Holocene environmental and climate change in the southern Levant: diatom-based palaeolimnology of Lake Kinneret (Israel)

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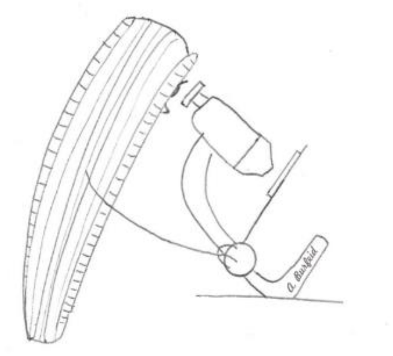

For Beate, Michael & Franz

Summary

The Eastern Mediterranean and especially the southern Levant are key regions for palaeoclimatological and palaeoenvironmental research due to their highly complex topography and climatic variabilty. Nevertheless, our knowledge and understanding of Holocene environmental variability and its possible drivers is still limited. Diatoms have a well-recognised potential to generate high-quality palaeolimnological data because they are often well preserved in lacustrine sediment records, which provide excellent high-resolution terrestrial palaeoarchives. To date, there has been surprising little Quaternary diatom research across the circum-Mediterranean, and the southern Levant in particular.

Therefore, this PhD thesis aimed to investigate and understand the potential of diatoms as palaeoenvironmental and palaeoclimate indicators in Eastern Mediterranean Quaternary research. Diatom death assemblages were analysed from modern sediment surface samples and, for palaeoenvironmental reconstruction, from an 18 m long sediment sequence recovered from Lake Kinneret (Israel) in 2010, covering the last 9,000 cal yrs BP. As part of the investigation, the formal description of a new diatom species, *Cyclotella paleo-ocellata* VOSSEL AND VAN DE VIJVER found in the lake sediment core was achieved, adding a taxonomic focus to the research.

This thesis provides a high-resolution diatom dataset for Lake Kinneret based on a robust chronology for the Holocene, which is unique in the southern Levant region. The results confirm that diatoms provide a powerful tool for Holocene palaeoenvironmental and climatological reconstructions in the southern Levant region, especially if they are interpreted in combination with multi-proxy datasets. The diatom data revealed the palaeolimnological history of Lake Kinneret for the past 9,000 cal yrs PB, i.e. changes in lake level and therefore regional climate variability. Our results show that the Early Holocene was characterised by fluctuating lake levels, which are linked to alternations between arid and more humid climate conditions at Lake Kinneret. Diatoms indicated a prolonged stable deep lake phase throughout the mid-Holocene and the onset of the Late Holocene due to long-lasting humid climate, which was possibly interrupted by smaller drought events (declined lake levels) occurring at around 4,600 and 3,600 cal yrs BP. During the Late Holocene, the diatom record indicates the initiation and subsequent pattern of anthropogenic impact on the lake's ecosystem by changing its trophic status from an oligotrophic to a meso-eutrophic system at around 2,200 cal yrs BP until present. Shifts in lake levels and the climate signal can therefore not be derived from the diatom dataset for this time.

The comparison between lake-level reconstructions from Lake Kinneret (based on the provided diatom data in this thesis) and the Dead Sea record indicates a close interaction between both lake systems as they seem to react in similar ways to major hydrological changes in the catchment, e.g. due to Holocene rapid climate changes.

Our investigations emphasize the need for further analysis of long, terrestrial diatom records with robust age-control in the southern Levant and the circum Mediterranean region. Moreover, more modern analogue studies from lakes, which are used for palaeoenvironmental reconstructions, would be very useful, improve calibration and interpretation of fossil datasets.

Acknowledgments

Firstly, I thank the Studienstiftung des deutschen Volkes (German Academic Scholarship Foundation) for funding my PhD studies. Without this support, my work would not have been possible. I also thank the Collaborative Research Centre CRC 806 “Our Way to Europe” and the German Science Foundation (DFG) for their financial support, which enables me to attend several research stays, conferences and workshops.

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especially from the CRC 806 and the IRTG, who supported me, shared their ideas and expertise with me during meetings and beers at the “Mauer”. I would like to thank Mordechai Stein, Dr. Ahuva Almogi-Labin, the Kinneret Limnological Laboratory and its employees and the Geological Survey of Israel for their collaboration and sample supply.

In the end, I thank my family and friends for their endless support and trust in me, that I can achieve this. I especially want to thank my parents, Beate and Michael, who taught me to fight for my dreams and ideas and that I can achieve everything, if I only try hard enough and really want it. I also especially thank my husband Franz, who is always there and makes me unbelievable happy and strong.

Thank you ! תודה רבה

Table of Contents:

Structure of the thesis

This PhD thesis generates new understanding of the power of diatoms as palaeoenvironmental indicators in Eastern Mediterranean Quaternary research, by analysis of modern and subfossil diatom assemblages in Lake Kinneret, Israel. The 18 m long sediment sequence recovered from the central part of the lake represents the longest and most continuous Holocene sequence yet retrieved. Taxonomical aspects are also covered by formal description of a new diatom species, so far only occurring in the subfossil material of Lake Kinneret.

This thesis has been written as a cumulative work, with individual chapters submitted and published in international peer-reviewed journals. It is possible, that smaller formal deviations (e.g. in abbreviations) may occur between all chapters due to different utilized journal author guidelines to prepare the publications. Each chapter is conceptualized and stands alone as a scientific work. To date, two of the chapters have been published, and a third will be submitted after performing some final analyses.

The main aims of the PhD thesis are to:

(I) Improve the understanding of the ecology of diatom communities (modern and subfossil) of Lake Kinneret and their distribution in the lake

(II) Investigate the applicability of diatoms as (palaeo-) ecological indicators, with a focus on lake-level and, hence, palaeoclimate reconstruction

(III) Provide a continuous, high-resolution diatom profile for the southern Levant covering the Holocene time period to
   a. improve understanding of Holocene climate variability in the southern Levant
   b. improve understanding of current and past human impact on the ecosystem of Lake Kinneret

To achieve these aims the following investigations were conducted:

Chapter 1 provides a general introduction to the thesis based on relevant published literature. This introduction gives a brief description of the study area “Lake Kinneret”, its geological setting and current climate situation. Diatoms and their usage as palaeoecological proxies are discussed. A summary of the current state of research based on Lake Kinneret and of diatom analysis in Israel is given.

Chapter 2 provides the formal taxonomic description of a newly discovered centric sub-fossil diatom species *Cyclotella paleo-ocellata* VOSSEL & VAN DE VIJVER from Lake Kinneret. This chapter comprises the following peer-reviewed publication:

Vossel, H., Reed, J.M., Houk, V., Cvetkoska, A., Van de Vijver B. (2015): Cyclotella paleo-ocellata, a new centric diatom (Bacillariophyta) from Lake Kinneret (Israel). Fottea 15: 63-75. Doi: 10.5507/fot.2015.006

Chapter 3 presents the results of a multi-proxy investigation from sediment cores Ki_10_I and Ki_10_II (1780 cm depth, approximately 9,000 cal yrs BP) from Lake Kinneret. The principal focus is the degree to which diatom shifts represent varying hydrological conditions and/or productivity changes of the lake system during the Holocene. Selected palynological (Langgut et al., 2013, 2016, Schiebel, 2013, Schiebel and Litt, 2018) and minero-geochemical proxy data are used to strengthen interpretation, determining whether shifts in the diatom flora are climate driven or are a function of varying trophic stages of the lake independent of climate forcing. Chapter 3 comprises the following peer-reviewed publication:

Vossel, H., Roeser, P.; Litt, T., Reed, J.M. (2018): Lake Kinneret (Israel): New insights into Holocene regional palaeoclimate variability based on high resolution multi-proxy analysis. The Holocene, vol. 28(9), 1395-1410. Doi: 10.1177/0959683618777071

Chapter 4 presents a semi-quantitative investigation of the modern distribution of diatom assemblages in Lake Kinneret based on analysis of surface sediment transect samples. The results indicate a strong relationship between water depth and relative abundance of planktonic, facultative planktonic and benthic diatom species (= P/B-ratio) in modern Lake Kinneret. This allows reanalysis and calibration of the fossil dataset to reconstruct lake-level changes (in m) for the Holocene. This chapter will be submitted after performing some final analyses.

Hartung, H. et al. (in preparation): Is the present the key to the past? Diversity and distribution of modern diatom communities in Lake Kinneret (Israel).

Chapter 5 presents a summary of the thesis and a brief discussion of future research needs.

1 General Introduction

1.1 Project background

This Phd thesis was funded by the German Academic Scholarship Foundation (Studienstiftung des deutschen Volkes) and is content-affiliated to the Collaborative Research Centre CRC 806 “Our Way to Europe”, which is supported by the German Science Foundation (Deutsche Forschungsgemeinschaft, DFG). The CRC focuses on culture-environment interaction and human mobility in the Late Quaternary and aims to improve the understanding of anatomically modern human (*Homo sapiens sapiens*) migration pathways out of Africa to Europe. To capture the complexity of various research areas, methods and theoretical concepts, the CRC uses an interdisciplinary approach in combining archaeology and geosciences (http://www.sfb806.uni-koeln.de). There is a particular focus on the Eastern Mediterranean region, which has a long history of human presence and represents one of the cradles of agriculture. Therefore, the CRC aims to investigate climate variability and how it has affected human societies and migration pathways over long time series (Richter et al., 2012). Long and continuous palaeoclimate datasets of many archaeologically rich areas, such as Israel, are lacking and prevented a complete understanding of climate-society interaction. As part of the project B3, a long and continuous sediment sequence was recovered from the centre of Lake Kinneret (Israel) in 2010, which lies on one of the possible migration corridors out of Africa (figure 1.1), to improve data availability within the southern Levant covering the Holocene period.

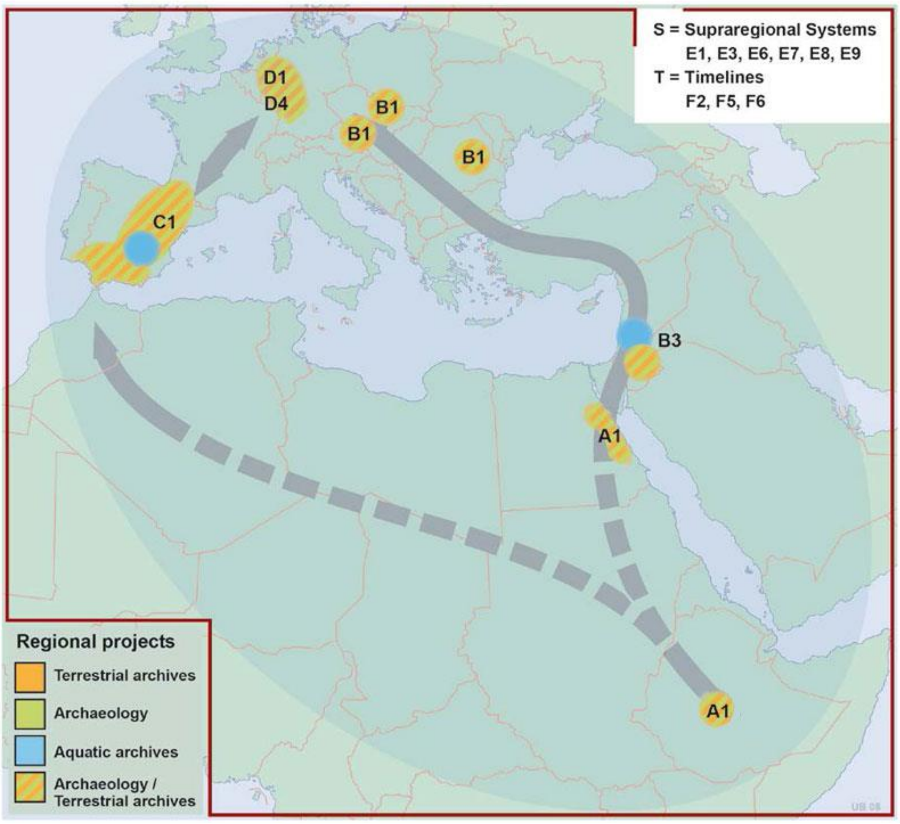

Figure 1.1 Overview of various projects covered by the CRC 806. The map shows the possible migration ways of anatomically modern humans out of Africa, where A) represents the source region East Africa, B) represents the eastern trajectory via the Near East (with project B3) and the Balkans, C) represents the western trajectory via North Africa and the Iberian Peninsula, and D) constitute the sink region in Central Europe (after Richter et al., 2012).

1.2 Study area: Lake Kinneret

Lake Kinneret is part of the so called Levant, which encompasses Cyprus, Israel, western parts of Jordan, Lebanon, Palestine, Syria and southern parts of Turkey. Lake Kinneret is located in the north of Israel in the northern part of the Jordan Rift Valley, representing the largest freshwater body (22 x 12 km; 167 km^2) in the region and, with a surface elevation of 210 mbsl the lowest-lying freshwater lake on Earth. The large catchment area of Lake Kinneret spans over 2,730 km^2 and extends to parts of Israel, Lebanon and Syria, incorporating four different hydrogeological units: the Jurassic mountainous karst of Mt. Hermon, the basalt plateau of the Golan Heights, the carbonaceous karst of the Eastern Galilee Mountains and the flat alluvial Hula Valley (Rimmer and Givati, 2014). The total annual water inflow into the lake system is about 629 x 10^6 m^3, comprising the inflow of the Jordan River, direct catchment runoff, saline springs, direct precipitation and other water sources (Rimmer and Givati, 2014). Modern lake level can fluctuate by up to 4 m a year depending on precipitation, evaporation (230 x 10^6

m^3/year) and water use for human consumption and agriculture (National Water Carrier, personal communication). Lake Kinneret is warm monomictic, being stratified with an anoxic hypolimnion from May to December and fully mixed from December to April (Gophen, 2003, Katz and Nishri, 2013).

1.2.1 Geological setting

Lake Kinneret is situated together with the Dead Sea Basin on the tectonically-active Dead Sea Transform Fault (DSTF; figure 1.2), which currently forms a more than 1000 km long fault system connecting the divergent plate boundary along the Red Sea with the Eastern Anatolian Fault (EAF) in Turkey (Hurwitz et al., 2002, Ben-Avraham, 2014). The Dead Sea fault is considered to be a major strike-slip fault (left-lateral slip), which is active since Neogene times, and separates the Sinai sub-plate in the West against the Arabian plate in the East with 2-6 mm per year (Klinger et al., 2000, Garfunkel et al., 2014), accompanied by the formation of narrow valleys and uplifting of its shoulders at the plate boundary (Garfunkel, 1997, Garfunkel and Ben-Avraham, 1996). Intense seismic activities and events, occurring in the past along the DSTF, are well documented by several geological archives and instrumental records (e.g. Klinger et al., 2015, Hofstetter et al., 2014, Migowski et al., 2004, Reches and Hoexter, 1981). The lake basin itself represents one of a series of pull-apart basins (from N to S: Hula Basin, Kinneret-Bet Shean basin, Dead Sea Basin and the Gulf of Elat; see figure 1.2), which have been formed as a result from plate tectonic movements. Pull-apart basins are depressions that are bounded by sideways-stepping, strike-slip faults parallel to their length. They from where the sense of stepping or bends along the faults have the same sense as fault motion (Garfunkel, 1981).

The Holocene Sea of Galilee has evolved from ancient water bodies that filled the Kinnarot tectonic depression during the Late Pleistocene, such as the former Lake Lisan (Hazan et al., 2005) and has only existed in its current configuration for around 18,000 yrs (Berman et al., 2014). The surrounding catchment area of Lake Kinneret (figure 1.3) is mainly composed of Cretaceous to Eocene carbonate rocks (limestones, dolostones, chalks and marls) with extensive karst (Sneh et al., 1998). Neogene and Pleistocene basalt is also common, especially in the Golan Heights, forming escarpments of up to 500 m in height at the eastern side of the lake (Sneh et al., 1998).

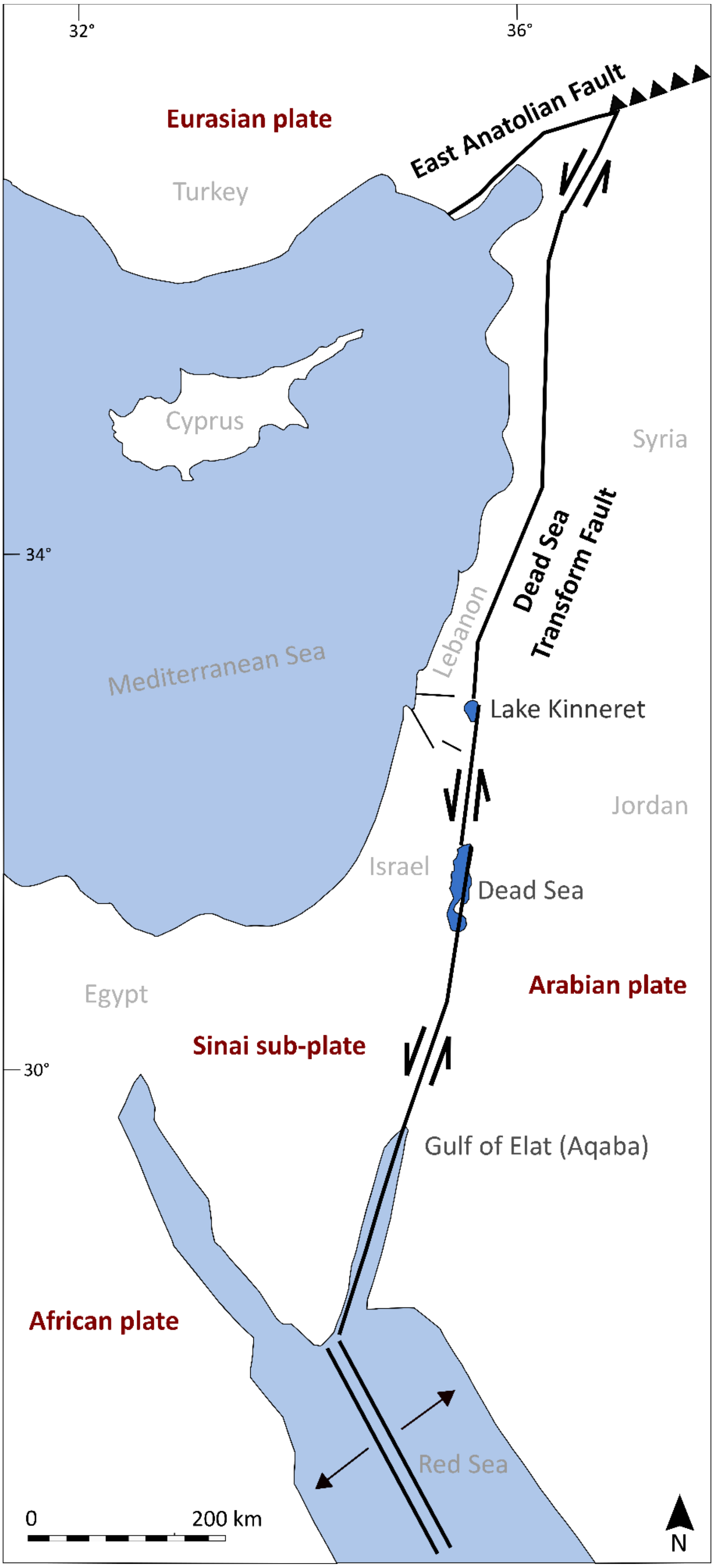

Figure 1.2 Simplified tectonic situation of the Dead Sea Transform fault (modified after Ben-Avraham, 2014).

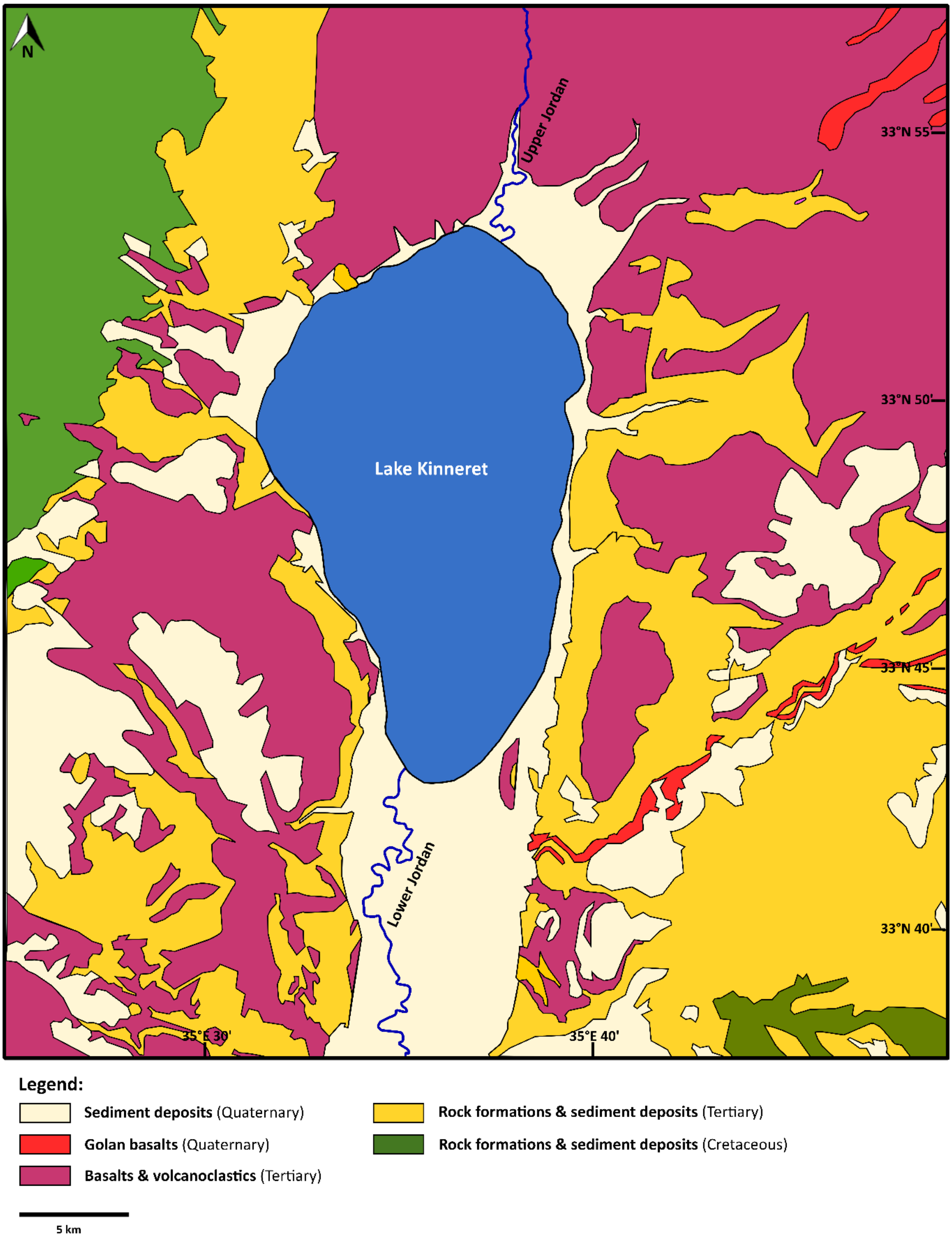

Figure 1.3 Exposed geological unites around Lake Kinneret (modified after Sneh et al., 1998).

