cm	285cm
Achnanthes exigua		
Anomoeoneis costata		
Anomoeoneis sphaerophora	71	11
Aulacoseira distans		
Aulacoseira granulata		
Cocconeis placentula		
Cyclotella meneghiniana	1	1
Cyclotella ocellata		
Cymbella muellerii		
Cymbella tumidula		
Epithemia sorex		
Epithemia zebra		
Fragilaria pinnata		
Fragilaria ulna +v. acus		
Gomphonema clevei		
Hantzschia amphioxys		4
Navicula aberrans	13	1
Navicula cryptocephala		
Navicula elkab	8	5
Navicula fossalis		
Navicula gawaniensis	47	36
Navicula grimmeii		
Navicula halophila		1
Navicula jakhalsensis	250	228
Navicula minisculoides		
Navicula mutica		1
Navicula platycephala		
Navicula pseudohalophila	5	1
Navicula pupula		
Navicula salinicola	17	13
Navicula tenella		
Nitzschia "group latens" (N. elliptica)		3
Nitzschia "group latens" (N. estohensis)	11	11
Nitzschia "group latens" (N. latens)	10	33
Nitzschia "group latens" (N. pura)		142
Nitzschia amphibia		
Nitzschia frustulum	1	3
Nitzschia sp. af. fonticola		
Pinnularia appendiculata	6	
Rhopalodia gibberula	2	2
Stauroneis salina		
Stauroneis wislouchii	71	11
Stephanodiscus minutus		1
Thalassiosira faurii		
Unidentified		1
TOTAL	513	508

Diatom counts MANE-87

Species/Depth 3-210cm	3cm	13cm	55cm	95cm	155cm	185cm	210cm
Achnanthes engelbrechtii							
Achnanthes exigua							
Anomoeoneis sphaerophora	36		3	5	5	8	43
Aulacoseira agassizii	37	27	1	1	1		
Aulacoseira granulata	5	10		1			
Campylodiscus clypeus		1	1		19	36	60
Cocconeis placentula				1			2
Cyclotella meneghiniana	6	178	405	132	312	143	62
Cymbella muellerii							
Cymbella ventricosa				1			
Fragilaria ulna +v. acus		2				1	
Hantzschia amphioxys					2	1	2
Mastogloia smithii							
Navicula gawaniensis							
Navicula elephantis							
Navicula elkab							
Navicula halophila	8						
Navicula sp. af. tenella							1
Nitzschia "group latens"	50	1					
Nitzschia frustulum	10		1	4		1	3
Nitzschia paleacea		5	1	1	5	4	5
Nitzschia sigma	8						
Nitzschia sp. af. fonticola	29	52	79	240	196	265	79
Nitzschia subrostrata			10				
Pinnularia borealis							
Rhopalodia gibba							
Rhopalodia gibberula		2	2	10	35	54	223
Stephanodiscus minutus	3	12		12	1		
Stephanodiscus rotula	283	138	7	30	1		
Surirella ovalis				1	4	13	17
Thalassiosira faurii	28	74	1	6		1	2
Thalassiosira rudolfi	5	3		62	1	11	5
Unidentified						1	2
TOTAL	508	505	511	507	582	539	506

Diatom counts MANE-87

Species/Depth 251-320cm	251cm	261cm	270cm	282cm	291cm	301cm	320cm
Achnanthes engelbrechtii	1	1					
Achnanthes exigua							
Anomoeoneis sphaerophora	8	20	28	5		5	
Aulacoseira agassizii							
Aulacoseira granulata	2						
Campylodiscus clypeus	27	108	53	13	6	13	
Cocconeis placentula	2	1			2		
Cyclotella meneghiniana	208	68	228	416	444	406	112
Cymbella muellerii							
Cymbella ventricosa							
Fragilaria ulna +v. acus					34	1	
Hantzschia amphioxys	1		1				
Mastogloia smithii			1				
Navicula gawaniensis							
Navicula elephantis		1					
Navicula elkab							
Navicula halophila							
Navicula sp. af. tenella							
Nitzschia "group latens"							
Nitzschia frustulum	1	12	7		4		
Nitzschia paleacea	7	2	8	45	16		6
Nitzschia sigma							
Nitzschia sp. af. fonticola	190	14	27	1	17	22	0
Nitzschia subrostrata							
Pinnularia borealis							
Rhopalodia gibba				1	5		
Rhopalodia gibberula	34	16	70	21			
Stephanodiscus minutus	9	2	6	2	4		
Stephanodiscus rotula					1		
Surirella ovalis	18	41	46	12		43	1
Thalassiosira faurii	9	7	26		3	28	40
Thalassiosira rudolfi	7	6	51	5	1	1	2
Unidentified	1	2					
TOTAL	525	301	552	521	537	519	161

Diatom counts MANE-87

Species/Depth 331-392cm	331cm	338cm	351cm	361cm	371cm	381cm	392cm
Achnanthes engelbrechtii							
Achnanthes exigua					1		
Anomoeoneis sphaerophora						5	17
Aulacoseira agassizii							
Aulacoseira granulata							
Campylodiscus clypeus		1					
Cocconeis placentula							
Cyclotella meneghiniana	257	179	252	407	480	459	325
Cymbella muellerii							1
Cymbella ventricosa	1						
Fragilaria ulna +v. acus		1			2		
Hantzschia amphioxys							
Mastogloia smithii							
Navicula gawaniensis							1
Navicula elephantis							
Navicula elkab							9
Navicula halophila							
Navicula sp. af. tenella							1
Nitzschia "group latens"					4	1	15
Nitzschia frustulum							4
Nitzschia paleacea	17	41	223	104	46	43	74
Nitzschia sigma							
Nitzschia sp. af. fonticola	0	0	0	10	7	6	45
Nitzschia subrostrata							
Pinnularia borealis							
Rhopalodia gibba							
Rhopalodia gibberula	1		1	4	7	6	9
Stephanodiscus minutus			1				
Stephanodiscus rotula							
Surirella ovalis					2	3	
Thalassiosira faurii	245	299	44	3	1		20
Thalassiosira rudolfi						1	10
Unidentified		1			1		1
TOTAL	521	522	521	528	551	524	532