1.2.2 Regional climate characteristics

The southern Levant is characterized by hot, dry summers and cold, wet winters due to its transitional location between the Mediterranean and Saharo-Arabian climate zones. Most of the present-day precipitation, aquifer recharge, stream flow and spring discharge in the Levant are generated by winter Mediterranean cyclones, which develop over Cyprus (the Cyprus Low) and the Aegean Sea, transferring moisture eastwards to the Levant (Ziv et al., 2006): mid-latitude westerly jet streams move eastwards and drive cold air-masses over the warm Mediterranean Sea, where they gain moisture and become conditionally unstable. This moisture is released as intensive rainfall over the Levant, mainly between December and February (Dayan and Morin, 2006). The Levant's topographic conditions in relation to the prevailing winds and the shape of its coastline control the distribution of precipitation over the adjacent landmasses (Ziv et al., 2006, figure 1.4). During summer (May to September), the North African tropical high-pressure system occupies the southern Levant and causes widespread droughts and high temperatures (Rohling et al., 2009).

Northern Israel in particular receives most of its precipitation from those mid-latitude lows, generated over Cyprus (Ziv et al., 2014). The mean annual precipitation and temperature vary considerably from northern to southern Israel, partly as a function of topography (see figure 1.4). Maximum precipitation occurs further north due to the high mountain ridges, e.g. on Mt. Hermon (Golan Heights), with an average of 1600 mm/year. In the Jordan Valley precipitation varies from 700 mm/year in the Hula basin to 300 mm in the Beth-Shean region (Langgut et al., 2016). There is a sharp transition to a fully arid climate in the south. Annual temperatures increase approximately linearly with decreasing precipitation (see figure 1.4). The Kinneret region itself is currently characterized by a typical semi-arid Mediterranean climate (Baruch, 1986), with an average annual precipitation of 400 mm and a mean annual temperature of 21 °C.

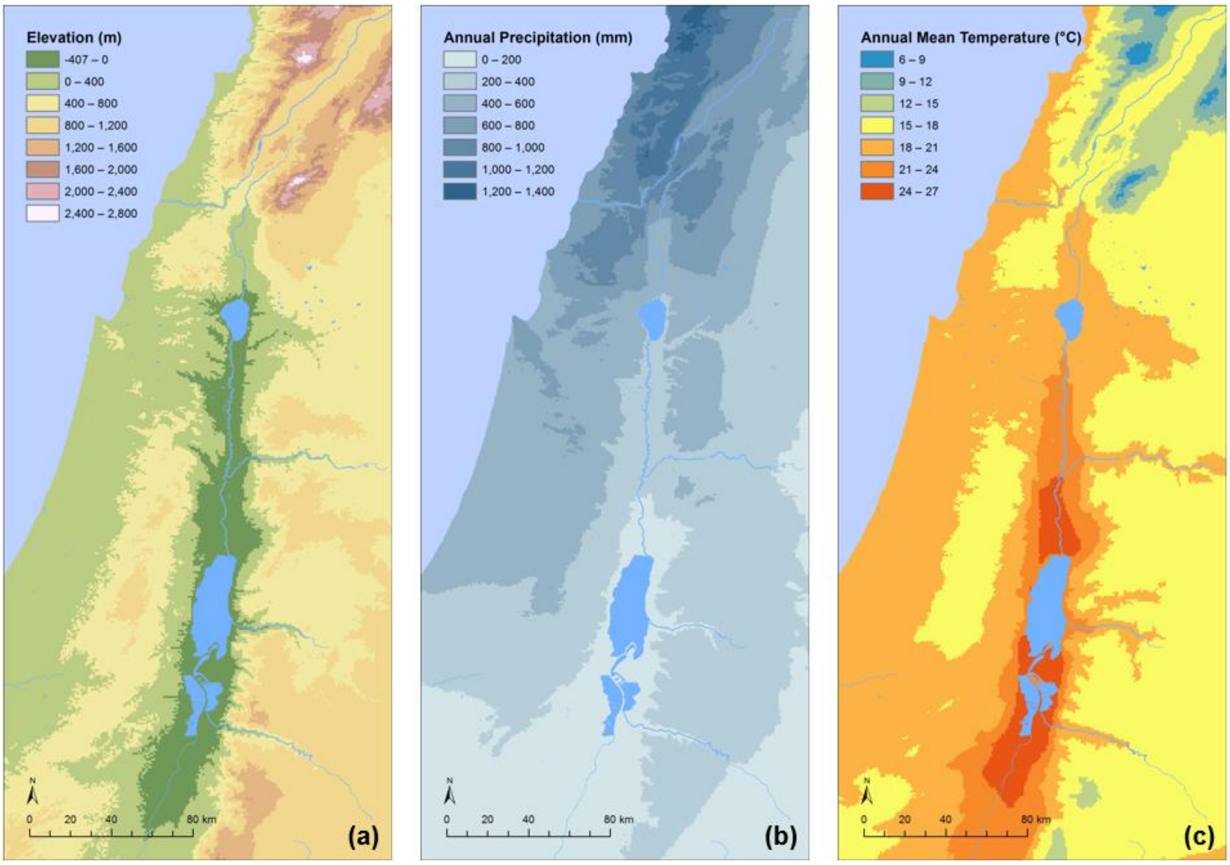

Figure 1.4 Maps show the distribution of (a) the elevation, (b) the annual precipitation (in mm), and (c) the annual mean temperature (in °C) across Israel. The mean annual precipitation and temperature vary considerably from northern to southern Israel, partly as a function of topography (maps are created with ArcGIS).

1.2.3 Current state of research on Lake Kinneret

As Lake Kinneret is the most important source of fresh water in the region it is not surprising that it is the subject of extensive modern aquatic monitoring programs. The book “Lake Kinneret – Ecology and Management” by Zohary et al. (2014) and references therein review the current state of the lake and aims to disentangle the mechanisms underlying the function of its ecosystem. It incorporates useful ecological data generated over the last ca. 50 years since monitoring began with the establishment of the Kinneret Limnological Laboratory in 1967.

Ancient Lake Kinneret (from Hebrew word *kinnṓr* = ‘harp’, reflecting the shape of the lake), which is also known as Lake Tiberias or the Sea of Galilee, has attracted people’s attentions since ancient times. The lake and its surroundings have served as an important backdrop for much of human history in the region, especially in biblical times: the life of Jesus Christ, his ministry, teaching and the accomplished miracles are strongly associated with Lake Kinneret (Berman et al., 2014). Therefore, it is not surprising that the lake has been a focus for palaeoenvironmental research in the past 50 years: The first multidisciplinary study on sediment cores covering the Late Holocene were implemented in the 1980's by Stiller et al. (1984), comprising isotopic and geochemical analysis as well as low resolution studies of diatoms, non-siliceous algae and pollen. Stiller and Kaufman (1985) revealed palaeo-climatic trends by the isotopic composition of carbonates in Lake Kinneret. Dubowski et al. (2003) reconstructed the lake's productivity and regional climatic conditions during the Late Holocene based on biochemical proxies including carbonates, organic C and N contents and their respective $\delta^{13}C$ values. Hazan et al. (2005) provided the first longer-term study by lake-level reconstruction and analysis of the sedimentological composition for the past ca. 40,000 years, based on sedimentological identification of radiocarbon-dated palaeo-shorelines and investigations at the Ohalo II archaeological site. Since palaeo-shorelines do not provide a continuous record, understanding of lake-level change during the Holocene in particular remains poor. Recently, Lev et al. (2007) investigated the possible usage of *Melanopsis* shells as radiocarbon chronometers for palaeo-lakes from different freshwater localities in the Jordan Valley, including Lake Kinneret. Quintana Krupinski et al. (2013) investigated the fire activity around Lake Kinneret by charcoal and black carbon analysis of a ca. 3 m long gravity sediment core, generating inferences concerning Late Holocene changes in moisture and human impact. Several palynological studies have been carried out, comprising Baruch (1986), and more recently by Langgut et al. (2013, 2016), Miebach et al. (2017) and Schiebel and Litt (2018), on different sediment core sequences retrieved from Lake Kinneret, revealing the palaeo-vegetational history of the region for the last 28 ka. To date, these latter provide the main source of continuous palaeoenvironmental data for the Holocene period.

1.3 Diatoms

Diatoms, or *Bacillariophyta*, are classified as unicellular, eukaryotic algae, which belong to the Phylum *Heterokontophyta*. They are characterized by their siliceous cell walls, which form a frustule (comprising two valves) and their yellow-brown pigmentation. The cells, which are variable in shape, are mainly solitary, but some taxa can form large filamentous colonies. The cell size can vary from 1 to 2000 µm in length, but most species have a size range from 10 to 100 µm.

Diatoms are found in almost every aquatic habitat (both marine and freshwater) where light penetration is sufficient to support photosynthesis, and also in damp terrestrial biotopes (Smol and Stoermer, 2010). They play an important role for a steady oxygen-saturated earth atmosphere as they are producing approximately 25 % of the oxygen existing on earth. Diatoms made their first appearance about 100 million years ago in the seas of the Middle Cretaceous

(Ehrlich, 1995). The oldest known freshwater diatom was found in Eocene sediments (Early Tertiary) and is around 40 million years old. So far there are 250 known genera and around 100 000 known species.

In lakes, diatoms live either in the water column as part of the phytoplankton (i.e. planktonic, free-floating in the open water) or near the bottom and/or on various submerged substrates of the littoral zone (i.e. periphytic, which means they grow on aquatic plants (epiphytic), stones (epilithic), sand grains (epipsammic) or mud (epipelic)) as part of the benthos. Some diatom taxa (e.g. some *Fragilaria*) have a tychoplanktonic lifestyle, i.e. they live attached to planktonic organisms or floating objects in the open water column. Diatoms are often an important component of the phytoplankton in lakes. In temperate and Mediterranean climate zones they tend to be particularly abundant at the beginning of spring (and in dimictic lakes also again in autumn), when the lake water contains plenty of nutrients including phosphate, nitrate and silicate, and when temperature, light intensity and daylength (and therefore photosynthesis) are increasing. In modern Lake Kinneret the phytoplankton flora is dominated by large dinoflagellate blooms, which occur in spring (March-May), and therefore replace the typical diatom spring bloom. Additionally, four stages of succession in the occurrence of phytoplankton assemblages are observable during a one-year-cycle due to the monomictic status of Lake Kinneret (Pollingher, 1981, Zohary, 2004): (1) Starting with thermal and chemical destratification during October and November with a slow increase in nutrients; typical occurrence of the genera *Erkenia* (=*Chrysochromulina*); *Rhodomonas* (=*Plagioselmis*), *Crytomonas*, *Cyclotella*, *Crucigenia*, *Chodatella*, *Tetraedon*. (2) Fully mixing of the lake in December to February with maximum nutrient concentrations and high turbulence conditions; resuspension of *Aulacoseira* filaments and *Peridinium* cysts, occurrence of small chlorphyte coenobia and unicells (e.g. *Pediastrum*, *Tetraedron*). (3) Beginning of stratification between March to May with higher temperatures, calmer water conditions and the beginning of gradual nutrient depletion (especially phosphorus); dominance of dinoflagellates, i.e. *Peridinium gatunense* and (4) ending with stratification in June to September with very low nutrient levels and high water temperatures, occurrence of species belonging to cyanobacteria (e.g. *Micocystis*), chlorophytes (e.g. *Pediastrum)* and nanoplankton (e.g. *Cyclotella spp.*, *Chroococcus spp.*).

1.3.1 Structure of the diatom frustule

Each diatom cell is surrounded by a cell wall, composed of more than 95 % of opaline silica, which is the reason why they are often well preserved as subfossils in lake deposits and can be used for long-term palaeoecological studies. These cell walls form a so-called frustule (figure 1.5), which is composed of two valves, separated by a series of ring- or hoop-like side walls called girdle bands. Each frustule exhibits a distinctive shape and ornamentation, which is often species-specific and important for morphological identification and classification. Frustules are usually either circular (centric) or elliptical (pennate) in valve view, which is the main character to differentiate between the two orders of diatoms: the Centrales and Pennales.

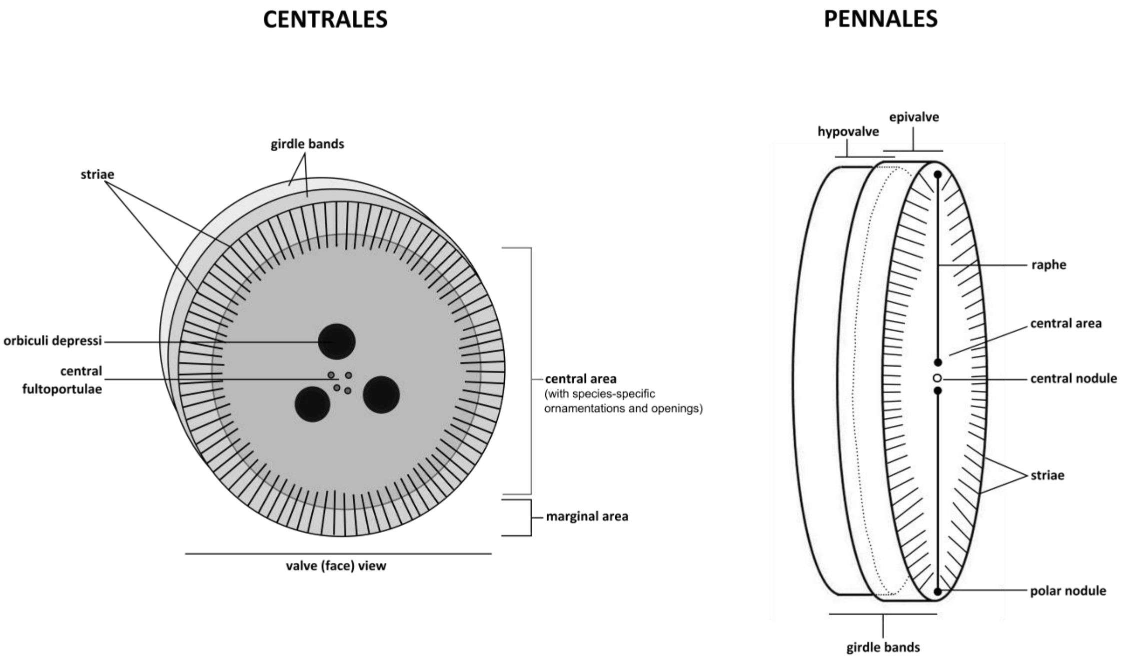

Figure 1.5 Schematic figure of a typical diatom frustule for each diatom order: Centrales (left); Pennales (right).

1.4 Diatoms as a palaeoecological proxy

Living diatom species are extremely sensitive to a wide range of physical and chemical aquatic parameters. Shifts in water chemistry and/or physical habitat characteristics can cause marked changes in the species assemblage composition and abundance, so they have great potential as ecological indicators in studies of modern water quality and reconstruction of past environments (Armstrong and Braiser, 2005, Smol and Stoermer, 2010). Diatoms are about the same size as pollen grains, and in many ways diatom analysis fulfils the same function for aquatic ecosystems that palynology does for terrestrial vegetation. Diatoms have two advantages compared to pollen: (a) a higher taxonomical resolution and (b) fossil diatom valves represent the organism itself rather than being a part of the reproduction process (Roberts, 2014).

Many diatom species are specialised to inhabit particular kinds of habitats (e.g. plankton, epiphyton, epilithon etc.) and have specific preferences that allow indicator values to be set for several important environmental parameters such as light, moisture conditions, temperature, current velocity, salinity, pH, oxygen, inorganic and organic nutrients (van Dam et al., 1994). Therefore, the quantitative analyses of modern and fossil diatom assemblages, often preserved in lake deposits, can be used to show (a) how lake characteristics have changed over time, (b) the relation to anthropogenic influences and (c) can help to reconstruct past climate conditions (i.e. by the reconstruction of lake-level variations through time), past water conditions and the palaeoenvironment.

1.4.1 Diatom-based palaeoenvironmental research in the Eastern Mediterranean and the southern Levant

Diatoms have been used as proxy indicators to reconstruct Holocene environmental changes across the Mediterranean. During the last decades the application of diatoms in environmental reconstruction has expanded considerably (Smol and Stoermer, 2010). Nevertheless, their potential still remains largely unexplored in the Eastern Mediterranean region as figure 1.6 shows. Figure 1.6 summarises the location of existing long sedimentary records recovered from lakes, which incorporate diatom analysis as a proxy indicator in palaeoenvironmental reconstructions. The absence of long, continuous, well-dated Holocene diatom sequences from the southern Levant is clear. To provide such a profile is one of the main motivations for this thesis.

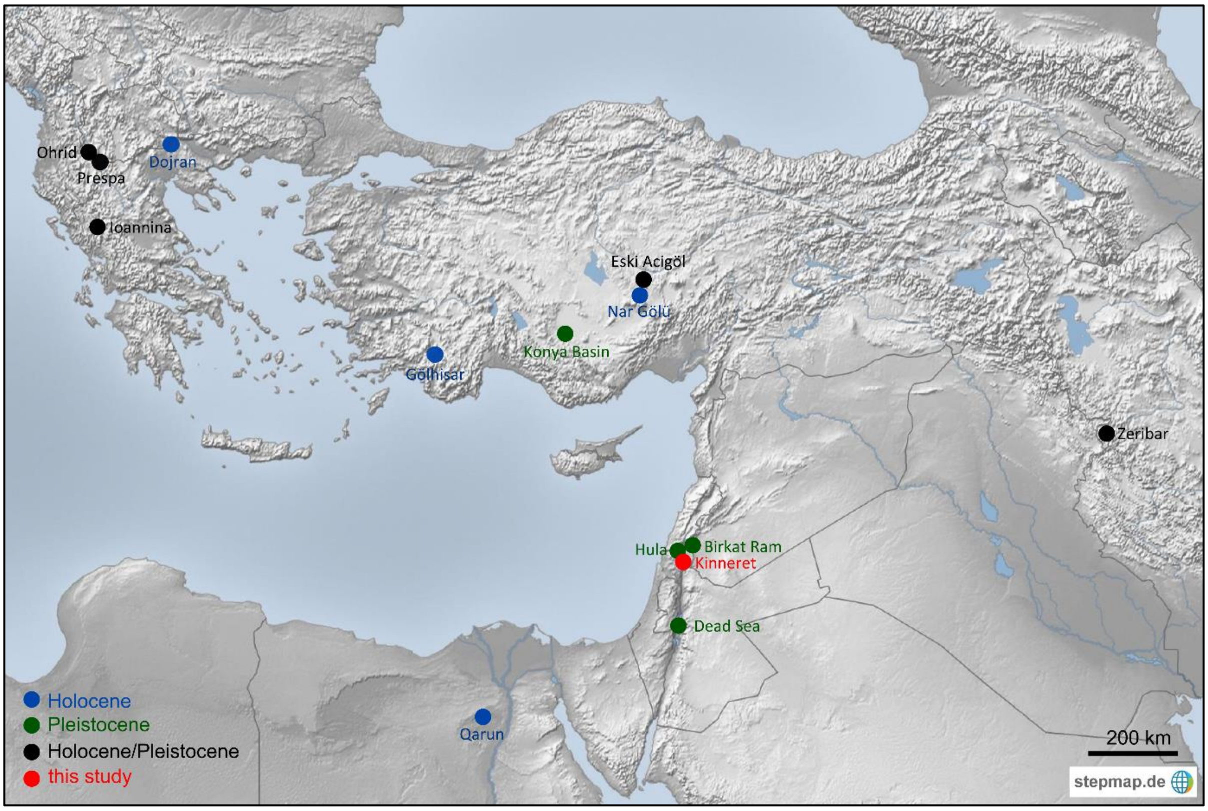

Figure 1.6 Overview map of existing diatom records across the Eastern Mediterranean/Near East region. Blue: diatom records encompassing the Holocene. Green: diatom records encompassing the Pleistocene. Black: diatom records encompassing parts of the Pleistocene and Holocene. Red: location of Lake Kinneret diatom record (this study) covering the Holocene.

The deep (284 m), ancient Lake Ohrid (Macedonia/Albania) diatom record (430 m sediment sequence covering the last 1.2 Ma) represents the longest continuous diatom record from the Eastern Mediterranean region (Wagner et al., 2014, Cvetkoska et al., 2012, 2016). Most other lakes are relatively shallow and exhibit a strong, if complex, response to Holocene shifts in moisture availability and, to a lesser extent, temperature. Zhang et al. (2014, 2016) investigated the complexity of diatom response to Late Glacial and Holocene climate variability on sediment sequences of Lake Ohrid and Lake Dojran. Cvetkoska et al. (2014) provided comparable analysis for neighbouring Lake Prespa. Wilson et al. (2008) investigated the diatom response within the Last Glacial-Interglacial transition in the Ioannina basin (NW Greece) and Jones et al. (2013) strengthened interpretation of Late Pleistocene and Holocene lake-level fluctuations in Ioannina by diatom analysis of multiple cores.

Several diatom-based studies have been carried out in Turkey (from W to E): Eastwood et al. (1999) inferred Holocene environmental changes for SW Turkey based on multi-proxy palaeoecological data (including diatom analysis) from Lake Gölhisar. Reed et al. (1999) evaluated the response of diatom communities to Late Quaternary environmental changes in two small lakes of the Konya basin and compared the results with stable isotope data from the same record to assess the sensitivity of different types of lake systems to local spatial climate variability. Roberts et al. (2001) presented the results of a multi-proxy study including diatom analysis for the last 16,000 yrs from a crater lake, Eski Acigöl, to assess the tempo of Holocene climatic changes for the Eastern Mediterranean region. This record provides the longest, continuous record for Turkey. Woodbridge and Roberts (2011) analysed diatoms from annually-laminated sediments from the Nar crater lake for ca. 2,000 yrs at a decadal time resolution to investigate how threshold and non-climatic effects like human influence may alter the diatom response to climate variability.

The study of Snyder et al. (2001) provides a diatom-based conductivity reconstruction of a 40,000 yrs old sediment sequence recovered from Lake Zeribar (Iran) and aims to estimate the hydrological balance of the lake to clarify the climatic history of the region as pollen records and lake-level reconstructions showed contrasting results (Roberts and Wright, 1993). Recently, Marks et al. (2018) published the results of a multi-proxy based palaeoenvironmental reconstruction (including diatoms) from Holocene lake sediments of the Qarun Lake (Egypt) to examine the climate history of the Faiyum Oasis and the evolutionary development of a permanent lake system.

All those diatom records demonstrated the strong potential of diatoms for palaeolimnological, palaeoenvironmental and palaeoclimate reconstructions in the Eastern Mediterranean region, especially if they are interpreted in combination with multi-proxy or multi-core approaches (e.g. Jones et al., 2013; Eastwood et al., 1999, Cvetkoska et al., 2014). Diatoms often revealed the palaeolimnological history of the analysed lake basins and indicated changes in lake level due to changing climate conditions, i.e. shifts in moisture availability being the strongest climatic forcing function in the semi-arid Mediterranean climate. In Lake Ioannina (Greece) for example, the comparison of three diatom records clearly indicated that lake-level fluctuations were the dominant driver for diatom assemblage composition changes (Jones et al., 2013). Moreover, the diatom record provided the first evidence for the Younger Dryas event in NW Greece (Wilson et al., 2008). Changes in the diatom data from Lake Prespa (Macedonia) were also interpreted as indicators for changing lake levels and therefore as function of varying moisture availability. Furthermore, the diatom record of Lake Prespa clearly demonstrated the high potential of diatoms for inferring past climate change at an orbital and sub-orbital scale. Cvetkoska et al. (2014) demonstrated that moisture availability clearly drove the changing diatom species assemblage composition during glacial-interglacial cycles. In most shallow Mediterranean lakes diatom response is mostly related to lake-level change linked to moisture availability rather than temperature or productivity variations. However, the study of Lake Ohrid diatom assemblages by Zhang et al. (2016) improved the understanding of the strength and complexitiy of diatom response to water temperature in deep, oligotrophic lake systems. These studies also highlight that diatoms demonstrate the strongest signal to lake-level variability, and therefore climate, in shallow, closed lake basins, while palaeoclimate reconstructions from deep, open-drainage freshwater lakes seem to be more complicated (Wolin and Stone, 2010). This could possibly also be one reason for the scarcity of quantitative diatom-based studies in the Eastern Mediterranean region.

1.4.2 Diatom-based research in Israel

Over the last few decades, few diatom-based palaeoecological studies have been carried out in Israel. Ehrlich (1973) and Kafri et al. (1981) described the freshwater diatom flora of ancient lake deposits from the Hula Basin covering the transition from the Late Pleistocene to the onset of the Holocene. The detailed study of Ehrlich (1973) based on several boreholes also contained the description of four new diatom species. Low-resolution studies focusing on the Late Pleistocene diatom succession in sediments from the ancient crater-lake Birkat Ram, located in the Golan Heights, were accomplished by Ehrlich and Singer (1976) and Singer and Ehrlich (1978). Diatoms are only sporadically preserved at low abundances in Holocene sediment samples of Birkat Ram, which makes detailed palaeoecological investigations impossible (Vossel, unpublished data). Begin et al. (1974) present brackish-hypersaline diatom assemblages preserved in some sections of the Late Pleistocene Lisan Formation, which crops out along the Dead Sea Rift valley. In Lake Kinneret, Holocene and sub-recent diatom-based palaeolimnological studies have been carried out previously: Pollingher et al. (1984) presented low-resolution analyses of the changing character of planktonic diatoms in the southern part of the lake over the last 5,000 years, and Ehrlich (1985, Stiller et al., 1984) carried out a palaeoecological assessment of recent environmental change in the diatom flora based on five short cores, including the description of two new planktonic species: *Cyclotella polymorpha* MEYER & HÅKANSSON and *Stephanodiscus galileensis* HÅKANSSON & EHRLICH (Håkansson and Ehrlich, 1987, Meyer and Håkansson, 1996). A detailed taxonomical description and overview of the Israelian diatom flora, collected from different habitat areas across Israel, was compiled by Ehrlich (1995) in the “Atlas of Inland-Water Diatom Flora of Israel”, which was used in this thesis beside other literature for taxonomical identification and ecological interpretations.

1.5 Holocene climate variability in the Eastern Mediterranean

The Holocene was once thought to have been climatologically stable (Dansgaard et al., 1993), but detailed and well-dated palaeoclimate records now show that Holocene climate was punctuated by several so called rapid climate changes (RCC's) occurring synchronously across the globe and triggered by different climatic forcing functions and their interaction, e.g. changes in ocean surface and atmospheric circulation systems, variation in solar insolation and volcanism (Mayewski et al., 2004). One of the well-known RCCs occurred around 8,200 years BP (the so-called 8.2 event), a second one at around 4,200 years BP (the 4.2 event) and a third one around 3,200 years BP (the 3.2 event). A rapid change towards cooler and more arid climate conditions during those events is recognizable around the globe, including the Eastern Mediterranean (Alley et al., 1997, Mayewski et al., 2004, Kaniewski et al., 2010). Additionally, it is highly debated as to whether RCCs can be linked to changes in societal structures, especially in the Eastern Mediterranean region (e.g. in Issar and Zohar (2004), Staubwasser and Weiss (2006), Kaniewski et al. (2010, 2015), Langgut et al. (2013, 2016)).

Across the Eastern Mediterranean, the Early Holocene is reported to be the wettest phase in the past 25, 000 years (Robinson et al., 2006), whereas a trend towards higher aridity with punctual short-term climate shifts, having notable impacts on human occupation patterns, is argued for the mid- to Late Holocene (Rambeau and Black, 2011). A series of reviews have recently been compiled discussing the (Holocene) climate variability in the Eastern Mediterranean in detail by considering the palaeoenvironmental evidence derived from proxies such as pollen analyses from lake sediments, stable isotopes (e.g. from speleothems, lake sediments or snails), from geomorphological indicators (such as palaeo-shorelines), and from the archaeological record (e.g. Issar, 2003, Mayewski et al., 2004, Robinson et al., 2006, Migowski et al., 2006, Finné et al., 2011, Rambeau and Black, 2011, Bar-Matthews et al., 2017, Litt and Ohlwein, 2017, Rosen and Rosen, 2017, Torfstein and Enzel, 2017).

1.6 Settlement history around Lake Kinneret

The oldest habitation site yet discovered in the surroundings of Lake Kinneret is located at Ubadiya (around 2 km SW from the lake) and is represented by the fossil remains of *Homo erectus* communities, which lived there around 1.4 million yrs ago (Belmaker et al., 2002, Berman et al., 2014). Other evidence for prehistoric settlement was found in the karst caves of Wadi Amund in the northwest of the lake: remains of the so called "Galilee man" were found with artifacts from the Middle and Upper Paleolithic periods (Freidline et al., 2012, and references therein, Berman et al., 2014).

With the onset of the Holocene, around 11 700 years ago (Walker et al., 2012), climate conditions rapidly improved from cooler conditions, which prevailed during the last ice age, towards more arid ones. Agriculture and a more sedentary lifestyle emerged to replace the previous hunter-gatherer lifestyle at around the same time and brought more people to the Eastern Mediterranean (Goring-Morris and Belfer-Cohen, 2011), with evidence for increasingly complex societal structure, although the reasons for the origins of agriculture remain an object of lively debate (e.g. Richerson et al., 2001, Gupta, 2004, and references therein). A few archaeological finds demonstrate the existence of smaller settlement communities close to Lake Kinneret (Bar-Yosef, 1995), but trade connections were limited during that time (Zwickel, 2017). During the Chalcolithic period (6,500-5,000 cal BP) settlement sizes increased and more complex structured and inter-regional well-connected societies developed (Epstein, 1998, Gibson and Rowan, 2006, Rowan and Golden, 2009). Many sites existed in the Upper Galilee (north of Lake Kinneret) and the central Golan (Epstein, 1998, Zwickel, 2017). Small, rural communities lived around Lake Kinneret (Epstein, 1977, Epstein, 1998), in which olive cultivation and oil production as well as basalt processing for trading already played a major role (Zwickel, 2017). In the Early Bronze Age (5,500-4,150 call BP) several settlement sites with high population densities are recorded nearby Lake Kinneret. Urban, well organized cities developed, e.g. Tel Bet Yerach (near Ohalo) with around 4,000-5,000 inhabitants (Greenberg, 2011). A decline of settlement density around the lake is reported from the Middle Bronze Age onwards (Greenberg and Paz, 2005). Especially during the Late Bronze Age, there is only little archeological evidence for settlement activity in northern Israel. Within the whole Levantine region unsteady times with many conflicts and intervals of the rise and decline of societal structures are reported (Finkelstein and Piasetzky, 2009), which can be possibly linked to enormous retrogression of trade activities (Zwickel, 2017) and climate (Langgut et al., 2013). The Iron Age is known as a period of resettlement. Societies mainly lived from agriculture and the Golan basalt industry. The Iron Age II period in particular seems to have been one of stabilization with a slight increase of settlement sites around Lake Kinneret (Zwickel, 2017). Less is known from Persian times as there is only limited proof of settlement activity within the archaeological record. With the onset of the Hellenistic period a marked increase in settlement activity is well documented in the archaeological record, with rising population density, bigger urban societies and continuous agriculture activities (Dar, 1993, Berlin, 1997) including the cultivation of large olive plantations. Major irrigation systems were introduced to this region in Hellenistic times and become common in the Roman era to ensure water-supply of bigger urban centres (Lemche, 2015), such as Tiberias, which was founded in the Roman period. During Roman and Byzantine time periods the surroundings of Lake Kinneret were densely populated and economically flourishing (Dar, 1993, Anderson, 1995, Chancey and Porter, 2001): perhaps around 50,000-100,000 people lived around the lake and many more settlements and towns were flourishing nearby in the region (Berman et al., 2014). The Early Islamic period was again marked by an economic regression and a decline in population density and agriculture activities in the whole southern Levant region (Safrai, 1994). The city of Tiberias was repopulated during the Ottoman period in the mid-sixteenth century by a group of autonomous Jewish settlers, but suffered in the following centuries from several different hazards including pillages, sieges and a devastating earthquake in1837 (Berman et al., 2014). In modern times the whole area around Lake Kinneret experienced economic revival by the development of industry and tourism. The first kibbutz “Degania” (at the south of the lake) was established in 1910 and increased the influx of Jewish settlements around the lake and its watershed, which strongly influence the lakes ecosystem till today (Berman et al., 2014). Tiberias, which is located at the western shore of the lake, is today with around 44,000 inhabitants the largest city at the shores of Lake Kinneret. Agriculture plays beside tourism still a major role for its inhabitants: a large proportion lives from the cultivation and export of fruits like bananas, dates and grapes.

1.7 References

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2 *Cyclotella paleo-ocellata*, a new centric diatom (Bacillariophyta) from Lake Kinneret (Israel)

Chapter 2 is based on Vossel, H., Reed, J.M., Houk, V., Cvetkoska, A., Van de Vijver B. (2015): *Cyclotella paleo-ocellata*, a new centric diatom (Bacillariophyta) from Lake Kinneret (Israel). Fottea 15: 63-75. Doi: 10.5507/fot.2015.006

2.1 Abstract

Large, subfossil populations of an unknown centric, planktonic diatom were observed in a lake sediment core from Lake Kinneret (Israel), which is here described as *Cyclotella paleo-ocellata* sp. nov. The new taxon, which belongs to the *Cyclotella ocellata* species complex, is described and separated from other similar taxa (e.g., *Cyclotella ocellata, Cyclotella kuetzingiana, Cyclotella polymorpha, Cyclotella paraocellata*) based on a combination of the following morphological characters: valve diameter, number of orbiculi depressi (circular depressions), number of striae/10 µm, stria length, number and position of rimoportulae and the number of central and marginal fultoportulae. *Cyclotella paleo-ocellata* can be distinguished mainly by two prominent characteristics: (1) the number and the arrangement of the orbiculi depressi (4–8) which increase with the valve diameter and (2) the marginal fultoportulae, situated on each, every second or third costa. Since *Cyclotella paleo-ocellata* is at present only known from the subfossil bottom sediments of Lake Kinneret, its ecological preferences are inferred simply from the associated diatom flora.

Key words: Bacillariophyta, *Cyclotella paleo-ocellata*, Lake Kinneret, morphology, taxonomy

2.2 Introduction

The genus *Cyclotella* (KÜTZING) BRÉBISSON is one of the most commonly occurring genera of the Stephanodiscaceae (Houk et al., 2010). Its species are centric and characterized by a distinct central area and a radially-striated marginal area (Håkansson, 2002). Genera in the family of Stephanodiscaceae are a dominant component of the plankton in freshwaters worldwide. The genus *Cyclotella* often dominates species assemblages in palaeolimnology, particularly in the circum-Mediterranean region, and can cause difficulties or loss of information in palaeoenvironmental reconstructions due to the ongoing taxonomic uncertainty in this group (Håkansson, 2002). The genus exhibits a high morphological variability that is still not completely understood, requiring more detailed analysis of recent and fossil diatom material.

Within the genus *Cyclotella*, it is possible to distinguish several groups of taxa that show a more or less similar morphology. One of these groups is the 'species complex' of *Cyclotella ocellata* PANTOCSEK, a term introduced by Hegewald & Hindáková (1997). Cvetkoska et al. (2012) recently reviewed the complex in detail. *Cyclotella ocellata* was first described by Pantocsek (1901, p. 104, fig.15: 318) as a flat valve with 3 "*margaritis majoribus*" (later named "orbiculi depressi" by Kiss et al., 1996) arranged in a triangular position in the central area with a ring of marginal striae.

As well as the high taxonomic variability within the taxon *C. ocellata* the ecological preferences are also still uncertain. According to several authors (Fritz et al., 1993, van Dam et al., 1994, Kiss et al., 1996, Schlegel and Scheffler, 1999, Cremer and Wagner, 2003, Houk et al., 2010). *C. ocellata* seems to have an extremely broad tolerance of nutrient status, extending (in rare cases) from ultra-oligotrophic [e.g., Lake Ohrid (Cvetkoska et al., 2012)] to eutrophic [e.g., Lake Dagow (Schlegel and Scheffler, 1999)]. Cremer & Wagner (2003) suggested that the *Cyclotella ocellata* complex must comprise several different species or ecological groups, exhibiting contrasting ecological preferences for nutrient status which may in part relate to the biogeographic region in which they grow. *Cyclotella ocellata* is known as a cosmopolitan taxon, often found in shallow lakes [e.g., Lake Las Madres (Kiss et al., 1996) and Laguna de Medina (Reed et al., 2001) in Spain], but can also dominate in very deep lakes such as Ohrid (Cvetkoska et al., 2012) or El'gygytgyn (Cremer and Wagner, 2003), perhaps particularly those with a sandy or gravel lake bed (Houk et al., 2010). It also occurs in slow flowing rivers as plankton or periphyton (Krammer and Lange-Bertalot, 1991, Ehrlich, 1995, Houk et al., 2010).

Few diatom-based palaeolimnological studies have been carried out previously in lake sediments of ancient Lake Kinneret. Pollingher et al. (1984) analysed the changing character of planktonic diatoms in Lake Kinneret over the last 5,000 yrs and Ehrlich (1985) carried out a palaeoecological assessment of recent environmental change in the diatom flora of five short cores. This included the description of two new planktonic species: *Cyclotella polymorpha* MEYER & HÅKANSSON and *Stephanodiscus galileensis* HÅKANSSON & EHRLICH (HÅKANSSON AND EHRLICH, 1987, MEYER AND HÅKANSSON, 1996). Ehrlich (1985) also observed a third unknown centric diatom which she denoted as *Cyclotella* sp. (Ehrlich 1985: Plate 1, Figs 13–14) without formal description.

Diatom-based palaeolimnological studies on a longer timescale have not yet been accomplished in Lake Kinneret. During a drilling campaign which took place as part of the Collaborative Research Center (CRC) 806 “Our Way to Europe” (http://www.sfb806.uni-koeln.de), a 17.8 m long sediment core was recovered which spans the last c. 8,200 cal yrs BP. The detailed diatom-based palaeolimnological analysis of this sediment sequence forms part of a multi-proxy study of Holocene climate change and human impact in the Levant region. During a preliminary analysis of the diatom succession in the sediment sequence of Lake Kinneret, large populations of an unknown *Cyclotella* species are often recorded as abundant in assemblages dominated by the classic *Cyclotella ocellata* type.

Following detailed light and scanning electron microscopy observation, the unknown taxon could not be identified based on the currently available literature. Here, we describe this new taxon as *Cyclotella paleo-ocellata* sp. nov. and discuss its morphology and separation from other taxa within the *Cyclotella ocellata* complex, also attempting the first delimitation of its ecological preferences.

2.3 Materials and Methods

2.3.1 Study site

Lake Kinneret (from Hebrew word *kinnṓr* = ‘harp’, reflecting the shape of the lake) is also known as the Sea of Galilee or Lake Tiberias and is located in the northern part of the Jordan Rift Valley in the North of Israel (32°48’08.12’’ N, 35°35’20.62’’ E; fig. 2.1). It is situated, together with the Dead Sea basin, on the “Dead Sea Transform Fault (DSTF)”. The DSTF currently forms a more than 1000 km long transform fault, connecting the divergent plate boundary along the Red Sea with the Alpine convergent zone in Turkey (Hurwitz et al., 2002). The modern and Holocene Sea of Galilee has evolved from ancient water bodies that filled the Kinneret tectonic depression in the northern Jordan basin during the Late Pleistocene (Hazan et al., 2004). The lake basin is mainly surrounded by volcanic igneous rocks (basalts in the Golan Heights), which were formed during the Oligocene, Miocene and Pleistocene and now form escarpments of up to 500 m in height around the lake.

The lake is 22 (N-S) km long, 12 km (W-E) wide and up to 43 m deep, and is situated 210 m below sea level (mbsl). The lake surface area is almost 167 km^2 and the catchment (total surface = 2730 km^2) extends to parts of the Upper Galilee in NE Israel, the Golan Heights, the Hermon range (with the peak of Mt. Hermon at 2814 m above sea level (masl)) and the southern Anti-Lebanon mountains (Baruch, 1986). The lake is mainly fed from the north by the River Jordan, which also drains the lake southwards to the Dead Sea. The lake is warm and monomictic, being stratified with an anoxic hypolimnion from May to December and fully mixed from December to April (Gophen, 2003). An overview of the main limnological parameters (i.e. chemical components of the lake water, composition of bottom sediments & secchi depth) are given in table 2.1. Lake level fluctuates by up to 4 m depending on precipitation, evaporation and water abstraction by the National Water Carrier operation. The Kinneret area has a Mediterranean climate, characterized by mild, rainy winters and hot, dry summers (Baruch, 1986).

Table 2.1 Table of typical annual limnological parameters for the epilimnion of Lake Kinneret based on the Lake Kinneret data base supplied by Ami Nishri (2014).

Chemical parameters:		
pH	8.6	
Salinity (as Cl)	250	mg/l
Silica (as SiO_2)	9	mg/l
Soluble P (as PO_4)	2	µg/l
Total phosphorus	20	µg/l
Nitrogen (as NO_3)	80	µg/l
Pelagic bottom sediments:		
Clay minerals	35	%
Calcium carbonate	55	%
Organic matter	5	%
Residual	3	%
Secchi depth	2.8-4.0	m

2.3.2 Field and laboratory methods

Two parallel sediment cores (core KI_10_I and KI_10_II) were recovered from a water depth of 38.8 m at the central, deepest part of the lake basin (32°49’13.8’’N, 35°35’19.7’’E; fig. 2.1 ‘red star’) in March 2010, using an UWITEC Universal Sampling Platform (http://www.uwitec.at) with a piston corer system. Sediment cores were transported for storage to the University of Bonn. The 17.8 m continuous master sequence covers approximately the last 8,200 cal yrs BP (Schiebel, 2013). This diatom study is based on analysis of taxa observed at various core depths between 4.5 m and 10.0 m, where the unknown species is abundant in the diatom flora.

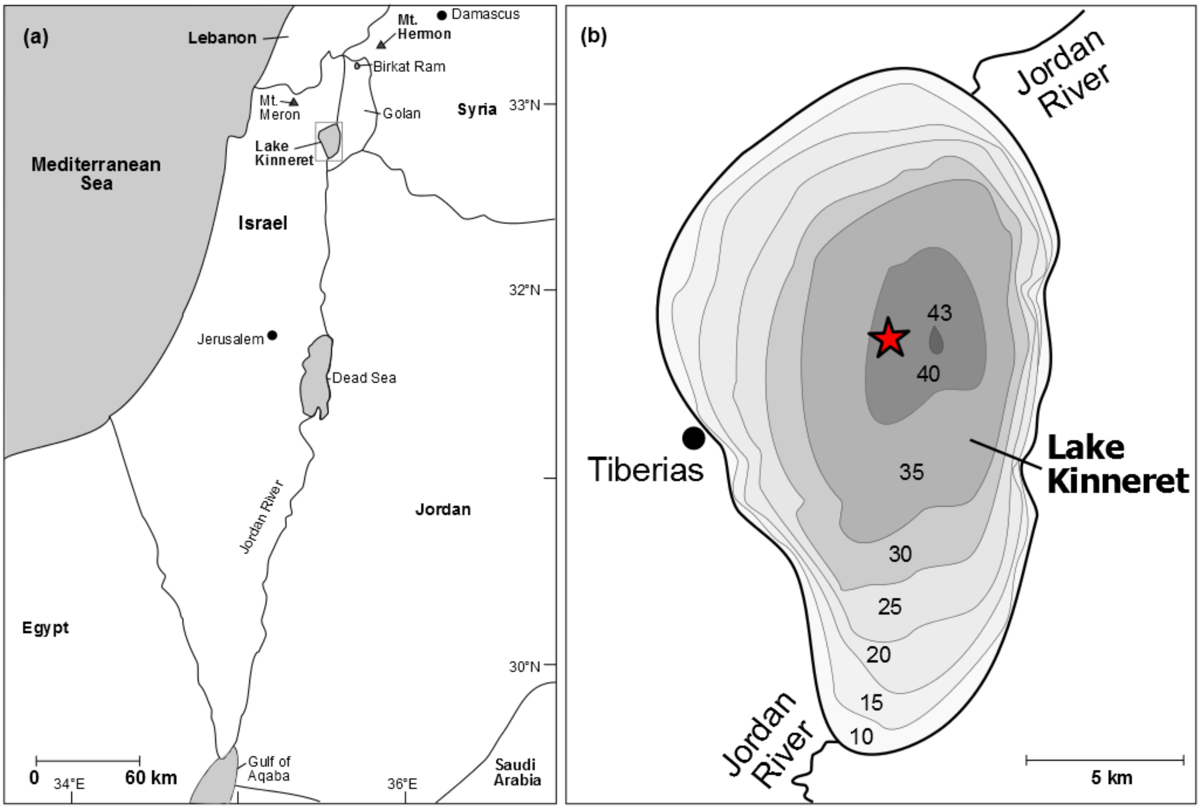

Figure 2.1 (a) Location of Lake Kinneret in the North of Israel; (b) Bathymetrical map of the lake (interval of isobathic curves is 5 m). The drilling location is marked by a ‘red star’ (modified after Schiebel, 2013).

All samples were prepared using standard techniques (Battarbee, 1986): 0.2 g of wet sediment was treated with H_2O_2 (30 %) and heated on a hotplate for several hours to oxidize organic matter. Afterwards a few drops of concentrated HCl (35 %) were added to the hot sample residual to remove carbonates. Samples were washed with distilled water and centrifuged several times (1200 rpm for 7 min) to eliminate the acid residual and avoid dissolution during storage. The cleaned sample material is stored at 4 °C in a cooling chamber at the University of

Bonn (Germany). A subsample from the cleaned, organic-free material was mounted in Naphrax™ for diatom community analysis using an Olympus BX53 light microscope (LM) at x1000 magnification, equipped with Differential Interference Contrast and an Olympus UC30 digital camera. For scanning electron microscopy (SEM), parts of the oxidized suspensions were filtered through a 1-µm Isopore™ polycarbonate membrane filter (Merck Millipore). The stubs were sputter-coated with a Gold-Palladium layer of 20 nm and studied using a ZEISS Ultra SEM microscope at 3 kV (Natural History Museum London, UK). Diatom terminology follows Ross et al., (1979), Kiss et al. (1996, 1999), Håkansson (2002) and Houk et al. (2010). The term ‘orbiculi depressi’ introduced by Kiss et al. (1996) is used to indicate the shallow central depressions.

Fifty non-dissolved valves were photographed and used for morphometric analysis of the following valve features: diameter (µm), length of the marginal striae (µm), number of striae in 10 µm, number of central fultoportulae, number of orbiculi depressi, number of rimoportulae and number of costae between the marginal fultoportulae.

Comparisons with other, similar *Cyclotella* taxa are based on Håkansson (1990a, 1990b, 2002), Kiss et al. (1996, 1999), Meyer & Håkansson (1996), Hegewald & Hindaková (1997), Genkal & Popovskaya (2008), Houk et al. (2010) and Cvetkoska et al. (2014).