Diatom counts MANE-87

Species/Depth 402-528cm	402cm	412cm	422cm	429cm	508cm	518cm	528cm
Achnanthes engelbrechtii				1	3	3	1
Achnanthes exigua							
Anomoeoneis sphaerophora		3	1		2	2	9
Aulacoseira agassizii							2
Aulacoseira granulata							2
Campylodiscus clypeus							
Cocconeis placentula							1
Cyclotella meneghiniana	418	416	491	281	347	381	41
Cymbella muellerii							
Cymbella ventricosa							
Fragilaria ulna +v. acus				1		1	
Hantzschia amphioxys							
Mastogloia smithii							
Navicula gawaniensis							
Navicula elephantis							
Navicula elkab		2		3			2
Navicula halophila							1
Navicula sp. af. tenella							2
Nitzschia "group latens"	1						273
Nitzschia frustulum		7			1	4	24
Nitzschia paleacea	45	31	3	100	13	25	36
Nitzschia sigma							
Nitzschia sp. af. fonticola	0	31	0	11	98	66	58
Nitzschia subrostrata							
Pinnularia borealis							
Rhopalodia gibba							
Rhopalodia gibberula	19	1	1	6	21	26	22
Stephanodiscus minutus				31	1	1	35
Stephanodiscus rotula							
Surirella ovalis		4	1	4	5	4	
Thalassiosira faurii	3	26	16	92	3		1
Thalassiosira rudolfi	13	3	6		22	4	1
Unidentified	1				1		3
TOTAL	500	524	519	530	517	517	514

Diatom counts MANE-87

Species/Depth 538-597cm	538cm	547cm	557cm	567cm	576cm	586cm	597cm
Achnanthes engelbrechtii		3					
Achnanthes exigua							
Anomoeoneis sphaerophora	25	7		5	1	3	
Aulacoseira agassizii	2						
Aulacoseira granulata					1		
Campylodiscus clypeus							
Cocconeis placentula	1						
Cyclotella meneghiniana	75	65	163	311	368	519	455
Cymbella muellerii							
Cymbella ventricosa							
Fragilaria ulna +v. acus	1			3			
Hantzschia amphioxys		1					
Mastogloia smithii							
Navicula gawaniensis							
Navicula elephantis							
Navicula elkab	3	3					
Navicula halophila	3	3					
Navicula sp. af. tenella	8	1					
Nitzschia "group latens"	135	141	8				
Nitzschia frustulum	37	13	16	3			3
Nitzschia paleacea	44	55	5	28	22	13	64
Nitzschia sigma	2						
Nitzschia sp. af. fonticola	55	204	43	66	22	1	1
Nitzschia subrostrata							
Pinnularia borealis	2						
Rhopalodia gibba							
Rhopalodia gibberula	35	18	18	6	1	1	1
Stephanodiscus minutus	78	3	9	69	14	3	
Stephanodiscus rotula							
Surirella ovalis			4	2			
Thalassiosira faurii	3						
Thalassiosira rudolfi	3	6	257	43	110		
Unidentified	3	3	1				
TOTAL	515	526	524	536	539	540	524

Diatom counts MANE-87

Species/Depth 604-635cm	604cm	625cm	635cm
Achnanthes engelbrechtii			
Achnanthes exigua			
Anomoeoneis sphaerophora	1	1	2
Aulacoseira agassizii			
Aulacoseira granulata			
Campylodiscus clypeus			
Cocconeis placentula			2
Cyclotella meneghiniana	447	424	216
Cymbella muellerii			
Cymbella ventricosa			
Fragilaria ulna +v. acus			
Hantzschia amphioxys			2
Mastogloia smithii			
Navicula gawaniensis			
Navicula elephantis			
Navicula elkab			
Navicula halophila			
Navicula sp. af. tenella			1
Nitzschia "group latens"			
Nitzschia frustulum	1	1	10
Nitzschia paleacea	34	25	8
Nitzschia sigma			
Nitzschia sp. af. fonticola	1	124	233
Nitzschia subrostrata			
Pinnularia borealis			
Rhopalodia gibba			
Rhopalodia gibberula	1	10	2
Stephanodiscus minutus	7		
Stephanodiscus rotula			
Surirella ovalis			1
Thalassiosira faurii			
Thalassiosira rudolfi	11	110	24
Unidentified			1
TOTAL	503	695	502