2.4 Results

2.4.1 Description of *Cyclotella paleo-ocellata* Vossel & Van de Vijver sp. nov. (Figs 2.2–2.18, 2.20–2.34)

2.4.2 Light microscopy (Figs 2.2–2.18):

Valves circular, nearly flat. Valve diameter (n=50): 14.1–28.7 µm. Three dome-shaped initial valves found (diameter 22.6–27.4 µm) (Figs 2.17, 2.18). Central area colliculate (Figs 2.2, 2.6, 2.13, 2.15), between ½ and ¾ of the valve diameter, clearly delimitable from marginal area. Orbicular depressions arranged concentrically in the central area (Figs 2.4, 2.14), presenting occasionally a star-shaped pattern (Figs 2.3, 2.7, 2.11). Number of orbicular depressions variable, 2.4–2.8 (Fig. 2.19B). Papillae present in between the depressions, in number always equal to the number of orbicular depressions (‘p’; Fig. 2.5). Initial cells lacking any depressions or papillae (Figs 2.17, 2.18). Central fultoportulae easily visible by changing focus level, 2.2–2.8 (Fig. 2.19A) near the orbicular depressions (‘cf’; Fig. 2.8). Rimoportulae, 1–2(3) present near the marginal striae (‘rp’; Fig. 2.8). Marginal fultoportulae usually visible, separated by (0)1–2 costae (‘mf’; Fig. 2.15). Near the rimoportulae, three costae separating adjacent marginal fultoportulae. Marginal striae, 12–20 in 10 µm (Fig. 2.19C), almost equal in length, 2.4–5.6 µm, throughout the entire valve, never penetrating into the central area (Figs 2.2, 2.6, 2.10, 2.15). Some interstriae forked (‘arrows’; Figs 2.13, 2.15, 2.16).

2.4.3 Scanning electron microscopy (Figs 2.20–2.34):

Valve exterior: Valve face central area colliculate, covered by irregularly shaped, sized and scattered, usually rounded, hillock-like protuberances (Figs 2.20, 2.21, 2.24). Orbiculi depressi (circular depressions) occurring as large, shallow depressions never penetrating the valve wall (‘o’; Figs 2.20, 2.21, 2.23), gradually decreasing in size towards the center. Ball-like silica granules, looking like large papillae, positioned outwards between the orbicular depressions, decreasing in size towards the valve center when positioned in series on a ridge (‘p’; Figs 2.20, 2.21, 2.23). When absent, the papilla postament (‘pp’) visible as a round small depression where the silica granule (papilla) was originally located (Figs 2.20, 2.21). Silica granules show an irregular colliculate surface sculptured by a series of ridges and small hillocks (Figs 2.23, 2.24). Externally striae multiseriate, usually composed of two (outer) rows of larger areolae and 1–2 (inner) rows of small areolae (Figs 2.20, 2.24, 2.26), the latter situated between the rows of larger areolae. Near the valve margin, striae merging due to shortening of the interstriae bearing a marginal fultoportula (‘mf’; Figs 2.24, 2.26). Interstriae of irregular width, slightly raised above the level of the striae (Fig. 2.24). Conical spinulae present on each interstria, near the central area (‘s’; Figs 2.24, 2.25). When absent, position of spinulae still visible as a shallow round depression (Figs 2.20, 2.24). Small granules (‘g’) scattered on the interstriae. A series of cylindrical, blunt spines present near the valve margin (‘ms’; Figs 2.20, 2.26 (‘arrows’), 2.27). External openings of the central fultoportulae visible as small, rounded pores (‘cf’; Figs 2.20, 2.21, 2.23). Marginal fultoportulae visible externally as small, rounded pores on each or every second or third interstria, usually shortening the interstriae near the valve margin (Figs 2.20, 2.24, 2.26). Rimoportula(e) positioned on the interstriae close to the central area, present as small, rounded pores (‘rp’; Figs 2.20, 2.24). When rimoportula present, marginal fultoportula absent, separating two adjacent marginal fultoportulae by 3 interstriae (instead of 1–2).

Valve interior: Valve face more or less flat with a slightly undulating central area. Internal openings of the central fultoportulae present as short tubuli with two satellite pores (‘cf’; Figs 2.28, 2.31). Near the valve margin interstriae (costae) composed of short stronger costae (ribs) without processes alternating thinner depressed costae bearing marginal fultoportulae, with small alveolar openings between them (‘mf’; Figs 2.28, 2.30, 2.32). Internal openings of the marginal fultoportulae surrounded by two satellite pores (Figs 2.32, 2.33). Rimoportula(e) present externally as a small circular opening, internally as a sessile labium with a wide slit with a variable orientation, usually radial (‘rp’; Figs. 2.28, 2.29, 2.30, 2.34).

Holotype (designated here): BR–4383 (Botanic Garden Meise, Belgium)

Isotypes (designated here): PLP–268 (University of Antwerp, Belgium); STIPB-Vossel-1 (Steinmann-Institute, Rheinische Friedrich-Wilhelms University of Bonn, Germany)

Type locality: Lake Kinneret, Israel, sediment core KI10_II_4.8-5.8, sample H44 (Leg. LITT et al.; coll. date 03/2010).

Etymology: The specific epithet (*paleo-ocellata*) refers to the similarity with *Cyclotella ocellata* and the fact that, to date, the species has only been found in subfossil material from a sediment core.

Associated diatom flora: *Cyclotella paleo-ocellata* is abundant over large parts of the sediment core (relative abundance often > 30 %), where *Cyclotella ocellata* is dominating the diatom flora. Other common taxa comprise various *Stephanodiscus* taxa including *S. galileensis*, *Amphora* taxa (e.g., *A. indistincta* LEVKOV and *A. ovalis* (KÜTZING) KÜTZING), unidentified *Staurosira* and *Staurosirella* taxa and *Aneumastus* taxa such as *A. stroesei* (ØSTRUP) D.G.MANN & STICKLE and *A. tusculus* (EHRENBERG) D.G.MANN & STICKLE.

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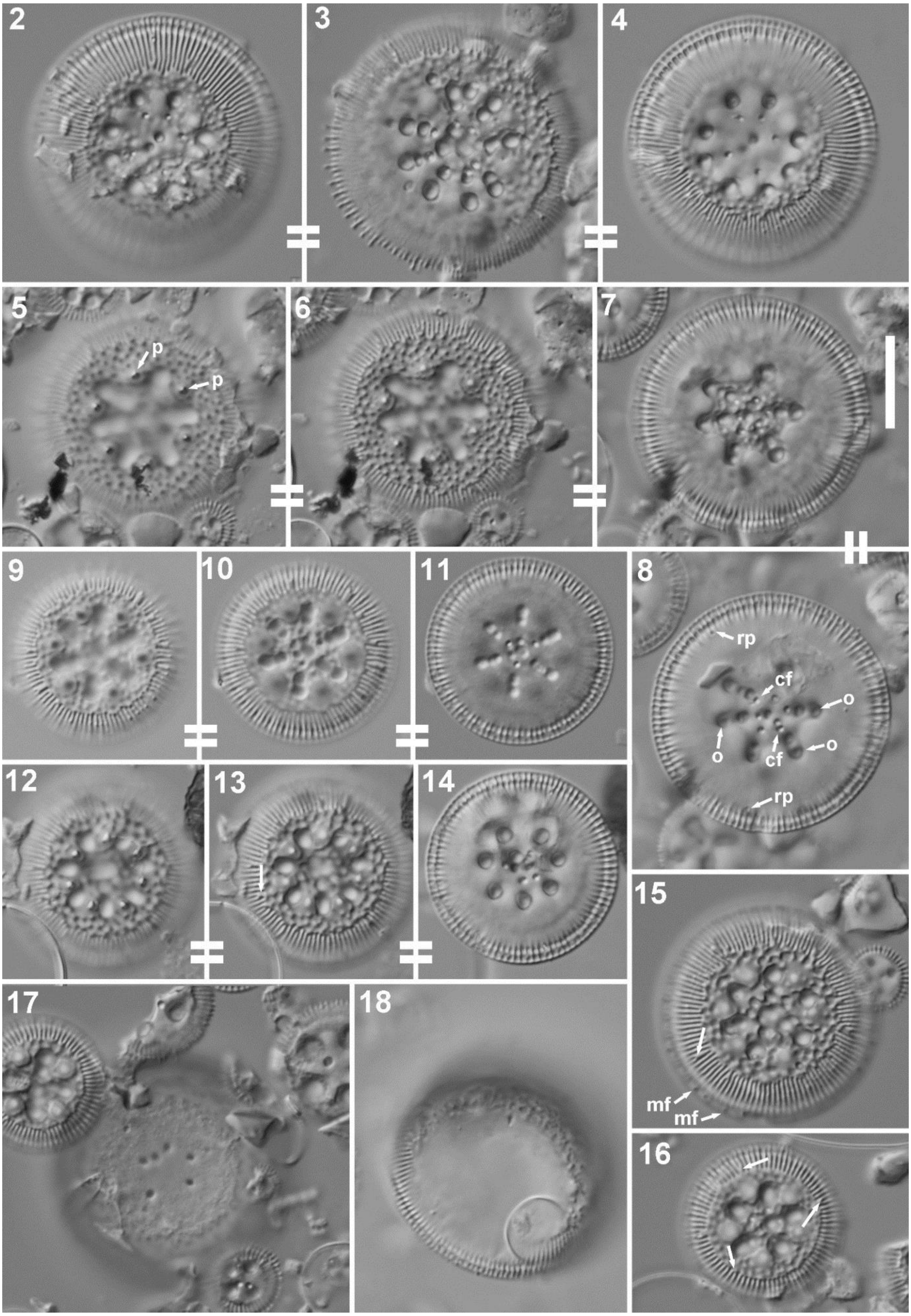
Figure 2.2-18 Photographs of the type population of *Cyclotella paleo-ocellata* sp. nov. from the subfossil bottom sediments of Lake Kinneret (sample H44) taken under a light microscope (magnification 1000 times); (2.2–2.16) Vegetative cells. Several valves are photographed at different focus levels (indicated by ‘=’) to show all morphological details; (2.17–2.18) Initial cells. Scale bar indicates 10 µm. Used abbreviations: ‘cf’ = central fultoportula, ‘mf’ = marginal fultoportulae, ‘o’ = orbiculi depressi, ‘p’ = papilla, ‘rp’ = rimoportula, arrows on Figs 2.13, 2.15–2.16 = forked interstriae.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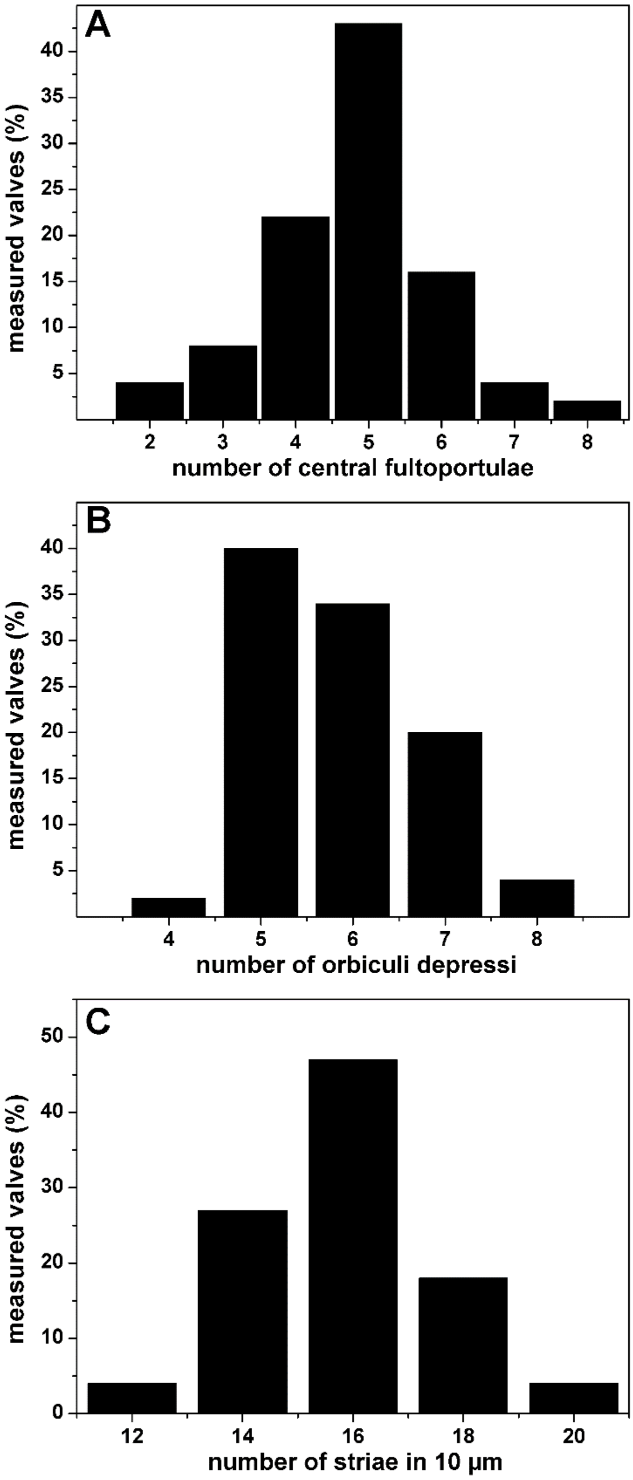
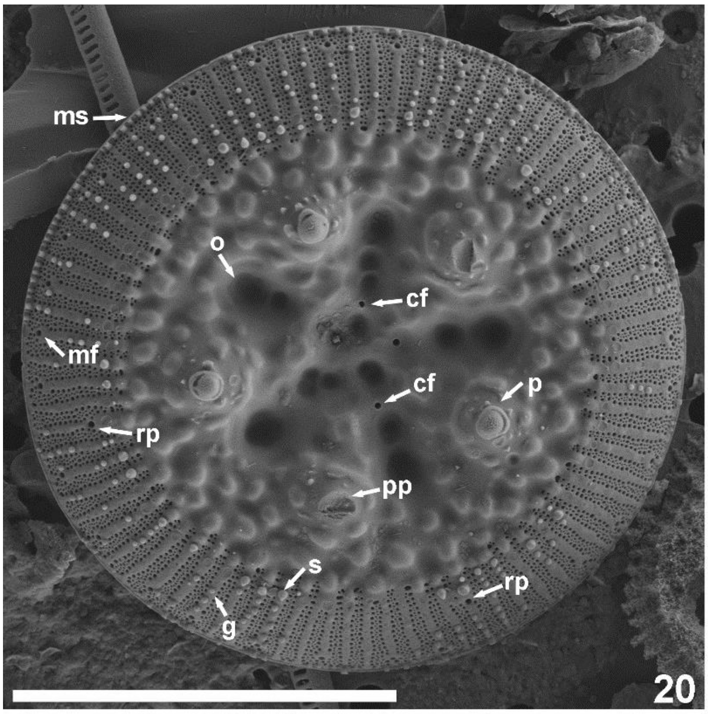


Figure 2.19 Relation between measured valves of *Cyclotella paleo-ocellata* (in percentage; n=50) and (A) the number of central fultoportulae; (B) the number of orbiculi depressi; and (C) the number of striae in 10 µm.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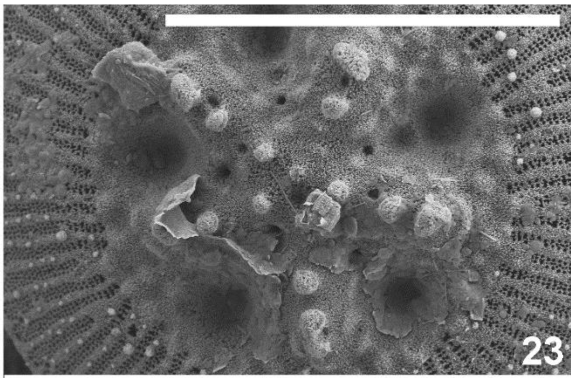
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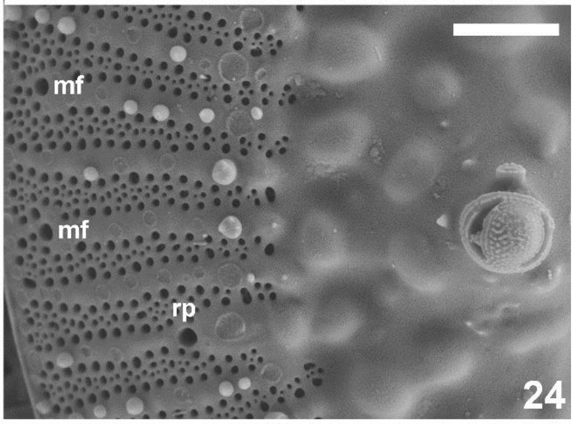
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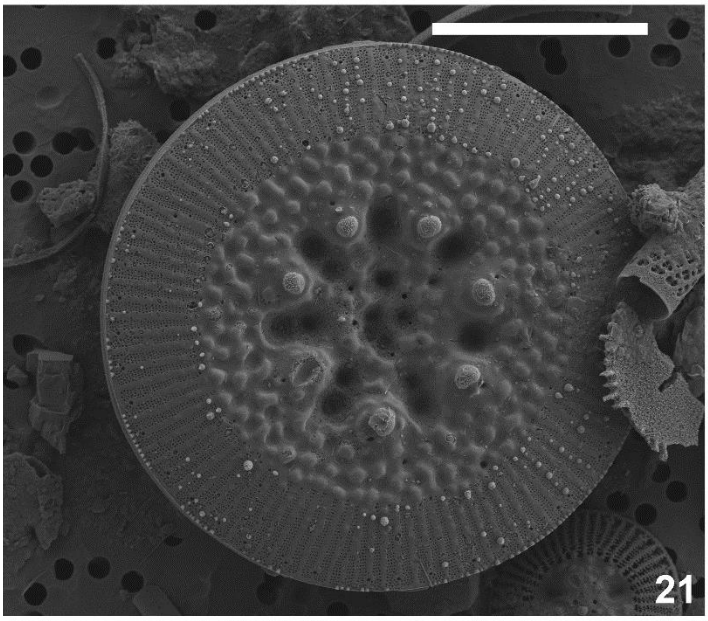
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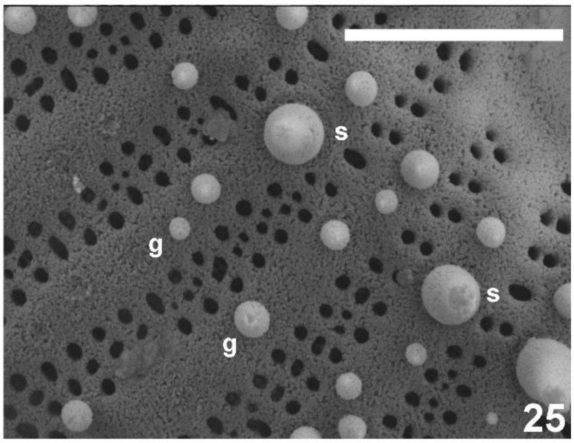
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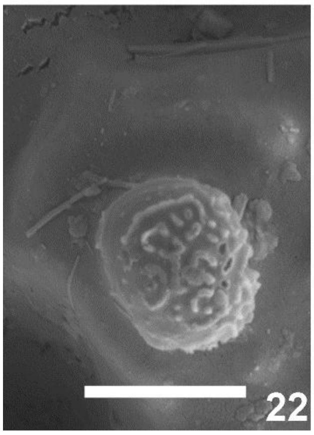
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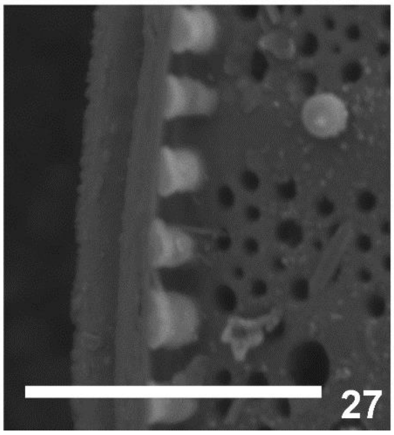
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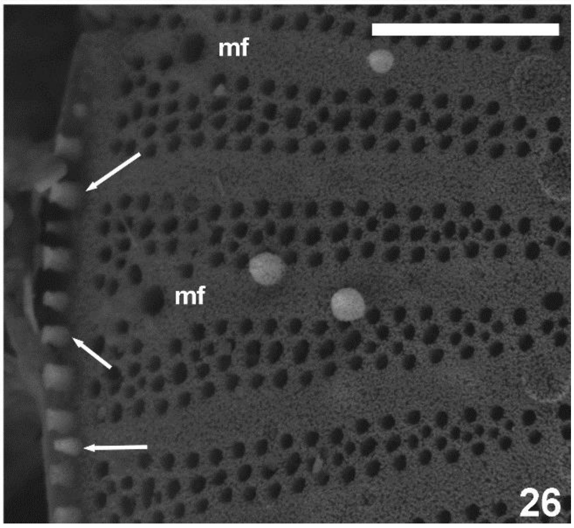
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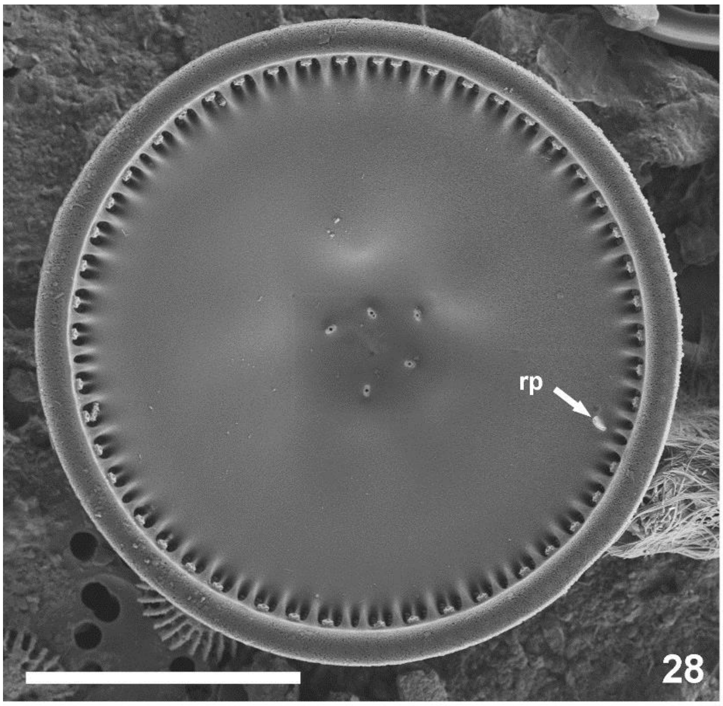
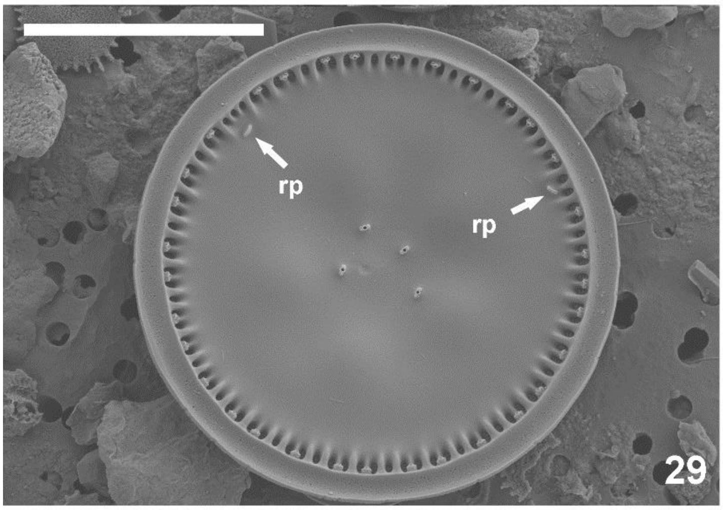
Figure 2.20-27 External scanning electron microscopy view of *Cyclotella paleo-ocellata* sp. nov. (type population, Lake Kinneret, sample H44). (2.20–2.21) External views of a complete valve face showing different organisations of the central area; (2.22) Detailed picture of a large silica granula (papilla) and its surface ornamentation (2.23) Detailed external view of the central area showing radial rows of papillae and central fultoportulae; (2.24) Detailed external view of the central area and the marginal striae. Note the presence of spinulae, granulae, rimoportula and the marginal fultoportulae; (2.25) Detailed external view of the marginal striae with a clear indication of the spinulae and granulae. Note the different rows of areolae in the striae; (2.26) Detailed external view of the marginal striae. Note the presence of blunt spines on the valve margin (‘arrows’); (2.27) Detailed picture of blunt spines. Scale bar indicates 10 µm for figs 2.20, 2.21 & 2.23 and 1 µm for figs 2.22, 2.24–2.27. Used abbreviations: ‘cf’ = central fultoportula, ‘g’ = granula ‘mf’ = marginal fultoportula, ‘ms’ = marginal spins, ‘o’ = orbiculi depressi, ‘p’ = papilla, ‘pp’papilla-postament, ‘rp’ rimoportula, ‘s’ = spinula.

Figure 2.28-34 Internal scanning electron microscopy view of *Cyclotella paleo-ocellata* sp. nov. (type population, Lake Kinneret, sample H44); (2.28–2.30) Internal view of complete valves with different organization of the central area; (2.31) Detailed view of the central fultoportulae showing two satellite pores per fultoportula; (2.32) Detailed picture of the marginal area showing two marginal fultoportulae (with two satellite pores) separated by one thickened costa; (2.33) Detailed picture of a marginal fultoportula showing two setallite pores; (2.34) Detailed picture of a rimoportula as a sessile labium with a wide slit. Scale bar indicates 10 µm except for figs 2.31, 2.32 & 2.34 where scale bar = 1 µm and fig. 2.33 where scale bar = 0.5 µm. Used abbreviations: ‘c’ = costa, ‘cf’ = central fultoportula, ‘mf’ = marginal fultoportula, ‘rp’ rimoportula.


rp
28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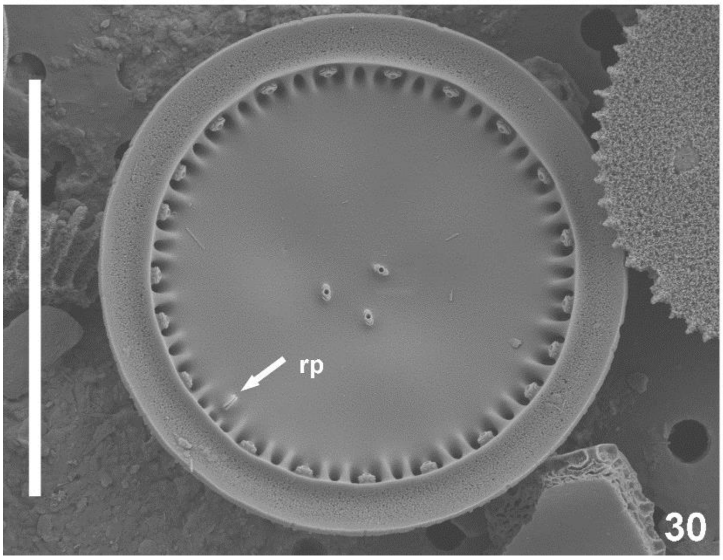
rp
29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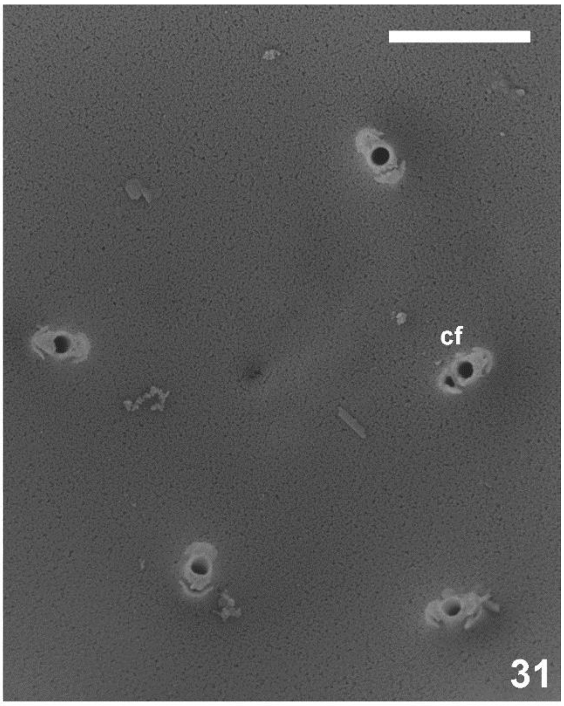
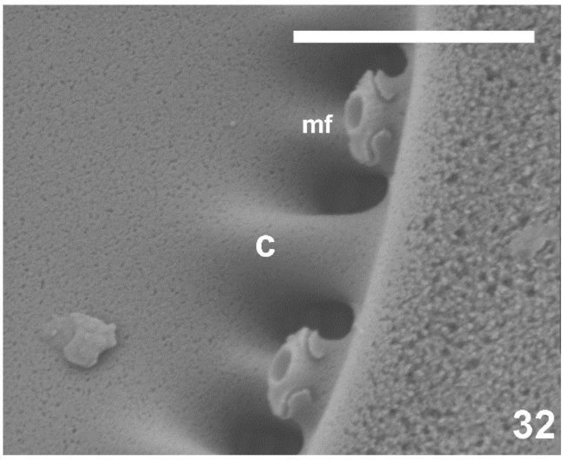
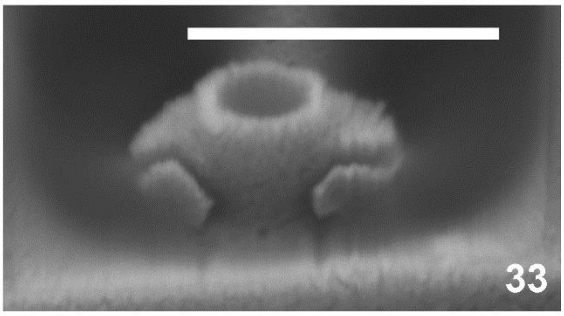

cf
31


mf
c
32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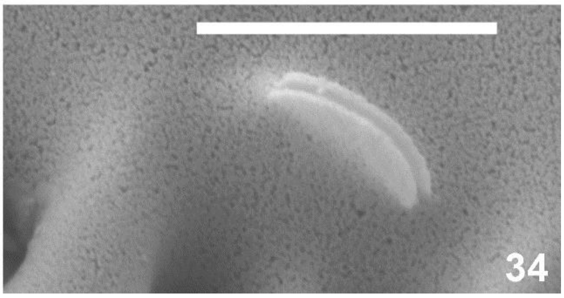
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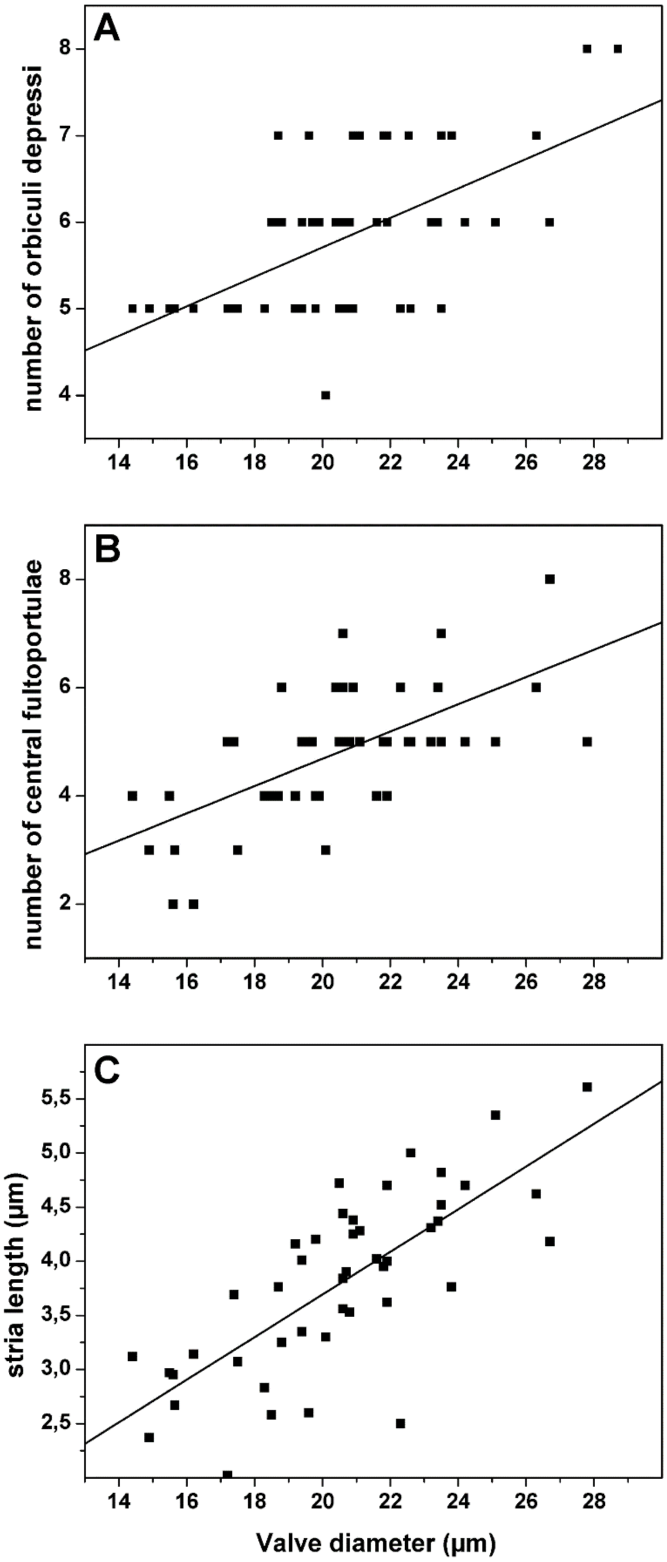

Figure 2.35 Relation between the valve diameter (µm) of *Cyclotella paleo-ocellata* and (A) the number of orbiculi depressi (R = 0.5955; $p < 0.0001$); (B) the number of central fultoportulae (R = 0.63352; $p < 0.0001$); and (C) the stria length (µm) (R = 0.74745; $p < 0.0001$). A regression line is added to all graphs.

2.5 Discussion

2.5.1 Comparison with other taxa

Cyclotella paleo-ocellata belongs morphologically to the *Cyclotella ocellata* species complex, based on the presence of orbiculi depressi and papillae in the colliculate central area, and on the arrangement and position of marginal striae, rimoportulae and fultoportulae. Table 2.2 describes other taxa with which *C. paleo-ocellata* may be confused, demonstrating that the new taxon is quite distinct based on the measured set of morphological characteristics. It differs from similar *Cyclotella ocellata* PANTOCSEK and *Cyclotella kuetzingiana* THWAITES first of all in having marginal fultoportulae situated on each, every second or third costa.

Cyclotella ocellata has a similar stria density but a contrasting stria organization, exhibiting marginal striae of unequal length whereas in *C. paleo-ocellata* all marginal striae have a more or less equal length. Moreover, *C. ocellata* is usually smaller (valve diameter 5–22 µm vs. 15–28 µm in *C. paleo-ocellata*) with a lower number of orbiculi depressi (3–6 in *C. ocellata* vs. 5–8 in *C. paleo-ocellata*), a lower number of central fultoportulae (up to 5 vs. up to 8 in *C. paleo-ocellata*) and the marginal fultoportulae are positioned on each 2–5 costae whereas in *C. paleo-ocellata* this is limited to 1–3 costae. Kiss et al. (1996, 1999) discussed various biometrical ratios for *C. ocellata*. Figures 2.35 A–C show the same ratios for *C. paleo-ocellata*. All measured parameters are highly significant. Figure 2.35A shows clearly that larger valves have a higher number of orbiculi depressi ($R = 0.5955$, $p < 0.0001$), in contrast to *C. ocellata* where the number of orbiculi decreases with increasing valve diameter (Kiss et al., 1996). Hegewald & Hindaková (1997) made a similar observation in a study of a *C. ocellata* population from the Gallberg pond in NW-Germany (although the pictures shown in their publication clearly differ from the *C. ocellata* type species and appear to resemble more closely *C. polymorpha*), clearly indicating this important morphological difference between *C. ocellata* and *C. paleo-ocellata*. The number of central fultoportulae in relation to the valve diameter (Fig. 2.35B) shows a trend that is comparable to *C. ocellata*: larger valves tend to have a higher number of central fultoportulae ($R = 0.6335$, $p < 0.0001$) (Kiss et al., 1996). Finally, stria length significantly increases with valve diameter (Fig. 2.35C) in *C. paleo-ocellata* ($R = 0.7475$, $p < 0.0001$), a feature not analysed in *C. ocellata*. Genkal & Popovskaya (2008) analysed a *C. ocellata* population from Lake Khubsgul (southern Baikal basin, Mongolia). They observed larger valves (up to 40 µm) with a highly variable number of costae (2–8) between the marginal fultoportulae, a high number of central fultoportulae (1–13), which are often positioned very close to each other, and

Table 2.2 Table of comparison between the morphology of *Cyclotella paleo-ocellata* and similar species belonging to the *Cyclotella ocellata*-complex.

	Cyclotella ocellata	***Cyclotella kuetzingiana***	***Cyclotella tripartita***	***Cyclotella rossii***	***Cyclotella pantanelliana***[a]	***Cyclotella polymorpha***	***Cyclotella paraocellata***	***Cyclotella paleo–ocellata***
reference	Kiss et al. (1999)	Houk et al. (2010)	Håkansson (1990a)	Håkansson (1990b)	Houk et al. (2010)	Meyer & Håkansson (1996)	Cvetkoska et al. (2014)	this study
valve diameter (µm)	5–22	8–45	2–18	5–18	12–70	4.5–16	9–34	15–28
central area	flat, smooth to colliculate	slightly undulate to nearly flat	colliculate, radially undulate	nearly flat, externally colliculate	concentrically (radially) undulate	circumferentially undulate, flat	flat, colliculate	flat, colliculate
orbiculi depressi	3–6	none or short radial rows of depressions	none, 3 depressions with triangular punctate field	none, 2–8 radial punctated rows	radial series of depressions	variable	3–6	4–8
number of striae (in 10 µm)	14–20	12–18	19–22	16–18	12–14	(18)20–22(24)	15–18	13–20
striae lenght	unequal	unequal	unequal	equal	nearly equal	equal to unequal	unequal	equal
central fultoportulae	1–5 (5)	1–5(7)	(1)2–3	2–3(5)	?	1–5(7)	3–5	1–8
satellite pores on central fultoportula	2	2	2	2	?	2(3)	2–3	2
marginal fultoportulae	on each 2–5 costae	on each (1)2–4(5) costae	on each (4)5–7 costae	on each 2–3(5) costae	on each costa	on each 2–5 costae	on each 3–5 costae	on each (1)2–3 costae
satellite pores on marginal fultoportula	2	2	2	2	?	2	2	2
rimoportulae	1	1	1	1	1–3?	1	3	1–3
location of rimoportula in valve interior	close to costae	in the marginal area	separated from costae	separated from costae	?	in between costae/next to it	close to costae	close to costae

[a] no SEM observations in literature

always 3–4 orbiculi depressi in the central area, regardless of the valve diameter. This combination of features has never been observed in *C. paleo-ocellata* and it is even highly likely that based on the differences between this taxon and the type species of *C. ocellata*, the Mongolian population may represent more than one taxon. *C. ocellata* and *C. paleo-ocellata* co-occur in our sediment samples but are easy to separate.

Cyclotella kuetzingiana THWAITES is similar to *Cyclotella paleo-ocellata* in the presence of depressions in the central area (see Håkansson, 2002, figs: 330–337; Houk et al., 2010, fig. 189: 1–6). However, *C. kuetzingiana* has a larger valve diameter (8–45 µm vs. 15–28 µm in *C. paleo-ocellata*) and marginal fultoportulae positioned on every 2–4(5) costae, while in *C. paleo-ocellata* the marginal fultoportulae are separated by (0)1–2 costae. Additionally, the central area depressions in *C. kuetzingiana* lack any pattern of arrangement. Valves sometimes have very few papillae (see Houk et al., 2010, fig. 188: 1–6, fig. 189:1–5) and their number and arrangement are not equal as it is in *C. paleo-ocellata*. Also, no valves with more than seven central fultoportulae have been reported for *C. kuetzingiana* (Håkansson, 2002, Houk et al., 2010). *Cyclotella kuetzingiana* var. *radiosa* FRICKE has a similar radial arrangement of the central area depressions, but lacks any papillae, has smaller striae density (12–14 in 10 µm), only one rimoportula and a large number of radially arranged valve face central fultoportulae (see Houk et al., 2010, fig. 192: 1–6).

Cyclotella tripartita Håkansson (1999b, p. 76, figs 1–4, 8–11, 13) has a smaller valve diameter (2–18 µm), fewer central fultoportulae (max 2–3 vs. 2–8 in *C. paleo-ocellata*) and there are 4–7 costae (instead of (0)1–2 in *C. paleo-ocellata*) between the marginal fultoportulae. Most definitively, *C. tripartita* lacks the typical orbiculi depressi. The central area is instead divided into six sections, three of them depressed having a triangular punctate field (Håkansson, 1990b). The rimoportula is located at a rather large distance from the costae, contrary to *C. paleo-ocellata* where the rimoportulae are located immediately next to the costae.

Cyclotella rossii Håkansson (1990a, p. 267, figs 18–27, 46–49) has an equal number of costae between the marginal fultoportulae but is smaller (valve diameter 5–18 µm vs. 15–28 µm) with 2–3, sometimes 5, central fultoportulae. The species again lacks the typical orbiculi depressi but is characterized instead by 2–8 radial rows of puncta (Håkansson, 1990a). The rimoportula in the valve interior is well separated from the costae, contrary to the new taxon.

Cyclotella pantanelliana CASTRACANE (1886, p. 171) is larger (valve diameter up to 70 µm) with a lower number of marginal striae (only 12–14 in 10 µm) and lacks the typical orbiculi depressi, being characterized by radial series of large, coarse puncta, clearly penetrating the cell wall, which can be observed in LM during focus changing (Houk et al., 2010). Therefore, eroded valves of *C. paleo-ocellata* might look somewhat similar to *C. pantanelliana*. The arrangement of the marginal fultoportulae is also similar (separation by only 1 costa; Houk et al., 2010) and can produce some confusion. The marginal area of *C. pantanelliana* shows typical forked thinner costae between thickened ribs, which could also be confused with the forked interstriae of *C. paleo-ocellata*. However, no SEM observations have been made on the taxon of *C. pantanelliana* due to the fact that type material from Italy is no longer available.

Cyclotella polymorpha MEYER & HÅKANSSON (1996, p. 64, figs 1–29) has a smaller valve diameter (4.5 µm – 16 µm) with a contrasting central area morphology which lacks the typical concentrically arranged orbiculi depressi. Both taxa are easy to distinguish by their characteristic central area: *Cyclotella polymorpha* shows a high variability of ornamentation patterns (i.e. radial rows of depressions with granulae on the raised area or 1–5 larger depressions having occasionally papillae in between (Houk et al., 2010) irregularly arranged in the central area in comparison to *C. paleo-ocellata*. Striae are usually of unequal length and usually penetrate deep into the central area. The central area is by this fact sometimes not clear to delimit in *C. polymorpha*, whereas it is easily in *C. paleo-ocellata.*

Cyclotella polymorpha becomes more abundant in the upper parts of the sediment sequence from Lake Kinneret and also occurs in the modern diatom flora. Its increase occurs at the expanse of *C. paleo-ocellata*, which is replaced completely at ca. 2,500 cal yrs BP (Vossel unpublished).

Finally, *Cyclotella paraocellata* CVETKOSKA, HAMILTON, OGNJANOVA-RUMENOVA & LEVKOV (2014, p. 317, figs 1–23, 30–45) is rather similar to *C. paleo-ocellata* but can nevertheless be separated based on the lower number of orbiculi depressi (3–6), unequal stria length, a constant, higher number of rimoportulae (3 vs. 1–3 in *C. paleo-ocellata*) and a lower number of central fultoportulae (3–5). The central area of *C. paraocellata* is smaller than that of *C. paleo-ocellata* (40–50 % vs. 50–75 % of the valve diameter). The largest difference is the arrangement of the marginal fultoportulae, separated by 3–5 costae in *C. paraocellata* compared to (0)1–2 costae in *C. paleo-ocellata*. Although Cvetkoska et al. (2014) reported valves with twinned orbiculi depressi and papillae, the authors did not report any valves with multiple papillae arranged in a series.

2.5.2 Palaeoecological remarks

It is remarkable that several new species of *Cyclotella* have evolved since the Miocene period in the Mediterranean region (Cvetkoska et al., 2014). *Cyclotella paleo-ocellata* in Lake Kinneret is a new example. The date of first appearance of *C. paleo-ocellata* is at present unknown, pending recovery of the pre-Holocene sediment record. It is not yet possible to identify the exact environmental preferences of *C. paleo-ocellata* since the taxon is only known from subfossil assemblages. Ecological preferences can be inferred instead based on its association with other taxa of known ecology. *Cyclotella paleo-ocellata* is often abundant where *C. ocellata* is dominating the diatom flora, together accounting for almost 90 % of the assemblage. Several *Aneumastus* taxa such as *A. stroesei,* are also present but at very low abundance. These taxa are known to prefer oligotrophic lakes (Lange-Bertalot, 2001).

As mentioned before, the broad ecological preference of *C. ocellata* makes ecological interpretations difficult. However, the period between 6,500 and 3,000 cal yrs BP is known as a humid phase (Litt et al., 2012), when the lake level of Lake Kinneret was higher than at present (Hazan et al., 2005). *Cyclotella paleo-ocellata* has large, thick robust silica frustules, suggesting based on life habit preferences of similar taxa [e.g., cylotelloid species from Lake Malawi, Afrika (Huisman and Sommeijer, 2002, Stone et al., 2011)] that it has an adaptive advantage in staying in suspension in deep turbulent open waters. Larger varieties of the *C. ocellata* complex often seem to occur in deeper open-water lakes [e.g., deeper phases of the Ioaninna sequence in Greece (Wilson et al., 2008)].

Both *Cyclotella paleo-ocellata* and *Stephanodiscus galileensis* disappeared at c. 2,500 cal yrs BP in the sediment record (Vossel unpublished). Since this disappearance coincides with human-induced eutrophication indicated by a phase of forest clearance and the cultivation of olive trees identified in the pollen record (Schiebel, 2013), it can be inferred that *C. paleo-ocellata* developed in an oligotrophic phase of lake development and has low tolerance of nutrient enrichment. Convincingly, the decrease of *Cyclotella paleo-ocellata* coincides with the rise of a range of centric taxa which are strong indicators for eutrophication, including *Cyclotella meneghiniana* KÜTZING, *C. polymorpha*, *Aulacoseira granulata* EHRENBERG and several small *Stephanodiscus* species including *S. hantzschii* GRUNOW, *S. minutulus* KÜTZING and *S. medius* HÅKANSSON also indicating a clear shift from oligotrophic to more eutrophic conditions (Krammer and Lange-Bertalot, 1991).

2.6 Acknowledgements

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3 Lake Kinneret (Israel): New insights into Holocene regional palaeoclimate variability based on high resolution multi-proxy analysis

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3.1 Abstract

The southern Levant is a Mediterranean climate zone of complex variability in which uncertainty remains in regional palaeoclimate reconstruction. In spite of the proven value of diatoms in circum-Mediterranean palaeoenvironmental research, their potential remains largely unexplored in the southern Levant region. In this study, we generate a new, high-resolution multi-proxy record for the last ca 9,000 cal yrs BP, supported by diatom data and key biological, mineralogical and geochemical indicators preserved in a 17.8 m long sediment sequence recovered from Lake Kinneret (the Sea of Galilee), Israel.