Diatom counts Surface samples

All species/Samples NFa-NFe	NFa	NFb	NFc	NFd	NFe
Anomoeoneis sphaerophora	22	43	37	124	40
Aulacoseira granulata					
Caloneis bacillium					
Cocconeis placentula					
Cyclotella meneghiniana					
Cyclotella ocellata					
Epithemia zebra					1
Fragilaria brevistriata		1			
Fragilaria construens					
Fragilaria ulna +v.acus					
Gomphonema clevei		2			
Hantzschia amphioxys				6	
Navicula abberans					
Navicula cryptocephala		2	10		
Navicula elkab					2
Navicula gawaniensis	10	10	3	1	16
Navicula halophila		1			2
Navicula hassiaca			8		
Navicula jakhalsensis	250	274	390	100	315
Navicula mutica	.			1	
Navicula pseudohalophila			2		
Navicula salinicola					
Navicula tenella		1			
Nitzschia 'group latens' (N. elliptica)	23	35	2	3	105
Nitzschia 'group latens' (N. latens)	36	8	8		19
Nitzschia 'group latens' (N. pura)	53	1			20
Nitzschia frustulum	25	4	34	2	8
Nitzschia hungarica					
Nitzschia paleacea	2				
Nitzschia sp. af. fonticola	10		3		2
Nitzschia subrostrata					
Rhoicosphena curvata	2				
Rhopalodia gibberula	62	100	26	45	59
Stauroneis phoenicentron	6	4	3	1	2
Stauroneis wislouchii	18	25	2	275	8
Stephanodiscus minutus					
Thalassiosira faurii					
Unidentified	1	5	1	3	3
Total	520	516	529	561	602

Diatom counts Surface samples

All species/Samples BRa-SWa	BRa	BRb	BRc	SWa
Anomoeoneis sphaerophora	370	430	186	315
Aulacoseira granulata			1	1
Caloneis bacillium			2	
Cocconeis placentula				
Cyclotella meneghiniana				1
Cyclotella ocellata			1	
Epithemia zebra			1	3
Fragilaria brevistriata				
Fragilaria construens			2	
Fragilaria ulna +v.acus			1	
Gomphonema clevei				
Hantzschia amphioxys		2	5	1
Navicula abberans		3		
Navicula cryptocephala				2
Navicula elkab	2	3	5	
Navicula gawaniensis	2	8	6	
Navicula halophila		1		1
Navicula hassiaca				
Navicula jakhalsensis	83	76	82	101
Navicula mutica			1	
Navicula pseudohalophila	4	2		
Navicula salinicola	2			
Navicula tenella			2	
Nitzschia 'group latens' (N. elliptica)				21
Nitzschia 'group latens' (N. latens)	10	7		27
Nitzschia 'group latens' (N. pura)	2			2
Nitzschia frustulum		2	4	7
Nitzschia hungarica				
Nitzschia paleacea				
Nitzschia sp. af. fonticola				1
Nitzschia subrostrata				
Rhoicosphena curvata				
Rhopalodia gibberula	1		20	1
Stauroneis phoenicentron		9	4	16
Stauroneis wislouchii	43	58	258	1
Stephanodiscus minutus				
Thalassiosira faurii				4
Unidentified	2		2	2
Total	521	601	583	507

Diatom counts dissolution experiments DE1 and DE3

DE1 Species/Samples	Control DE1	1.1	1.2	1.3	1.4	1.5
Achnanthes spp.	1					1
Anomoeoneis sphaerophora	5	1	3	3	3	4
Campylodiscus clypeus	3	5	3	5	7	4
Cocconeis placentula	1					1
Cyclotella meneghiniana	180	176	180	190	170	172
Cymbella spp.				1		
Diatoma vulgare			2			
Navicula spp.	2					
Nitzschia frustulum	1		1		1	
Nitzschia paleacea	1		2	2		
Nitzschia sp. af. fonticola	102	100	92	100	104	102
Nitzschia subrostrata						
Rhopalodia gibberula	15	16	18	15	12	15
Surirella ovalis	2	2	3	3	3	5
Thalassiosira faurii	1					
TOTAL	315	300	304	319	300	303
DE1 Species/Samples (contd.)	**1.6**	**1.7**	**1.8**	**1.9**	**1.11**	**1.12**
Anomoeoneis sphaerophora	2	17	2	12	11	7
Campylodiscus clypeus	9	35	18	64	49	35
Cocconeis placentula		1				
Cyclotella meneghiniana	189	216	116	203	221	102
Nitzschia rostellata			1		2	1
Nitzschia sp. af. fonticola	90	9	1	3	7	
Rhopalodia gibberula	16	13	9	19	19	5
Surirella ovalis	3	10	3	4	4	
TOTAL	309	301	150	305	313	150
DE3 Species/Samples	**Control DE3**	**3.1**	**3.2**	**3.3**		
Campylodiscus clypeus	1					
Cyclotella meneghiniana	241	245	262	252		
Nitzschia paleacea	4	4	3			
Nitzschia sp. af. fonticola	60	75	46	54		
Nitzschia subrostrata	2		5			
Rhopalodia gibberula		4	1			
Stephanodiscus minutus	1	2				
Stephanodiscus rotula	3					
Surirella ovalis	1					
Thalassiosira rudolfi	1	3	1	1		
TOTAL	314	333	318	307		