During the Holocene, well-correlated shifts in the diatom, minero-geochemical and palynological data indicate marked lake-level variation over time as well as changes in the trophic state of Lake Kinneret. Our results are particularly important in improving the reconstruction of Holocene lake-level variation, and thus past moisture availability. Diatom-inferred lake-level oscillations correlate well with the output from climatic models from the Levantine region and clarify previous uncertainty concerning regional variation in moisture availability. The Early Holocene (from ca. 9,000 cal yrs BP to 7,400 cal yrs BP) was characterized by lake-level shifts due to fluctuating dry-wet climate conditions. During the mid-Holocene (from 7,400 to 2,200 cal yrs BP), a stable, deep lake-level phase persisted due to high humidity. The lake level of modern Lake Kinneret fluctuates seasonally with available moisture, but has also been influenced for ca. 2,000 years by the impacts of water abstraction for human consumption and agriculture.

Over the last 9,000 cal yrs BP, the trophic state of Lake Kinneret has changed from an oligotrophic to a meso- to eutrophic environment, mainly triggered by increased human impact from around 2,200 cal yrs BP onwards. The lake's ecosystem status was not strongly affected by the documented major changes in human occupation patterns during the mid-Holocene, when a relatively stable environment persisted.

Key words: diatoms, human activity, lacustrine carbonates, Levant, palaeoecology, Sea of Galilee

3.2 Introduction

The Eastern Mediterranean is a key region for palaeoclimate research due to its considerable sensitivity to climate change because of its location between the North Atlantic pressure systems, the monsoons of East Africa and India and the continental climate of Europe (Lionello et al., 2006). This complexity translates itself into considerable complexity in palaeoenvironmental archive data, with climate change manifesting itself in the combined influence of precipitation and temperature change on lake levels and limnological processes, which may be mediated to a greater or lesser extent by other factors including catchment processes and human activities, to name but a few. In spite of expansion of Holocene circum-Mediterranean research in recent decades (Robinson et al., 2006, Finné et al., 2011), our understanding of past environmental variability and its possible drivers is still limited.

The Levantine region, located in the transition zone between the Saharo-Arabian desert belt and the subtropical Mediterranean, on the western end of the Fertile Crescent, has a long history of human occupation and therefore represents an ideal area for investigating the complex relationships between climatic, environmental and societal changes (Issar and Zohar, 2004, Frumkin et al., 2011, Richter et al., 2012). The Early Holocene is reported as the wettest phase in the past 25,000 years across the eastern Mediterranean (Robinson et al., 2006), whereas a trend towards more aridity with punctual short-term climate shifts, having notable impacts on human occupation patterns, is assumed for the mid- to Late Holocene (Rambeau and Black, 2011). A series of reviews have recently been compiled which consider the palaeoenvironmental evidence derived from proxies such as pollen analyses, stable isotopes (e.g. from speleothems, lake sediments or snails), from geomorphological indicators (such as palaeo-shorelines), and from the archaeological record for the southern Levant during the Holocene (e.g. Issar, 2003, Robinson et al., 2006, Finné et al., 2011, Rambeau and Black, 2011, Bar-Matthews et al., 2017, Litt and Ohlwein, 2017, Rosen and Rosen, 2017, Torfstein and Enzel, 2017). Establishing a coherent linkage between different sources of data in the southern Levant (e.g. lacustrine and marine sediment records, speleothem data) can be challenging due to distinctive gradients in topography and moisture availability. It is not understood whether apparent discrepancies are a result of real spatial variability in climate response (Rambeau, 2010), that of differences in response thresholds between palaeoenvironmental archives, or are a function of data quality. The uncertainty is probably due in part to the rarity of well-dated, continuous multi-proxy records in the southern Levant spanning the entire Holocene. With several lakes in the region, palaeolimnology offers the potential to reduce uncertainty surrounding continental variability.

Lake-level reconstructions from the past Lake Lisan, the Dead Sea (Torfstein et al., 2013, Kushnir and Stein, 2010) and the northern freshwater body of Lake Kinneret (Hazan et al., 2004, Hazan et al., 2005) have been achieved, but uncertainties remain. Current understanding of Dead Sea lake-level variability during the Holocene is reviewed by Kushnir and Stein (2010). A lake-level reconstruction from Lake Kinneret based on sedimentological identification of radiocarbon-dated palaeo-shorelines (Hazan et al., 2004, Hazan et al., 2005) offers a fragmentary Holocene reconstruction. Lake Kinneret is thought to have stood at ~ 212 m below sea level (mbsl) during most of the Holocene, i.e. similar to the modern lake, yet there were periods when the lake level declined and the shallower southern sediments were exposed (Hazan et al., 2005, Stein, 2014). There is no existing evidence for full desiccation of the lake during the past 10,000 years (Langgut et al., 2015). Several authors emphasize the still incomplete picture of Holocene lake-level evolution, and thus the uncertain character of local changes in moisture availability (Hazan et al., 2004, Hazan et al., 2005, Stein, 2014, Schiebel and Litt, 2017).

To date, palaeolimnological reconstructions based on diatoms (single-celled siliceous algae; Bacillariophyceae) have been limited in the southern Levant, in spite of their high sensitivity to a wide range of limnological variables (van Dam et al., 1994) and proven potential in palaeoclimate research in Mediterranean climate zones (Battarbee et al., 2001, Cvetkoska et al., 2014, Zhang et al., 2014). Previous diatom-based palaeolimnological studies at Lake Kinneret comprise a low-resolution analysis of the changing character of planktonic diatoms in the southern part of the lake over the last 5,000 years (Pollingher et al., 1984), and a palaeoecological assessment of recent environmental change in the diatom flora of five short cores (Ehrlich, 1985). A detailed mineral and geochemical investigation based on sediments from Lake Kinneret covering the entire Holocene was also lacking.

In this study, we present the results of high-resolution diatom analysis combined with minero-geochemical analysis of a 17.8 m long sediment sequence from Lake Kinneret. Our results are compared to previously-published palynological data from the same core (Langgut et al., 2013, 2015, 2016, Schiebel, 2013, Schiebel and Litt, 2017), the longest and most continuous Holocene sequence yet retrieved from the lake. This study aims to exploit the value of diatoms as palaeolimnological proxy indicator for lake-level variation, and thus local changes in moisture availability. We assess critically evidence for confounding factors of additional ecological change such as shifts in lake productivity (Wilson et al., 2008) or human impact since Neolithic times (e.g. Rollefson and Köhler-Rollefson, 1992, Maher et al., 2011), which may affect interpretation. Our results are set in the context of known regional records, considering short-term climate events, to test whether there is coherency in regional patterns of climate change during the Holocene.

3.3 Site description and limnology of Lake Kinneret

Lake Kinneret (Sea of Galilee or Lake Tiberias) is with a surface elevation of 210 mbsl the lowest-lying freshwater lake on Earth. The lake is located in the north of Israel in the northern part of the Jordan Rift Valley (32°48’08.12’’ N, 35°35’20.62’’ E; figure 3.1), which is filled with alluvial and lacustrine sediments of Neogene and Pleistocene age. The lake is situated, together with the Dead Sea Basin, on the tectonically-active Dead Sea Transform Fault (DSTF), which currently forms a more than 1000 km long fault system connecting the divergent plate boundary along the Red Sea with the Eastern Anatolian Fault (EAF) in Turkey (Hurwitz et al., 2002). The Holocene Sea of Galilee has evolved from ancient water bodies that filled the Kinneret tectonic depression during the Late Pleistocene, such as the former Lake Lisan (Hazan et al., 2005). The lake catchment is mainly composed of Cretaceous to Eocene carbonate rocks with extensive karst. Neogene and Pleistocene basalt is also common, especially in the Golan Heights, forming escarpments of up to 500 m in height around the lake (Sneh et al., 1998).

The Kinneret region is currently characterized by a typical semi-arid Mediterranean climate (Baruch, 1986), with an average annual precipitation of 400 mm and a mean annual temperature of 21 °C (figure 3.1). Northern Israel receives most of its precipitation from mid-latitude Cyprus lows, which generate westerlies and transport moist air from the Mediterranean Sea into the region (Ziv et al., 2014). The mean annual precipitation and temperature vary considerably from northern (up to 1600 mm/year; Golan Heights) to southern (up to 300 mm/year; Beth Shean region) Israel, partly as a function of topography. Annual temperatures increase approximately linearly with decreasing precipitation.

The lake is the largest natural freshwater body in Israel (22 x 12 km; 167 km^2) and by water abstraction a major source of drinking and irrigation water. A bathymetric map is provided in figure 3.1. The catchment area (2730 km^2) extends to parts of the Upper Galilee in NE Israel, the Golan Heights, the Hermon range and the southern Anti-Lebanon mountains (Baruch, 1986). The Jordan River flows into and out of the lake and is its main freshwater input (434 x 10^6 m^3/year), draining southwards to the Dead Sea. The lake is also fed by several saline springs, which influence its salinity and geochemical composition (Stiller et al., 2009, Stein, 2014, Kolodny et al., 1999, Nishri et al., 1999), such that the water is slightly oligosaline (table 3.1, total dissolved solids ca. 600 mg L^{-1}, Nishri et al., 1999, Katz and Nishri, 2013). Analysis of the modern diatom flora (Vossel unpublished) shows the presence of halophilous diatom taxa close to the saline springs, confirming that these, rather than evaporative concentration, are the main cause of the subtle increase in salinity.

Total annual water inflow is about 629 x 10^6 m^3 comprising the inflow of the Jordan River, direct catchment runoff, saline springs, direct precipitation and other water sources (Rimmer and Givati, 2014a). Modern lake level can fluctuate by up to 4 m a year depending on precipitation, evaporation (230 x 10^6 m^3/year) and water use for human consumption and agriculture (National Water Carrier, personal communication).

Table 3.1 Summary of key limnological parameters for the epilimnion of Lake Kinneret based on the Lake Kinneret data base (Sukenik et al., 2014, Nishri, 2014, Katz and Nishri, 2013).

Chemical parameters:		
pH	8.6	
Alkalinity (as HCO_3^-)	165	mg/l
Anions (as Cl^- + SO_4^{2-})	340	mg/l
Cations (Na^+ + Mg^{2+} + Ca^{2+} + K^+)	236	mg/l
Silica (as SiO_2)	10	mg/l
Soluble P (as PO_4^{3-})	2	µg/l
Total phosphorus	15-60	µg/l
Nitrate (as NO_3^-)	800	µg/l
Pelagic bottom sediments:		
Clay minerals	35	%
Calcium carbonate	55	%
Organic matter	5	%
Residual	3	%
Secchi depth	2.8-4.0	m

Lake Kinneret is warm monomictic, being stratified with an anoxic hypolimnion from May to December and fully mixed from December to April (Gophen, 2003, Katz and Nishri, 2013). The mixing cycle of the water column is closely linked to the bio-geochemical signature imprinted in the sediments, and directly affects the fluxes of calcite precipitated from the water column towards the bottom of the lake (Katz and Nishri, 2013). Biologically-induced calcite precipitation occurs in spring and early summer (Katz and Nishri, 2013).

The modern phytoplankton flora of Lake Kinneret is dominated by dinoflagellates, with a low proportion of diatoms, cyanobacteria and chlorophytes. As diatoms are a minor component of the phytoplankton biomass (Pollingher et al., 1984), they have not previously been a focus for ecological research, although, with more than 200 reported species (Round, 1978), they are an important component of the benthic flora. The most common planktonic taxa are *Cyclotella* spp., *Stephanodiscus* spp., *Aulacoseira granulata*, which are often accompanied by the periphytic *Brachysira* spp. The most common benthic taxa are *Amphora pediculus*, *Achnanthes* sensu lato spp., *Navicula* spp., *Synedra ulna* and *Rhoicosphenia curvata*. A detailed species list is provided in Zohary et al. (2014).

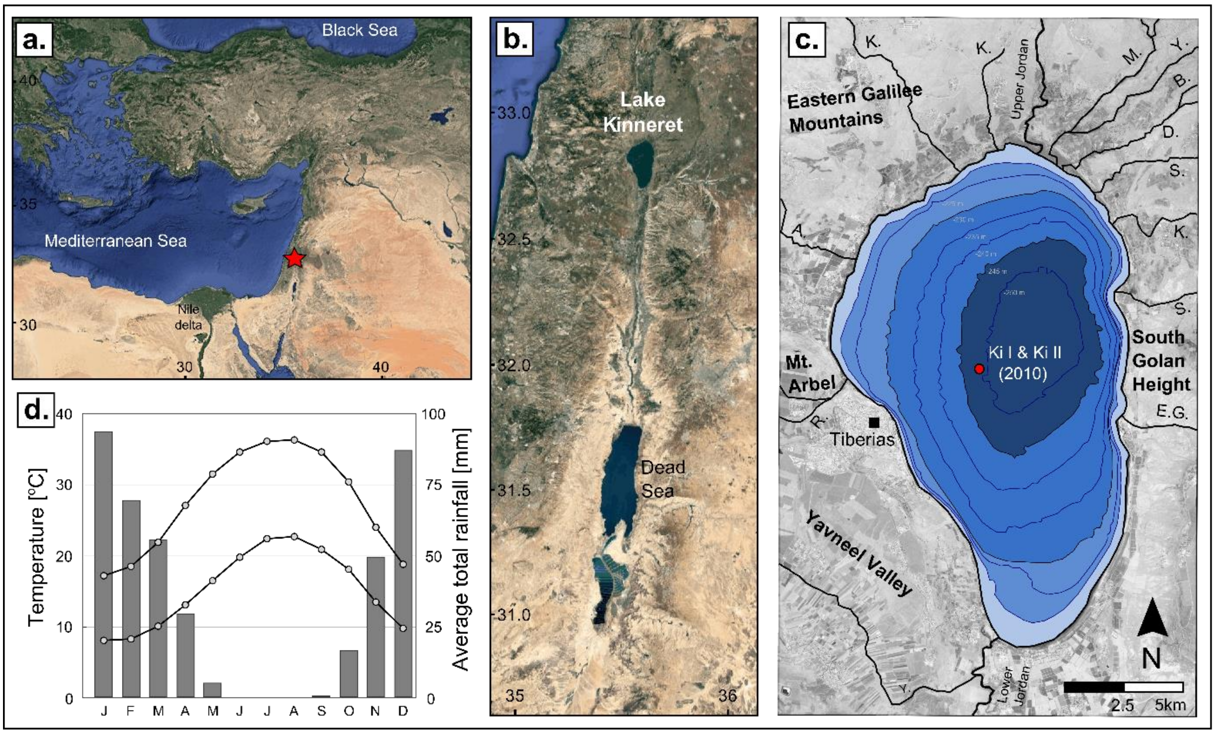

Figure 3.1 (a) Location of Lake Kinneret (star) in the Eastern Mediterranean Region; (b) Jordan Rift Valley (satellite images for (a) and (b) are from Imagery$^{©}$2016 TerraMetrics); (c) Lake Kinneret with location of two 2010 coring sites Ki I and Ki II. Bathymetry given in 5 m intervals (after Berman et al., 2014, background after NASA) and (d) average monthly rainfall and average temperatures (daily maxima and minima) for the city of Tiberias (time-series from 1976-1995, www.worldweather.org).

3.4 Material and Methods

3.4.1 Sediment cores, sedimentology and chronology

In March 2010, two parallel sediment cores (core KI_10_I and KI_10_II) were recovered from a water depth of 38.8 m at the deepest part of the lake basin (32°49’13.8’’N, 35°35’19.7’’E;

figure 3.1). Cores were retrieved from a UWITEC Universal Sampling Platform (http://www.uwitec.at), using a piston corer for successive two-meter sections. Sediment cores were offset by 0.5 m to allow construction of a continuous composite profile (Schiebel, 2013). The recovered sediment cores consist of homogenous greyish to brown silt and clay deposits (figure 3.5); only the upper 25 cm of sediments show lamination, possibly due to the construction of the Degania Dam in 1932 (A. Nishri, personal communication). Only one notable sediment disturbance is apparent at 4.64 to 4.57 m depth (figure 3.7) and there is otherwise no variation in colour or texture of the sediments (Schiebel and Litt, 2017).

As this sediment sequence shows no evidence for full desiccation (e.g. desiccation cracks or crusts) of the lake during the past 10,000 years (Langgut et al., 2015), it can be assumed that sedimentation is continuous in the deepest parts of the Kinneret basin. The 17.8 m composite sequence covers approximately the last 9,000 cal yrs BP (figure 3.2, Schiebel and Litt, 2017). The age-depth model, which is presented in full detail in Schiebel and Litt (2017), relies on radiocarbon determinations on bulk organic material (n=21), and selective encountered terrestrial macrofossils (n=10). Age determinations on both materials at the same stratigraphic depth show that bulk organic ages are subject to a reservoir offset ranging from ca. 800 to ca. 1,600 years. The linear age-depth model (figure 3.2) assumes a constant sedimentation rate of 1.9 mm/year for the Holocene and a gradual decrease of the reservoir offset from the beginning of the Holocene until present day, at a rate of ca. 70 years offset per 500 years (or 0.14 per year).

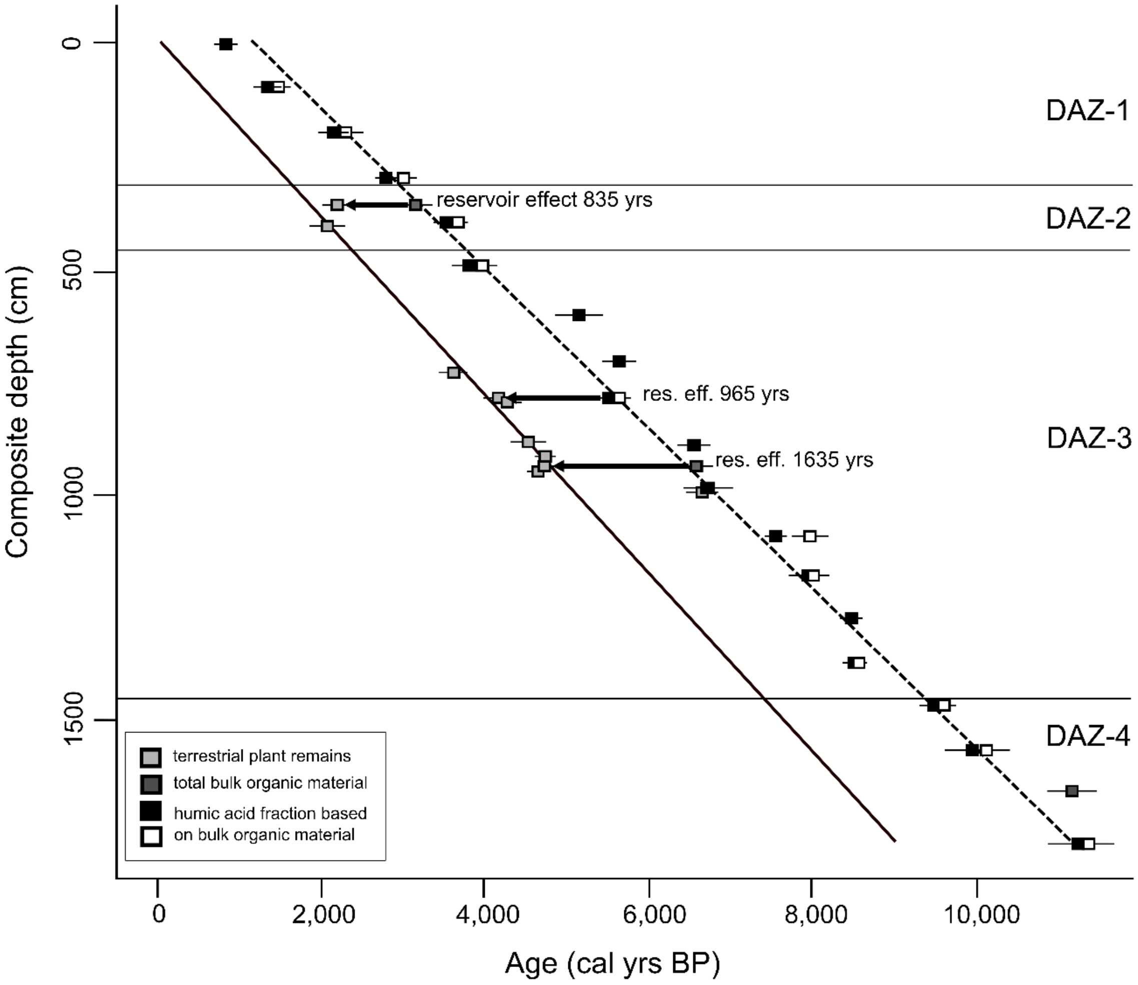

Figure 3.2 Age-depth model of the Lake Kinneret composite profile based on calibrated radiocarbon data. Error bars indicate 2 σ-range. Black arrows display reservoir correction at depth horizons (358 cm, 794 cm, and 944 cm) with available macro- and bulk organic samples. Diatom assemblage zones (DAZ)-1 to DAZ-4 correspond to defined DAZs (modified after Schiebel and Litt, 2017).

3.4.2 Diatom and other micropalaeontological analyses

For diatom analysis 165 samples were taken at 10 cm intervals, corresponding to a resolution of ca. 50 years. Sample resolution was increased to 2 cm (10 yrs) or 5 cm (25 yrs) in two sections: 17.8-14.8 m and 4.6-3.5 m, intervals in which the diatom concentration was low or a complete turnover of the diatom community was recognized. All samples were prepared using standard techniques (Battarbee, 1986): 0.2 g of wet sediment was treated with H_2O_2 to oxidize organic matter, followed by concentrated HCl (35 %) to remove carbonates. Known quantities of microspheres were added to allow the calculation of diatom concentrations (valves/g) for each sample. Subsamples were mounted in Naphrax™. Where diatoms were well preserved, more than 500 valves were counted using a Zeiss Axio Lab.A1 light microscope at x1000 magnification. In some samples, counts were lower (up to 200 valves) due to preservation problems or the complete lack of diatoms. Phytoliths were counted at a similar sample resolution in relative abundance to diatom counting. Diatom taxonomy and nomenclature follow Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), Lange-Bertalot (2013) and the Diatom Flora of Israel (Ehrlich, 1995). Following several authors (Cruces et al., 2010, Hobbs et al., 2011, Zhang et al., 2014) *Stephanodiscus minutulus* (KÜTZING) CLEVE & MÖLLER and *S. parvus* STOERMER & HÅKANSSON are merged into *S. minutulus/parvus*. Current changes in nomenclature are applied following the Catalogue of Diatom Names (Fourtanier and Kociolek, 2009). Diatom counts were converted to percentage data and displayed stratigraphically using Tilia, version 1.7.16 ($^{©}$1991-2011 Eric C. Grimm). Stratigraphically constrained cluster analysis using square root transformation was applied using CONISS (Grimm, 1987) to define zone boundaries, based on taxa present at > 5 % abundance.

Palynological data from pollen analysis of 73 samples (parallel sampling depth to diatom samples) at a resolution of 25 cm (150/yrs) is published in detail in Schiebel (2013, Schiebel and Litt, 2017).

The application of a transfer function to reconstruct lake-water nutrient concentrations from the taxonomic composition of diatom communities was not appropriate. The dominant taxon *Cyclotella ocellata*, has an extremely broad tolerance for nutrient availability (Fritz et al., 1993, van Dam et al., 1994, Kiss et al., 1996, Schlegel and Scheffler, 1999, Cremer and Wagner, 2003, Houk et al., 2010), and another common taxon, *C. paleo-ocellata*, is newly described (Vossel et al., 2015) and without a modern analogue.

3.4.3 Diatom-based lake-level reconstruction

Diatom-based lake-level reconstruction is based on the assumption that the variability in the ratio of planktonic to benthic (P/B) diatom taxa can be interpreted as a response to varying basin morphology as lake level fluctuates (Jones et al., 2013). As a lake shallows, benthic habitats may increasingly disperse into regions that were previously inhabited by planktonic diatoms living in a deeper water column, thereby changing the P/B-ratio. Effectively, decreasing lake level shortens the transport distance from littoral habitats to the deepest region of the lake (the favoured coring site), coupled with a reduction in area suitably deep for planktonic diatoms (Stone and Fritz, 2004). The plankton/benthos-ratio may also be affected by shifts in productivity. Therefore, supporting evidence for lake-level change, coupled with regional shifts in moisture availability, is sought from the comparison with known palynological datasets and

climate models as well as speleothem data from other study sites. Known trophic preferences of diatom taxa and the geochemistry data can help to disentangle if changes in the diatom assemblage reflect fluctuating lake-level conditions or are the result of productivity shifts.
The ratio of planktonic to benthic diatoms was calculated using the following formula provided by Wang et al. (2013):

$$\frac{P}{B} = \frac{\sum(\text{planktonic taxa})}{\sum(\text{planktonic} + \text{benthic taxa})}$$

Following the allocation of Pollingher et al. (1984), facultative planktonic taxa such as *Pseudostaurosira brevistriata, Staurosira venter* and *Staurosirella pinnata* and epiphytic species such as *Cocconeis spp.* were assigned as benthic (i.e. littoral) taxa in this calculation.

3.4.4 Geochemistry and Mineralogy

Geochemistry was determined by non-destructive high resolution (1cm) XRF core scanning (Itrax, Cox Analytical Systems, Sweden) at the University of Cologne, equipped with a Cr X-ray source, operated under the following conditions: voltage (kV): 30, current (mA): 30 and exposure time (s): 10.

For mineral analysis 50 samples were taken from various depths (approx. intervals of 20-30 cm) in parallel with palaeoecological samples. Mineralogy was obtained from the powdered bulk fraction measured with a Siemens D5000, equipped with a CuKα1, 2 target tube. Operation conditions were: voltage (kV): 40, current (mA): 30, scan range (°2Theta):4-70, step-size (°2Theta): 0.02, counting time (s):1, divergence slit (°): 1, anti-scatter slit (°): 1, mask (mm):15. Mineral assemblage was identified using the software, MacDiff (Petschick et al., 1996) and X'Pert High Score Plus (PANanalytical B.V.). The Rietveld refinement was applied using Profex v. 3.10.2 (Döbelin and Kleeberg, 2015) with additional structure files from the American Mineralogist Crystal Structure Database (Angel et al., 1990, Bailey, 1969, Maslen et al., 1995). Compositional data analysis was applied to the geochemical data (Aitchison, 2003, Comas-Cufí and Thió-Henestrosa, 2011) and gives further insights to the inter-element and possible source relationship (Aitchison and Greenacre, 2002). Biplots of complex data-sets can be used as a simple tool to investigate the structure of these data-sets (Greenacre, 2010).

3.5 Results

3.5.1 Diatom analysis

A total of 143 diatom taxa were identified within the subfossil sediment sequence of Lake Kinneret, most of which can be classified as oligohalobous-indifferent, requiring alkaline water for optimal growth (Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b, Ehrlich, 1995, Lange-Bertalot, 2013). The summary diagram (figure 3.3) shows that diatoms were well preserved in most samples. They were rare (valves dissolving and fragmented) in two intervals (17.8-16.9 m; 15.4-14.8 m depth) and absent in one sample (4.57 m depth).

Planktonic taxa from the genera *Cyclotella*, *Stephanodiscus* and *Aulacoseira* dominate the sequence. Small, facultative planktonic fragilarioid taxa (e.g. *Pseudostaurosira brevistriata, Staurosira venter, Staurosirella pinnata*) are also common. Salt-tolerant diatom species such as *Amphora coffeaeformis* are present sporadically at low abundance.

Four major diatom assemblage zones (DAZ-1-4) could be recognized from the results of CONISS (Grimm, 1987). Adopting the opposite of stratigraphic convention, zones in this study are numbered from the top down (DAZ-1 representing the recent past) to allow coherent sequencing of zone numbers in future studies of a longer sequence. A detailed description of each DAZ, its species composition and criteria for defining the lower zone boundaries are given in table 3.2. Although anthropogenic influences might have caused a shift in the modern diatom composition compared to the fossil one, the modern flora still contains many of the taxa present in the fossil record.

The P/B-ratio (given in figure 3.3, 3.5 and 3.6) shows some significant variations within the record, being particularly low within DAZ-4 and DAZ-2, which also exhibit low diatom concentration and high counts of phytoliths and high potassium values.

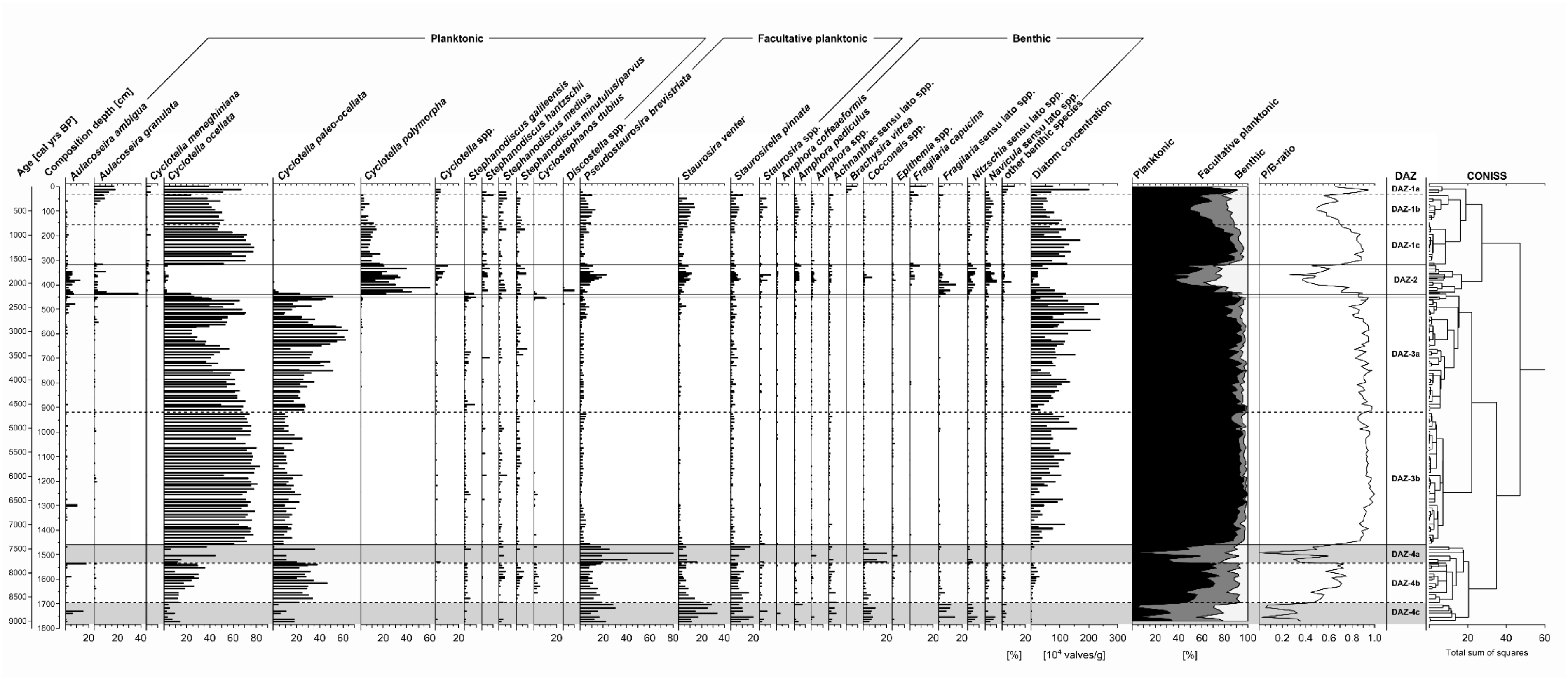

Figure 3.3 Summary diatom diagram from Lake Kinneret (composite profile from core KI_10_I and KI_10_II) showing selected taxa (present at > 5 % abundance), diatom concentration and Plankton/Benthos (P/B)-ratio. Some of the rare benthic taxa are grouped together at genus level (e.g. *Amphora* spp., *Achnanthes* spp., *Nitzschia* spp., *Navicula* spp.). Diatom assemblage zones (DAZ) are defined by CONISS cluster analysis. The calibrated radiocarbon chronology (Schiebel and Litt, 2017) is marked at 500-year intervals, with an estimated age of 9,000 cal yrs BP at the base of the sequence. In the marked sections of the diagram (grey pattern) diatoms were rare (17.8-16.9 m; 15.4-14.8 m depth) or not well preserved and absent in one sample (4.57 m depth).

Table 3.2 Table with detailed description of diatom assemblage zones and their species composition (DAZ = diatom assemblage zone; DA = diatom assemblage; DC = diatom concentration; LB = lower boundary; P = Planktonic; FP = Facultative Planktonic; B = Benthic)

DAZ	Depth [cm]	Age [cal kyrs BP]	Diatom assemblage	P [%]	FP [%]	B [%]
1a: *Aulacoseira granulata* DAZ	30-1	0.2-present	**DA:** dominated by *C. ocellata* and *A. granulata* (increasing up to 20 % and forming long filament chains); *C. meneghiniana* and benthic species such as *Fragilaria capucina* become more common **DC:** low (< 50 [10^4 valves/g]) to high (> 200 [10^4 valves/g]) with rapid changes **LB:** increase in *A. granulata*, *C. meneghiniana* and DC	60-80	< 5	5-15
1b: *Stephanodiscus* DAZ	160-30	0.9-0.2	**DA:** dominated by *C. ocellata* (35-55 %); *C. polymorpha* and small *Stephanodiscus* species are common as well as facultative planktonic fragilarioid taxa such as *P. brevistriata*, *Staurosira venter* and *Staurosirella pinnata*; Naviculoid taxa increase slightly; occurrence of *A. granulata* increases towards top of this subzone **DC:** low (< 50 [10^4 valves/g]) to moderate (> 100 [10^4 valves/g]) **LB:** decrease in *C. ocellata*; increase in FP and B species	50-80	10-30	5-15
1c: *Cyclotella* DAZ	320-160	1.6-0.9	**DA:** strong dominance of *C. ocellata* (up to 80 %); *C. polymorpha* is present (10-15 %); facultative planktonic and benthic diatoms are present at low abundance (< 5 %) **DC:** moderate (> 50 [10^4 valves/g]) to high (up to 175 [10^4 valves/g]) **LB:** increase in *C. ocellata* and DC	> 80	< 5	< 5
2: *Cyclotella polymorpha* DAZ	440-320	1.6-2.2	**DA:** dominated by *C. polymorpha* (strong increase up to 55 %); *A. ambigua*, *A. granulata* (showing strong occurrence at base of this zone: 35 %) and smaller *Stephanodiscus* taxa are common; only occurrence of *Discostella* spp. in record; strong decrease in occurrence of *C. ocellata* (< 5 %) and complete disappearance of *C. paleo-ocellata* and *S. galileensis* from record, fragilarioid and benthic species (e.g. *Amphora pediculus* at 5 %) show higher abundance (up to 10 % per species); complete shift in diatom assemblage composition compared to other DAZs **DC:** low; lack of diatom preservation in some samples **LB**: decrease in *C. ocellata*/*C. paleo-ocellata*/other planktonics; strong decrease in DC; strong increase in *C. polymorpha*, *A. granulata* and benthic taxa	40-70	10-50	5-40

Table 3.2 to be continued

DAZ	Depth [cm]	Age [cal kyrs BP]	Diatom assemblage	P]%}	FP [%]	B [%]
3a: *Cyclotella paleo-ocellata* DAZ	920-440	4.7-2.2	**DA:** strongly dominated by *Cyclotella* species: *C. paleo-ocellata* is often exhibits higher relative abundances (up to 65 %) than *C. ocellata;* both species strongly co-dominating DA; at top of this subzone *Cyclostephanos dubius* (maximum peak of 15 %) and *Stephanodiscus galileensis* become more abundant **DC:** moderate to high (maximum values in record: 250 [10^4 valves/g]; various rapid fluctuations **LB:** remarkable increase in *C. paleo-ocellata*	> 80	< 5	< 5
3b: *Cyclotella ocellata* DAZ	1460-920	7.4-4.7	**DA:** dominated by planktonic *Cyclotella* species: *C. ocellata* is the most common diatom in this DZ (often > 75 %) and *C. paleo-ocellata* is common at 10-25 %; *Stephanodiscus* species (all sizes) are abundant at 5-10 %; abundance of facultative planktonic and benthic species is very low **DC:** low (< 20 [10^4 valves/g]) to high (> 130 [10^4 valves/g]) with various fluctuations **LB:** increase of *C. ocellata*, other planktonic taxa & DC; decrease in FP and B species	> 80	< 5	< 5
4a: *Pseudo-staurosira brevistriata* DAZ	1535-1460	7.9-7.4	**DA:** dominated by robust fragilarioid species such as *P. brevistriata* reaching its maximum (ca. 80 %) in record; *Cocconeis* spp. are common, reaching maximum abundance of up to 20 % **DC:** very low; lack of diatom preservation in some samples **LB:** decrease in planktonic species & DC; increase in *P. brevistriata* & *Cocconeis* spp.	5-60	35-80	10-25
4b: *Fragilarioid* DAZ	1695-1535	8.6-7.9	**DA:** dominated by planktonic taxa such as *C. ocellata* (10-35 %), *C. paleo-ocellata* (20-45 %) & smaller *Stephanodiscus* species (< 10 %) and some small fragilarioid species (~ 25 %) **DC:** low (<20 [10^4 valves/g]) **LB:** increase of planktonic species and DC	45-75	20-40	10-20
4c: *Aulacoseira* DAZ (lower boundary not defined)	1772-1695	9.1 -8.6	**DA:** dominated by robust fragilarioid species (< 50 %), *Cocconeis* spp. common (up to 10 %) and *Navicula* and *Nitzschia* are also present; presence of planktonic diatoms low; besides *C. ocellata, A. ambigua* is abundant up to 15 % **DC:** very low; lack of diatom preservation in some samples **LB:** not defined (start of record)	5-35	45-56	20-45

3.5.2 Sediment minero-geochemistry and compositional data analysis

The major mineral assemblage of Lake Kinneret sediments is composed of calcite [$CaCO_3$], dolomite [$CaMg(CO_3)_2$], quartz [SiO_2], muscovite/illite [$(K,H_3O)(Al,Mg,Fe)_2(Si,Al)_4O_{10}[(OH)_2,(H_2O)]$] - probably in the fine fraction, and feldspars (plagioclase and alkali feldspar). In the diffractograms the feldspars were best explained by anorthite [$CaAl_2Si_2O_8$] and microcline [$KAlSi_3O_8$]. The structure that best resolved the phylossilicates was that of a muscovite. The major mineral assemblage remained qualitatively constant throughout the sediment sequence and changes in abundance of the major minerals correlate well with DAZ boundaries (table 3.3). Minerals in trace amounts, e.g. pyrite, occurred at specific depths. Pyrite concentrations larger than 1% occurred particularly in DAZ-1, reaching up to 2.25 w%.

From XRF-scanning, the elements Si, S, Cl, K, Ca, Ti, Fe and Sr were present at detectable concentrations, with reduced scattering throughout the profile; apart from sulphur and chlorine, these elements were also retained in the lattices of the identified minerals. The S/Ti-ratio plotted versus depth shows covariance with the Ca/Ti-ratio (figure 3.5).

First observations from the centered log ratio of the compositional data (*clr*-biplot, figure 3.4) show, that the defined diatom assemblage zones also have distinct geochemical fingerprints. For geochemical elements, the pair [Ca, Sr] shows relatively small variance, as do the elements [Fe, Ti, K, Si] between each other. Hence, Ca and Sr represent the carbonate accumulation; and Ti, K, Fe and Si, represent the detrital fraction. The high variance between any pair of variables from these two groups arises from the fact that Ca and Sr in the Kinneret sediments are reflecting lake internal carbonate precipitation, whereas a detrital source for the carbonate input is here of secondary order. One representative element from each group was chosen for following interpretations.

Table 3.3 Average major mineral composition for each DAZ

Diatom Assemblage Zone	Depth [cm]	Quartz [w%]	Muscovite/Illite [w%]	Feldspars [w%]	Dolomite [w%]	Calcite [w%]
DAZ-1	320 - 0	2.1	9.2	2.4	1.1	84.1
DAZ-2	440 - 320	4.0	14.7	2.4	1.2	76.7
DAZ-3	1460 - 440	6.8	15.3	3.7	2.4	70.5
DAZ-4	1772 - 1460	10.2	21.4	4.4	1.5	60.9
Event Layer	at 457	24.7	23.3	5.8	10.2	35.2

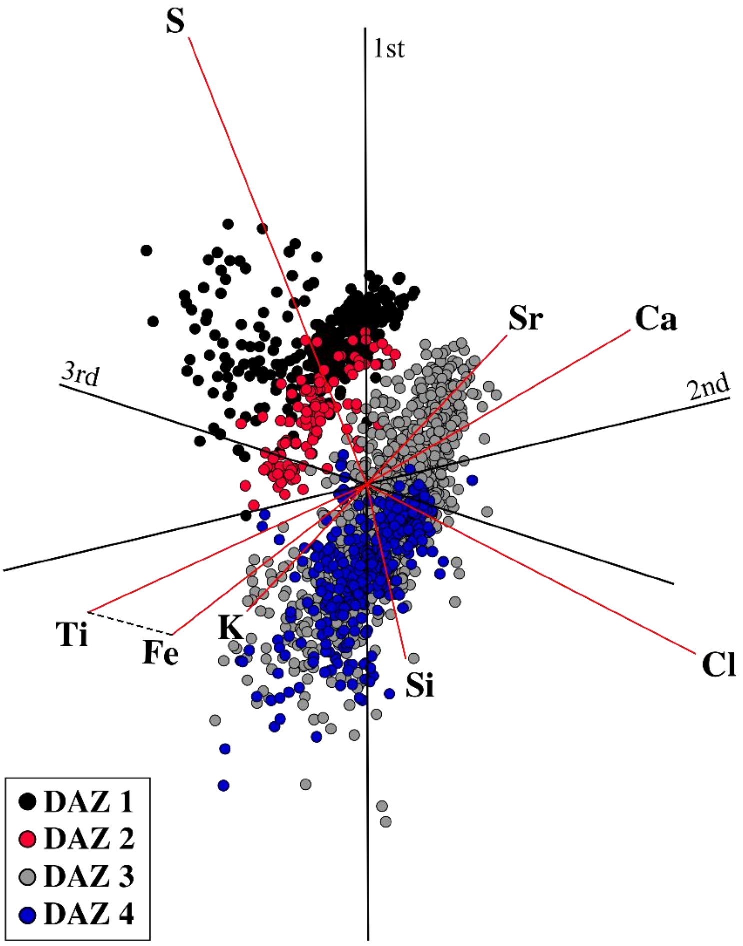

Figure 3.4 The presented *clr*-biplot for the geochemical data of Lake Kinneret segregates the individual diatom zones (DAZs; different coloured dots). The variables, herein geochemical elements, are represented by *rays* emanating from the origin. Interpretations are mainly based on *links*, i.e. distances between the end-points of these *rays*. The length of the link between Fe and Ti (dashed line) shows, for example, that the variance between the pair of elements [Fe, Ti] is smaller than the variance between the pair [Fe, Si]. Thus, pairs of elements with low variance in between each other have *rays* pointing to similar directions and are correlated to each other.

3.5.3 Sediment geochemistry and implications for palaeoenvironmental reconstruction

In the sediments of Lake Kinneret, Ca is retained in the lattices of plagioclase, dolomite and calcite. The positive correlation between Ca/Ti-ratio and calcite/quartz (figure 3.5) indicates that the calcium accumulation in Lake Kinneret is mainly driven by calcite. Pelagic bed sediments from Lake Kinneret consist with up to 60 % of calcite (table 3.1, Serruya, 1978, Dubowski et al., 2003), that is mostly of autochthonous origin (Katz and Nishri, 2013). This chemical precipitation of calcite in the water column is a major process in the lake, favoured by the waters' alkalinity and is associated to the lake mixing cycle (Katz and Nishri, 2013). The carbonate precipitation is strongly biogenic induced, as maximum calcite accumulation in the lake occurs between February and March due to intensive photosynthesis, occurring concomitant with bloom periods of the dinoflagellate *Peridinium gatunense* (Koren and Klein, 2000). The necessary carbonate and calcium ions are fed to the lake system in dissolved form from the catchment (Nishri and Stiller, 2014, Leng and Marshall, 2004) and picoplankton seems to serve as nuclei for calcite crystal growth (Nishri and Stiller, 2014). Thus, the primary carbonate accumulation in Lake Kinneret is a potential indicator for lake productivity, given that carbonate precipitation from the water column of alkaline lakes is usually triggered by algal production and consequent changes in the carbonate equilibria (Ohlendorf and Sturm, 2001, Matter et al., 2010, Roeser et al., 2016).

Lake Kinneret data (figure 3.5) show good correspondence between the diatom concentration, the carbonate accumulation (Ca/Ti), the sulphur accumulation (S/Ti) and calcite/quartz, suggesting that they mainly reflect internal lake processes and together are indicative of lake productivity. Lacustrine processes participating in sulphur cycling are largely biogeochemical such that sulphur is added to the sediments (a) as organic compounds or (b) dissolved sulphate that might be reduced to sulphides (Berner, 1971, Mackereth, 1966). Thus, sulphur might indicate primary organic production or diagenetic processes.

The detrital (clastic) input from the catchment is well reflected in the *clr*-biplot from the low variation between the elements Si, K, Fe, and Ti. From these elements, variations in potassium (K) counts are positively correlated to the sum of minerals representing the clastic fraction (quartz+feldspars+clays) and the phytolith counts (see figure 3.5). The detrital input can increase: (a) with enhanced humidity/rainfall, (b) with a lower lake level due to: (1) a reduction in lake water volume also reduces internal biomass and calcium production, which can cause a relative increase in detrital material, and (2) because a shallow lake exposes sediment surfaces in shallower littoral zones; (c) with open vegetation cover on the surrounding landscape, which increases sediment and nutrient input to the lake system, whereas a dense vegetation cover stabilizes the soil.