Diatom counts dissolution experiments DE4

Species/samples	Control	4.1.	4.2.	4.3.	4.4.	4.5.	4.6.	4.7.	4.8.
Achnanthes spp.								2	
Anomoeoneis sphaerophora	2	4	5	1	1	1	1	4	2
Campylodiscus clypeus	1	5	4	5	1	2	1	10	3
Cocconeis placentula			1						1
Cyclotella meneghiniana	221	216	153	253	246	193	219	159	225
Cymbella spp.									
Fragilaria spp.			3	1			1		
Navicula spp.					1	1		1	
Nitzschia sp. af. fonticola	49	47	38	17	18	30	20	24	16
Nitzschia frustulum	4		2						1
Nitzschia "group latens"		3	1	3	2		3		
Nitzschia palaeacea	69	35	55	57	50	29	29	11	19
Nitzschia rostellata	1		3		1				
Rhopalodia gibberula	18	42	24	28	26	25	18	41	17
Rhopalodia gibba			1						
Stephanodiscus minutus	5	1	1			1			
Surirella ovalis	3	12	3	8	4	5	3	7	5
Thalassiosira faurii	9	3	3	1	1	5	4	5	5
Thalassiosira rudolfi	11	23	8	7	2	14	1	41	6
Unidentified							1		
TOTAL	393	391	305	381	353	306	301	305	300
Species/samples	4.9.	4.10.	4.11.	4.12.	4.13.	4.14.	4.15.	4.16.	
Achnanthes spp.									
Anomoeoneis sphaerophora	6	5		1	3	3	3	1	
Campylodiscus clypeus	1	2	2	2	4		1		
Cocconeis placentula									
Cyclotella meneghiniana	257	243	252	280	236	271	247	257	
Cymbella spp.			1					1	
Fragilaria spp.	1								
Navicula spp.					1				
Nitzschia sp. af. fonticola	10	11	18	10	10	9	7	6	
Nitzschia frustulum			1				2		
Nitzschia "group latens"					1				
Nitzschia palaeacea	11	8	13	6	13	4	13	5	
Nitzschia rostellata									
Rhopalodia gibberula	20	18	12	12	21	7	19	25	
Rhopalodia gibba									
Stephanodiscus minutus									
Surirella ovalis	4	3	2	5	4	2	5	4	
Thalassiosira faurii	2	2		3	3	3	4	2	
Thalassiosira rudolfi	5	8	8	2	6	2		2	
Unidentified		1							
TOTAL	317	301	309	321	302	301	301	303	

Diatom counts dissolution experiments DE5

Species A-G.l/Samples Con-5.5	Control	5.1.	5.2.	5.3.	5.4.	5.5.
Achnanthes engelbrechtii		1				
Achnanthes exigua			3		1	1
Achnanthes minutissima	1	2	1	3	2	
Amphora ovalis	1	2			4	1
Amphora pediculus		1				
Anomoeoneis sphaerophora	1		1		2	3
Aulacoseira granulata	14	21	15	24	12	12
A. granulata v. angustissima	20	17	15	21	8	22
Caloneis bacillium	1		2		1	
Campylodiscus clypeus	1	1	2	3		4
Cocconeis placentula	5	4	12	3	1	1
Cocconeis thumensis	2		1		2	
Cyclotella iris	1	2	1		2	
Cyclotella meneghiniana	38	40	42	67	61	58
Cyclotella ocellata	21	3	10	10	1	4
Cyclotella stelligera	5	2		3	1	
Cymbella affinis	1	1	6	5	2	5
Cymbella cistula	2	1	2		5	1
Cymbella microcephala	10	4	11	7	2	5
Cymbella muelleri	2	4		2	2	1
Cymbella turgida	3			2		
Diploneis elliptica		2	1	2		3
Diploneis ovalis			3			
Diploneis subovalis	1					
Epithemia sorex	12	27	23	21	11	18
Epithemia zebra	6	13	6	7	12	11
Fragilaria acus + v. ulna	15	8	6	3	4	5
Fragilaria brevistriata	16	19	8	6	8	2
Fragilaria construens	6	5	2	1	1	4
Fragilaria pinnata	12	3	1	2	1	4
Gomphonema clevei	2		1	1	3	
Gomphonema gracile	8	5	12	3	10	8
Gomphonema intricatum				2		
Gomphonema lanceolatum			1	3		

Diatom counts dissolution experiments DE5

Species A-G.I /Samples 5.6-5.10	5.6.	5.7.	5.8.	5.9.	5.10.
Achnanthes engelbrechtii		1			
Achnanthes exigua	2		1	2	1
Achnanthes minutissima					
Amphora ovalis					1
Amphora pediculus		1			
Anomoeoneis sphaerophora	1	1	2	1	2
Aulacoseira granulata	16	11	13	16	21
A. granulata v. angustissima	20	13	11	20	27
Caloneis bacillium	1		2		
Campylodiscus clypeus		2	1	5	
Cocconeis placentula	5	1	5	3	5
Cocconeis thumensis		1			
Cyclotella iris				1	
Cyclotella meneghiniana	34	53	56	72	156
Cyclotella ocellata	7	6	3	1	3
Cyclotella stelligera	1				1
Cymbella affinis	2	4	5	2	3
Cymbella cistula	1	3	2	1	7
Cymbella microcephala	6	2	1	7	2
Cymbella muelleri			1		4
Cymbella turgida					
Diploneis elliptica			1	1	1
Diploneis ovalis					
Diploneis subovalis					
Epithemia sorex	16	16	14	21	33
Epithemia zebra	12	13	4	5	16
Fragilaria acus + v. ulna	6	3	2	5	5
Fragilaria brevistriata	5	1	9	5	13
Fragilaria construens	4	2	1	3	3
Fragilaria pinnata	1	1	6	6	4
Gomphonema clevei		3	3		
Gomphonema gracile	8	4		5	3
Gomphonema intricatum					
Gomphonema lanceolatum	1	5	3		

Diatom counts dissolution experiments DE5

Species G.p-Tot./Samples Con-5.	Control	5.1.	5.2.	5.3.	5.4.	5.5.
Gomphonema parvulum			4		1	
Hantzschia amphioxys	3	1	1	5	1	3
Mastogloia elliptica	5	2		1		
Mastogloia smithii	5	2	11	9	4	10
Navicula elephantis	1					
Navicula elkab	40	50	49	48	60	55
Navicula gastrum		1			1	3
Navicula halophila	1	3		1		1
Navicula minima	1		3	3	1	
Navicula mutica	2	1	1	1	3	
Navicula platycephala						
Navicula pupula	2					
Navicula radiosa	2	4	2		6	2
Navicula tenella	6	8	6	4	2	
Nitzschia "group latens"	9	11	14	14	16	23
Nitzschia amphibia	5	3	4		5	7
Nitzschia denticula	4	1	4	2		1
Nitzschia frustulum	12	12	23	10	21	7
Nitzschia lancettula	2	3	1			
Nitzschia palea	2	2				
Nitzschia paleacea	2	4	3	2	1	
Nitzschia sigma		4	1		1	2
Nitzschia sp. af. fonticola	49	53	31	24	35	39
Nitzschia subrostrata	113	111	125	135	137	144
Pinnularia borealis	1			1	2	
Pinnularia microstauron	1	1	4			1
Rhopalodia gibba	5	6	6	5	14	16
Rhopalodia gibberula	17	6	6	14	8	18
Stephanodiscus minutus	1	4	2		2	
Surirella ovalis						1
Terpsinoe mutica					1	
Thalassiosira faurii	18	15	16	23	18	30
Unidentified	2	6	1	5	10	5
TOTAL	501	475	486	481	488	524

Diatom counts dissolution experiments DE5

Species G.p-Tot./Samples 5.6-5.1	5.6.	5.7.	5.8.	5.9.	5.10.
Gomphonema parvulum	4	1			
Hantzschia amphioxys	6	7	2	1	3
Mastogloia elliptica			2		
Mastogloia smithii	13	8	3	6	9
Navicula elephantis					
Navicula elkab	80	74	61	49	8
Navicula gastrum					1
Navicula halophila					
Navicula minima			1	2	1
Navicula mutica			1	2	1
Navicula platycephala	1				
Navicula pupula	1			2	
Navicula radiosa	2			4	5
Navicula tenella	4	3	2	1	3
Nitzschia "group latens"	20	13	19	8	
Nitzschia amphibia	5	3	1	3	7
Nitzschia denticula	1	1	1		
Nitzschia frustulum	23	11	4	5	8
Nitzschia lancettula	1	1	1	1	
Nitzschia palea					
Nitzschia paleacea	1			8	
Nitzschia sigma	2			4	
Nitzschia sp. af. fonticola	38	34	56	40	29
Nitzschia subrostrata	129	143	149	121	155
Pinnularia borealis	1	1			
Pinnularia microstauron					
Rhopalodia gibba	16	7	7	17	13
Rhopalodia gibberula	16	13	10	12	9
Stephanodiscus minutus	1		2		
Surirella ovalis					1
Terpsinoe mutica					
Thalassiosira faurii	28	26	27	41	23
Unidentified		7	7	11	11
TOTAL	523	486	486	501	573

Appendix 3: Photomicrographs of diatoms from Magadi and Manyara.

Plate A3.1.

a-c *Anomoeoneis sphaerophora*. Modern sample from Flamingo Nursery, Magadi.

d *Anomoeoneis costata*. Modern sample from Flamingo Nursery, Magadi.

e-f *Navicula gawaniensis*.Modern sample from Flamingo Nursery, Magadi.

g-p *Navicula jakhalsensis*. Modern sample from Flamingo Nursery, Magadi.

(a) (b) (c) (d)

(e) (f) (g) (h) (i) (j) (k)

(l) (m) (n) (o) (p)

0 5 10
µm

Plate A3.1.

Plate A3.2.

a-c *Stauroneis salina*. Modern sample from Flamingo Nursery, Magadi.

d-e *Stauroneis* sp. af. *wislouchii*. Modern sample from Flamingo Nursery, Magadi.

f-g *Navicula pseudohalophila*. Modern sample from Flamingo Nursery, Magadi.

h *Thalassiosira faurii*. Fossil sample from core MANE-87, Manyara.

i-k *Thalassiosira rudolfi*. Fossil sample from core MANE-87, Manyara.

(a)

(b)

(c)

(d)

(e)

(f)

(g)

(h)

(i)

(j)

(k)

0 5 10
µm

Plate A3.2.

(a) (b) (c) (d)

(e) (f) (g) (h) (i)

(j) (k) (l) (m) (n) (o) (p) (q) (r)

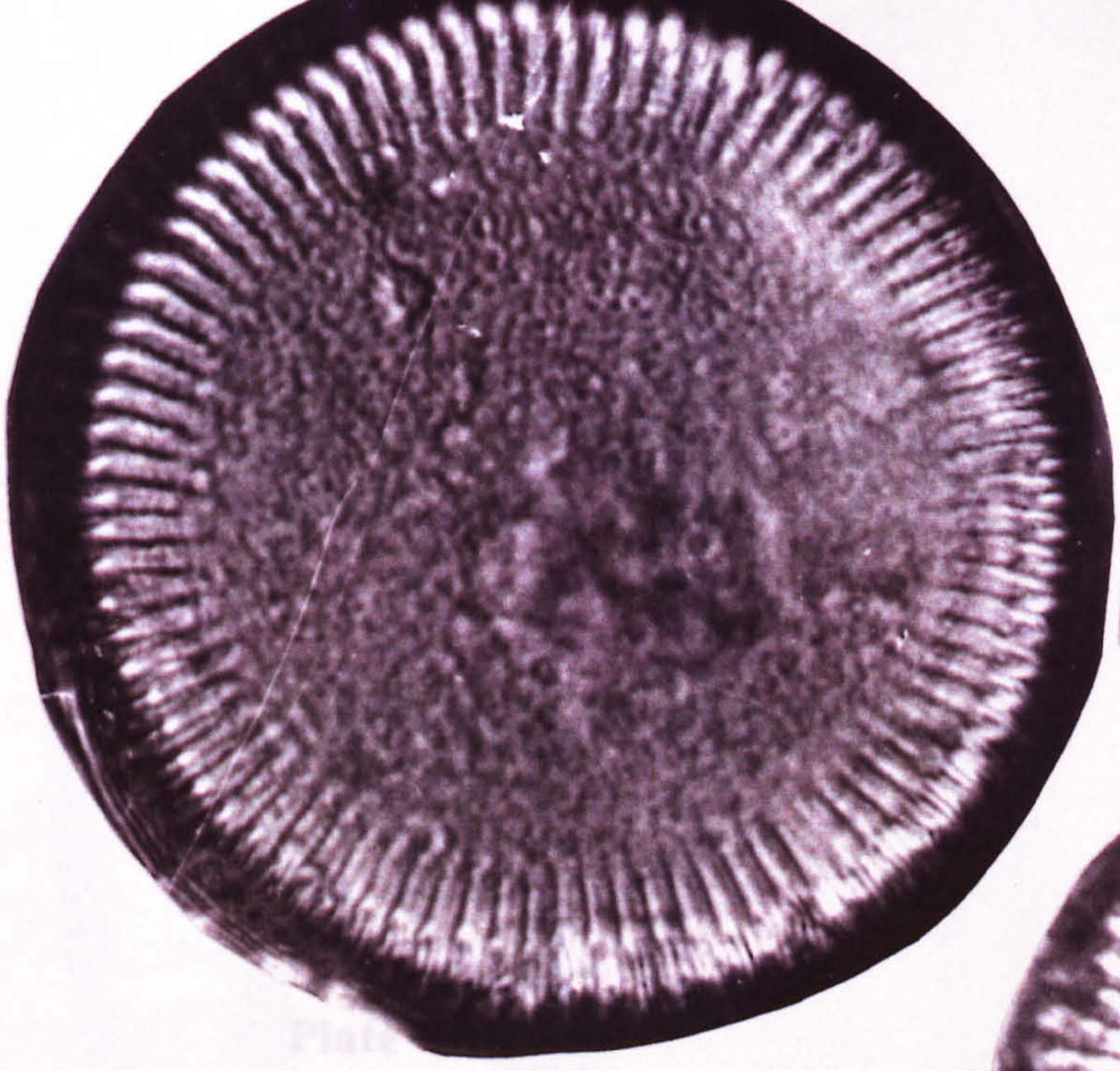
0 5 10
µm

Plate A3.3

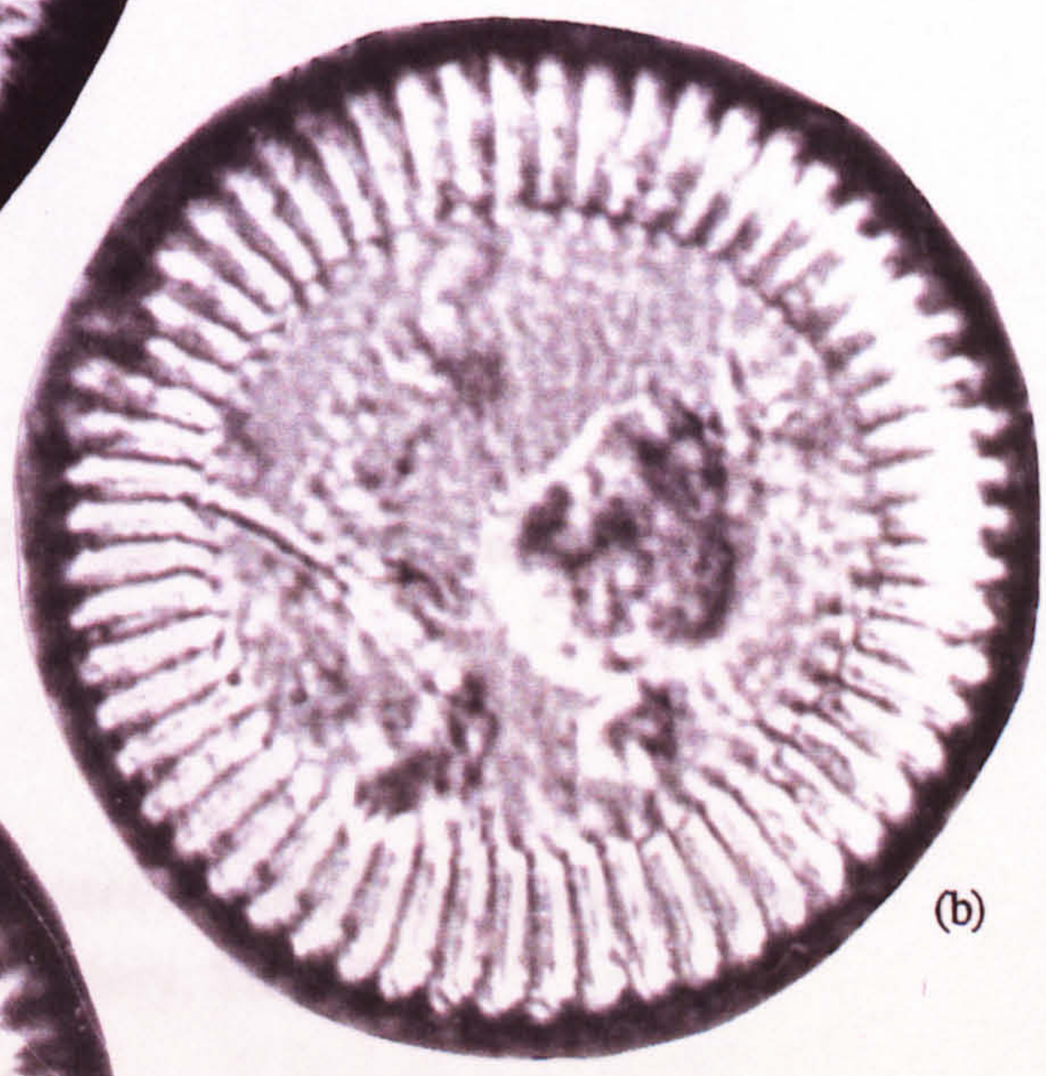
Plate A3.4.

a-e *Cyclotella meneghiniana*. Fossil sample from core MANE-87, Manyara.

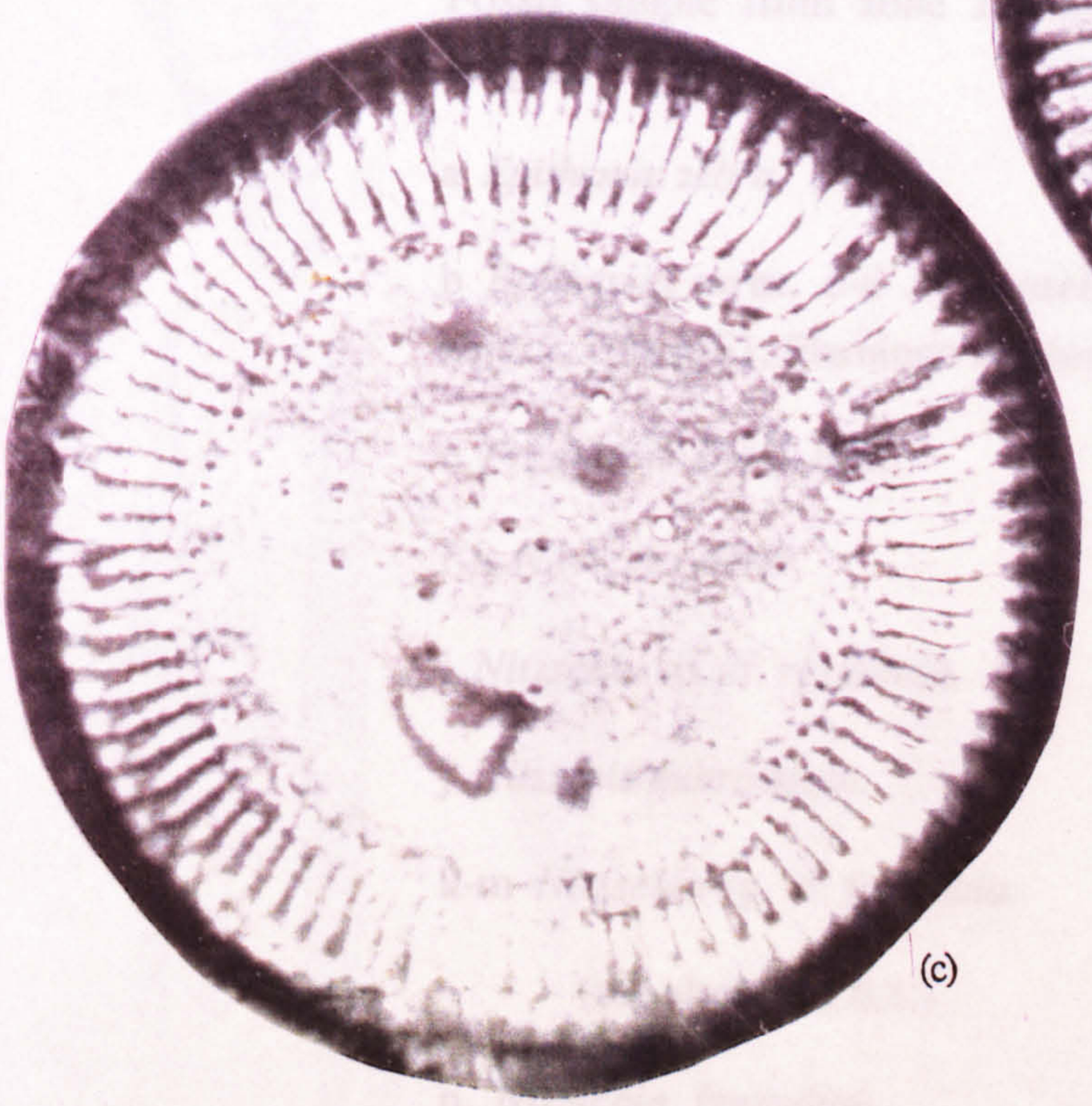
f. *Stephanodiscus rotula*. Fossil sample from core MANE-87, Manyara.



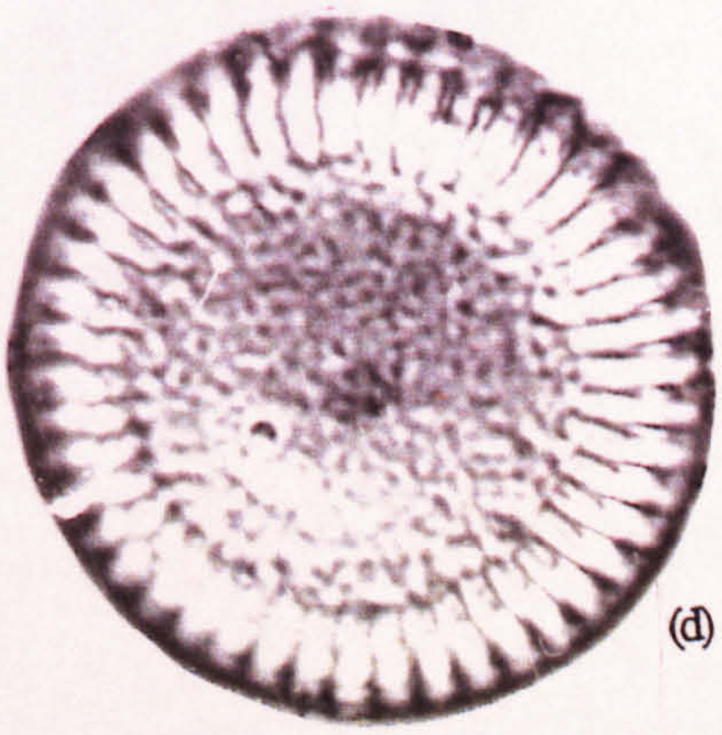
(a)



(b)



(c)



(d)

(e)

(f)

0 5 10
µm

Plate A3.4.

Plate A3.5.

Fossil sample from zone 2, core NF1, Flamingo Nursery, Magadi.

a *Epithemia zebra.*

b *Epithemia sorex.* c-d *Aulacoseira granulata.* Fossil sample zone 2, core NF1, Flamingo Nursery, Magadi.

e *Fragilaria ulna* v. *acus.*

f-h *Navicula elkab.*

i *Nitzschia* sp. af. *rostellata.*

j *Nitzschia subrostrata.*

k-m *Nitzschia* sp. af. *fonticola.*

(see also plate 6.1.)

n. *Nitzschia frustulum.*

o *Mastogloia elliptica.*

p *Cymbella muelleri*

q *Fragilaria brevistriata.*

r *Cyclotella ocellata.*

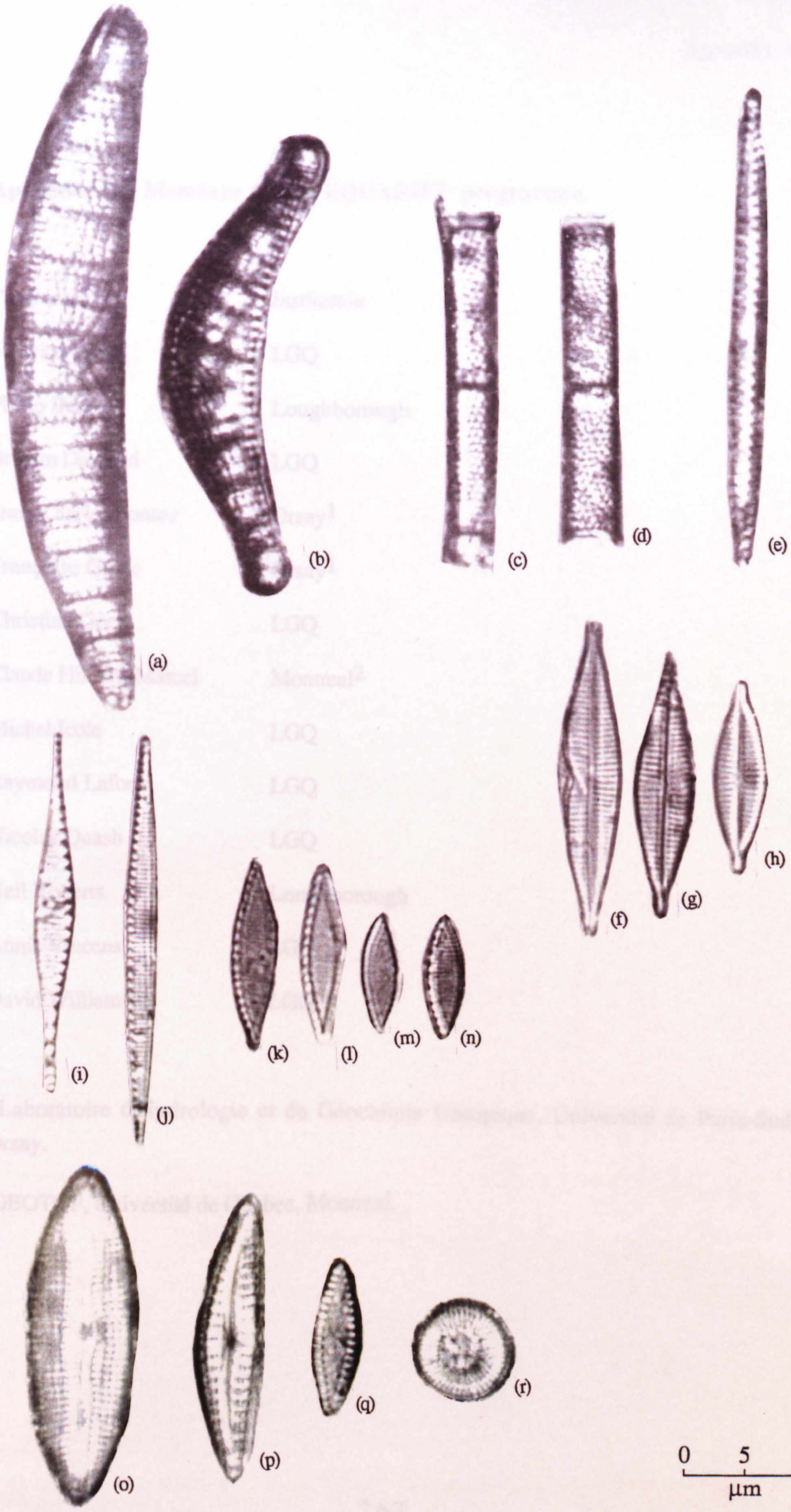


Plate A3.5.

Appendix 4: Members of the EQUARIFT programme.

Participant	*Institution*
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Brahim Damnati	LGQ
Jean-Charles Fontes	Orsay[1]
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Michel Icole	LGQ
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Nicolas Quash	LGQ
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