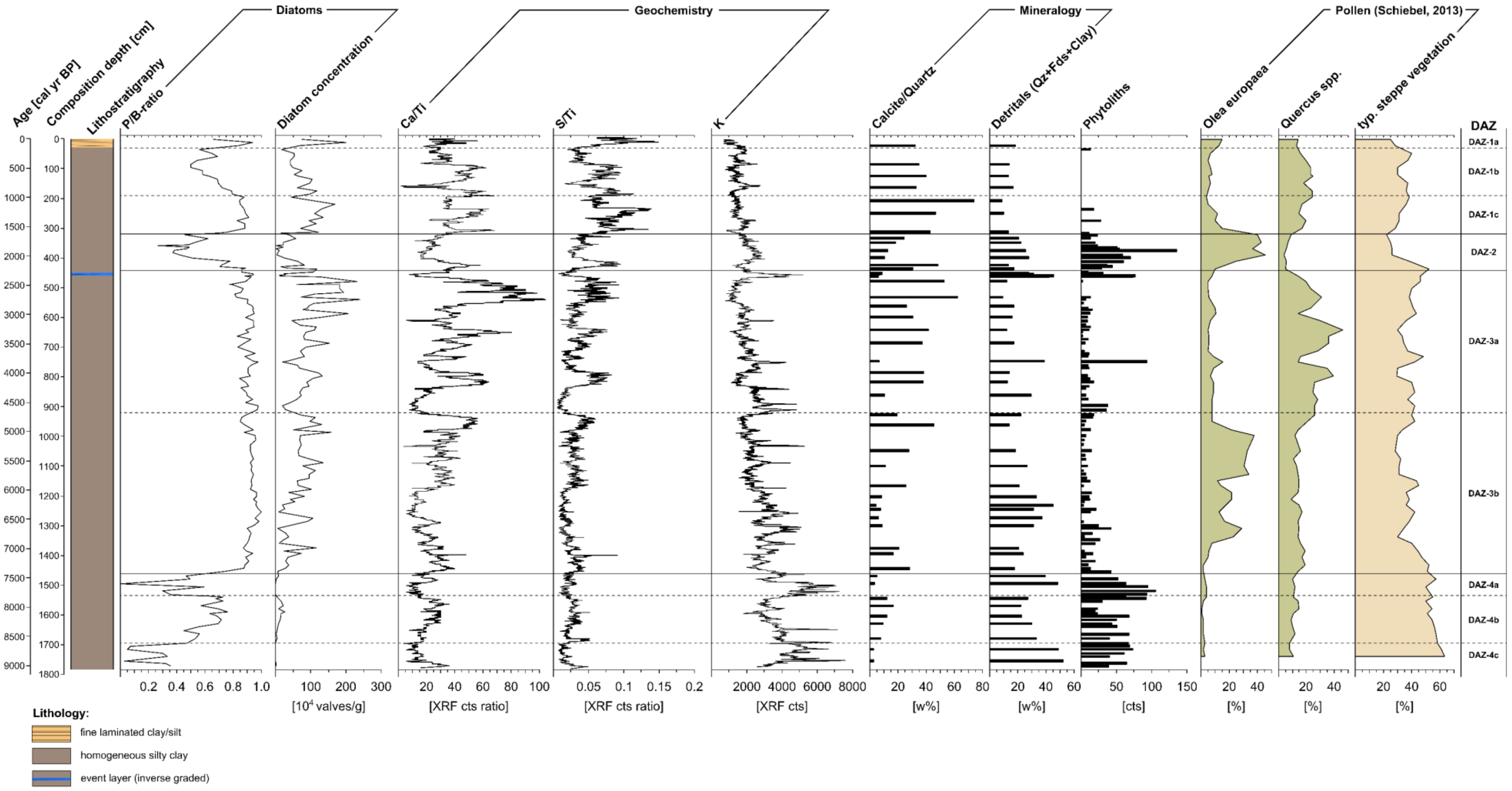

Figure 3.5 Multi-proxy data from Lake Kinneret (composite profile from core KI_10_I and KI_10_II) showing a selected dataset of diatoms, geochemistry, mineralogy and palynology plotted against age [cal yrs BP] and depth [cm]. Pollen data was provided by Schiebel (2013): “typical steppe vegetation” here includes all species of the following families: *Apiaceae*, *Asteraceae*, *Chenopodiaceae*, *Poaceae* and *Polygonum*. A detailed pollen analysis is published in Schiebel and Litt (2017).

3.6 Discussion

In the following sections we discuss major palaeolimnological and environmental changes inferred from diatom analysis and minero-geochemistry data of a 17.8 m long sediment sequence of Lake Kinneret. The study spans the last 9,000 cal yrs BP and emphasis is given to disentangling climate-driven lake-level variation from shifts in trophic status and the impact of past human activities. A summary multi-proxy diagram is provided in figure 3.5 for a comparison of key limnological indicators and selected previously-published palynological data (Schiebel, 2013, Schiebel and Litt, 2017, Langgut et al., 2013, 2015, 2016). For interpretation of regional trends in moisture availability, a comparison of existing Holocene lake-level reconstructions from the Dead Sea (Kushnir and Stein, 2010) and Lake Kinneret (Hazan et al., 2005) are given in figure 3.6. The sparse occurrence of obligate halophilous diatom taxa (e.g. *Amphora coffeaeformis)* indicates an essentially freshwater lake and a hydrologically open lacustrine system throughout the Holocene. Palaeolimnological interpretation and implications for palaeoclimate reconstruction are discussed according to diatom assemblage zone boundaries below. Calibrated ages are provided (according to the age-depth model given in figure 3.2; Schiebel and Litt, 2017), with associated archaeological periods for comparison with the wider literature.

3.6.1 Holocene history of Lake Kinneret – a multi-proxy interpretation

From 9,000 – 7,400 cal yrs BP (DAZ-4, Pottery Neolithic Period)

At the base of the sequence, diatom assemblage zone (DAZ) 4 is characterized by very low diatom concentration or even an absence of diatoms (figure 3.3), in subzones DAZ-4c and DAZ-4a in particular. The low diatom concentration may (1) result from poor preservation rather than being a reliable indicator of lake productivity (Battarbee et al., 2001), as many valves were broken or showed early signs of dissolution and/or (2) reflect an increased sediment accumulation rate in a phase of shallowing and sediment in-wash.

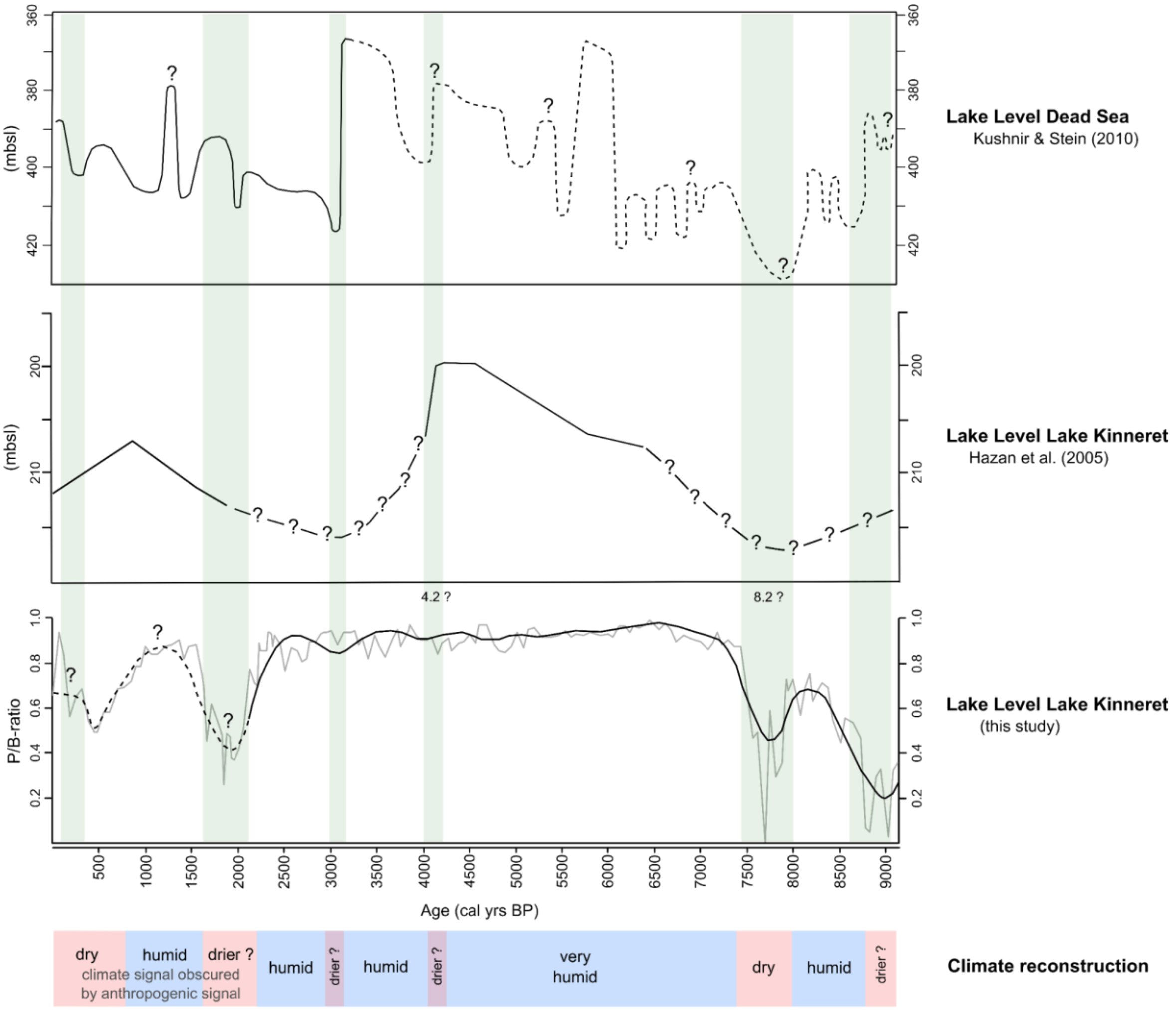

Figure 3.6 Comparison of currently known, fragmentary Holocene lake-level reconstructions from the Dead Sea (Kushnir and Stein, 2010) and Lake Kinneret (Hazan et al., 2005) compared to the reconstructed lake-level curve inferred from shifts in the ratio of planktonic to benthic (P/B) diatom taxa (grey curve shows P/B-ratio for diatoms in high resolution; black curve is a 10 point average for the P/B-ratio). The presented lake-level reconstruction for the Dead Sea is a combination of absolute lake-level curves (based on the identification of palaeo-shorelines and knowledge of their age and original elevation) and relative lake-level curves (based on estimates of relative water depth identified by lithological changes in sediment cores) and were compiled for the Holocene by Kushnir and Stein (2010). The presented lake-level reconstruction for Lake Kinneret by Hazan et al. (2005) is based on sedimentological identification of radiocarbon-dated palaeo-shorelines. Note that some intervals of the curves are dashed and labelled with question marks, indicating that they are assumptions and not robust curve reconstructions. Assumed correlations between the Dead Sea and Lake Kinneret curves are marked for a better comparison.

Where diatoms were identifiable, the diatom community of subzone DAZ-4c (9.1-8.6 cal kyrs BP; table 3.2) is dominated by robust facultative planktonic species, such as *Pseudostaurosira brevistriata*, *Staurosira venter* and *Staurosirella pinnata*, and fragmented valves of benthic genera such as *Cocconeis* (growing on submerged water plants in the littoral zone), *Navicula* and *Nitzschia*. As fragilarioid species are associated with environmental stress and physical disturbance (Schmidt et al., 2004), the high proportion of benthic and facultative planktonic taxa, can be linked with an expansion of the littoral zone, i.e. are a strong indicator for relatively shallow waters (Barker et al., 1994). The occurrence of *Aulacoseira* spp. in these subzones, and low abundance of *Cyclotella ocellata*, can be indicative of turbulent mixing of the water column and a temporary breakdown of stratification (Owen and Crossley, 1992, Anderson, 2000), since *Aulacoseira* have highly silicified valves and require a turbulent water column to stay within the photic zone. A combination of low lake level and high wind exposure can provide the turbulent, high nutrient condition favoured by this genus (Wolin and Stone, 2010). Shallow and turbulent water conditions can often enhance dissolution of diatom valves (Flower, 1993), which is here well reflected in the low diatom concentration.

Mineralogical and geochemical data indicate a phase of long-lasting and high detrital input, supported by palynological data: The poorest diatom preservation (DAZ-4c and DAZ-4a) occurs in phases of maximum inferred detrital input: increased potassium (K) counts, phytolith counts and detrital mineral concentrations with values up to 50 w% (clays+feldspars+quartz), and the unique presence of anorthite and microcline only in this sediment unit. DAZ-4 as a whole shows maximum abundance of steppic pollen taxa, indicating an natural open vegetation cover (not influenced by human activities) and arid climate conditions in the catchment area (figure 3.5, Schiebel and Litt, 2017). The open steppe vegetation would also favour soil erosion processes (Zuazo and Pleguezuelo, 2008) and increase the sediment discharge, serving to dilute the diatom concentration. A high sediment discharge into the lake likely causes a turbid water column, limiting the light availability for the photosynthetic processes necessary for diatom growth, especially for species with a planktonic life habit. In addition, Barker et al. (1994) stated that planktonic diatom taxa can be restricted by turbidity during phases of enhanced catchment erosion. Tychoplanktonic fragilarioid species, which here occur at their peak abundance (table 3.2; figure 3.3), would be favoured by a turbid, sediment-loaded water column. The inferred phase of shallow lake levels for Lake Kinneret until ca. 8,600 cal yrs BP is consistent with pollen-climate model reconstructions from the Dead Sea (Litt et al., 2012), which document an arid (precipitation values < 350 mm/a) and warm period.

In subzone DAZ-4b, the shift towards dominance of the planktonic *Cyclotella ocellata*-complex (45-75 %, table 3.2), i.e. *Cyclotella ocellata* and *C. paleo-ocellata*, suggests a slight increase in lake levels around 8,600 cal yrs BP lasting till 7,900 cal yrs BP. Total diatom concentration and the Ca/Ti-ratio remains low in spite of better diatom preservation, indicating reduced lacustrine productivity. As *Cyclotella ocellata* is known for its extremely broad tolerance for nutrient availability (Fritz et al., 1993, van Dam et al., 1994, Kiss et al., 1996, Schlegel and Scheffler, 1999, Cremer and Wagner, 2003, Houk et al., 2010), the co-occurrence of *C. ocellata* with *C. paleo-ocellata* is interpreted in this record as an indicator of oligotrophic conditions in a deeper open-lake system (Vossel et al., 2015, and references therein). Notably, the peak in the S/Ti-ratio at the beginning of DAZ-4b (~ 8.6 cal kyrs BP) differs from the Ca/Ti signature, possibly indicating changes in lacustrine mixing related to a deeper water column. This can result as a transient state after a rapid lake-level increase, as known for other east Mediterranean lakes (e.g. Lake Van, Turkey; (Kaden et al., 2010)).

An excursion towards more humid climate conditions with higher precipitation values is recognized between 8,600 to 7,900 cal yrs BP from speleothem records of the nearby Soreq cave, Israel (Bar-Matthews et al., 2000) and Jeita cave, Lebanon (Verheyden et al., 2008) with reconstructed precipitation values up to 550-700 mm/a. These shifts in moisture availability also affected the Eastern Mediterranean basin, as seen by the formation of sapropel (e.g. S1; Kallel et al., 1997, De Rijk et al., 1999). Our data are strongly in accord with the hypothesis of a humid Early Holocene in the southern Levant, clarifying the uncertainty generated previously by low lake levels reported in the Dead Sea (Kushnir and Stein, 2010). A slight rise in Dead Sea lake level does occur at this time (figure 3.6), reflecting a subdued response or local variation in climate.

As noted above, conditions in subzone DAZ-4a (7,900 – 7,400 cal yrs BP) return to a relatively arid state with a low lake level similar to that reported for DAZ-4c, even though diatom communities show higher relative abundance of fragilarioid and *Cocconeis* spp. rather than a diversity of benthic taxa, indicative of an unstable, fluctuating environment (Schmidt et al., 2004, table 3.2). Although later, according to the age-depth model (figure 3.2), it is within the error range (a reservoir effect of nearly 1,000 years; Schiebel and Litt, 2017) to argue that this subzone represents the Early to mid-Holocene boundary, coinciding with the so-called 8.2 k yrs abrupt climate event (Walker et al., 2012). The 8.2 k yrs cold (arid) event is the most prominent rapid climate change (RCC) at northern high latitudes during the Holocene (Johnsen et al., 2001, Pross et al., 2009) and its influence on terrestrial records in the Eastern Mediterranean is strongly debated (Robinson et al., 2006). The observed strong diatom response also occurs in some other Mediterranean sites (e.g. Cvetkoska et al., 2014, Ariztegui et al., 2001); here, other proxy data also show a peak, e.g. K – indicative for enhanced erosion, but no marked shift in palynological evidence for its impact on catchment vegetation is recognizable. Bar-Matthews et al. (1999) reported a sudden cooling and decrease in precipitation around 8.2 cal kyrs BP for the Soreq cave (Israel). Moreover, geomorphological lake-level reconstructions from Lake Kinneret (Hazan et al., 2005, and this study) and the Dead Sea (Kushnir and Stein, 2010, Litt et al., 2012) show low lake-level stands between 8,000-7,500 cal yrs BP (figure 3.6), indicating a region-wide response to shifts in moisture towards more arid climate conditions. Kushnir and Stein (2010) conclude that marked Holocene arid events, which are expressed as abrupt and relatively large drops in the Dead Sea lake level (10 m or more), correlate with pronounced cooling episodes recorded in Eastern Mediterranean winter sea surface temperatures (SST, reconstructed from planktonic foraminifera in marine sediment cores) and with cold events in northern latitudes.

From 7,400 – 2,200 cal yrs BP (DAZ-3, Transition Neolithic/Chalcolithic Period – Bronze Age–Iron Age)

DAZ-3 is characterized by the consistently high abundance of planktonic diatom taxa (> 80%) mainly belonging to the *Cyclotella ocellata*-complex (table 3.2), indicating stable, high lake levels and an oligo-mesotrophic state throughout this subzone (Vossel et al., 2015, and references therein). The marked transition to plankton dominance represents strong evidence for a rapid increase in lake level around 7,400 cal yrs BP, which is also observed in the diatom data from Lake Prespa, further north (Cvetkoska et al., 2014).

From a geochemical perspective, in phase primary carbonate accumulation (Ca/Ti-ratio) and diatom concentration indicate long-lasting increased productivity phases between 6,000 and 5,000 cal yrs BP and between 4,000 and 2,200 cal yrs BP (figure 3.5). In general, DAZ-3 is a phase of moderate detrital input. Abrupt, marked excursions of potassium also occur, indicating pulses of terrigenous input, which might be caused by flood events or other external triggers. Most of the punctual increases in detrital input have no influence on the diatom flora.

The interpretation of enhanced humidity is supported by palynological evidence for an increase of summer-green oak (*Quercus ithaburensis*-type), especially in subzone DAZ-3a and a slight decrease in steppic vegetation, which seems to be natural and not anthropogenically induced (Schiebel and Litt, 2017). The pollen evidence alone was not definitive since the climate signal is strongly overprinted by human activities from the Chalcolithic period onwards. Fluctuating human settlement size and activities around Lake Kinneret during this time period (Langgut et al., 2013, 2015) seem not to have a remarkable effect on the lake's ecosystem and trophic state, as interpreted from the high-resolution diatom record.

In summary, all analysed proxies indicate a stable, oligo-mesotrophic lake system for the mid-Holocene with a maximum lake-level high-stand lasting from 7,500 till 2,200 cal yrs BP. This is in accord with climate models based on palynological data, providing evidence for an extended humid phase with precipitation values up to 650 mm/a for the Levantine region (Litt et al., 2012). Additionally, our dataset is in accord with other diatom records in the Eastern Mediterranean, which also exhibit an inferred mid-Holocene phase of maximum lake levels (e.g. Lake Ioannina; (Jones et al., 2013); Lake Prespa (Cvetkoska et al., 2014) and Lake Dojran (Zhang et al., 2014)). A mid-humid Holocene is also documented by increasing lake levels in Lake Iznik (Turkey) based on high resolution grain size analysis and carbonate accumulation (Roeser et al., 2016). Many localities in the Levant support the hypothesis of a humid climate optimum, e.g. speleothem records from Soreq cave, Israel (Bar-Matthews and Ayalon, 2011) and Jeita cave, Lebanon (Verheyden et al., 2008) and a new, high-resolution pollen record from Lake Kinneret (Langgut et al., 2016).

Previous lake-level reconstructions for Lake Kinneret (Hazan et al., 2005) and the Dead Sea (Kushnir and Stein, 2010) (figure 3.6) had shown inconsistencies, which were thought to reflect differences in patterns of evaporation and local differences in freshwater supply (Stein, 2014). From our results, the stability of the Kinneret high stand accentuates the apparent discrepancy further, standing in stark contrast to the major fluctuations in lake level inferred for the Dead Sea. Although our results are more closely in accord with other records of the region, it is possible that, as a closed-lake basin, the Dead Sea exhibits far higher sensitivity to changing moisture availability. Furthermore, our results support the hypothesis that the strong north to south climate gradient of today (see also 3.3 Site description section) operated through most of the Holocene, which might explain independent changes in the limnological behaviour of the two lake systems. These observations support the analysis of Enzel et al. (2008), who argued that the present north-south climatic gradients between arid and Mediterranean zones were already established during the Late Pleistocene.

The diatom record of Lake Kinneret shows, in contrast to the 8.2 k yrs event, no evidence for the so-called 4.2 cal kyr BP drought event appearing across the Northern Hemisphere between 4.2-3.8 cal kyrs BP (Mayewski et al., 2004). The lack of response might be caused by the fact that the lake was a deep, stable ecosystem during this time. A similar lack of diatom response was observed in Lake Prespa (Cvetkoska et al., 2014). Nevertheless, there is subtle evidence in the pollen record (Schiebel and Litt, 2017) comprising decreased arboreal pollen percentages around 4,000 cal yrs BP (figure 3.5).

During the Late Bronze Age (around 3,200 cal yrs BP) a subsequent pronounced dry episode has been identified from palynological analysis of Lake Kinneret (Langgut et al., 2013, 2015, Schiebel and Litt, 2017). This event lasted probably slightly more than a century and is represented by a reduction in arboreal pollen percentages (low *Quercus* spp. in figure 3.5), clearly not induced by human deforestation as settlement activity was low in many areas during that time. Again, the stable, deep lake-level state in Kinneret during this phase might cause a buffering effect on the diatom response, possibly similar to observations made in Lake Eski Acigöl, Turkey (Roberts et al., 2001). A remarkable drop in lake levels does appear to occur in the Dead Sea at this time (Kushnir and Stein, 2010, Stein et al., 2010), however.

Sediment disturbance at 2.3 k cal yrs BP

In the rather homogenous Holocene sediment sequence of Lake Kinneret, a major shift in palaeolimnological proxy data at 4.64 to 4.57 m depth (ca. 2.3 cal kyrs BP; figure 3.7), indicates the occurrence of an event layer. This 4 cm thick sediment sequence shows abrupt lithologic and mineralogical boundaries, and grain size shows inverse grading, which is indicative of a rapid depositional event. Concentrations of microcline, detrital dolomite and quartz are the highest of the profile (table 3.3) and potassium and phytolith counts exhibit clear peaks.

This distal deposit of a turbidity current/gravity flow might have originated from two distinct natural triggers (a) seismic activity or (b) climate, as a result of a flash flood event. Terrestrial deposits of palaeo-earthquakes with Holocene age are encountered at the south-eastern margin of Lake Kinneret (e.g. Klinger et al., 2015, Reches and Hoexter, 1981). Given the lake's location on the active Dead Sea transform fault system, it is conceivable that the observed event layer originated from a seismic event. On the other hand, deposits of flood events are known from Lake Kinneret, however appearing closer to the shore and under direct influence of river discharge. For example, Williams (2016) recently recorded two flood deposits in a short sediment core (143 cm; 4,000 years) from the western shore of Lake Kinneret, providing strong evidence for fluctuating dry-wet conditions of the Roman-Byzantine periods due to climate instability.

Another possible human-induced explanation for the sediment disturbance could be the start of olive tree cultivation and the previous clearance of the natural vegetation visible in the gradual decrease of *Quercu*s spp. in the pollen data (Schiebel and Litt, 2017) at the top of DAZ-3a. Natural vegetation clearance and heavy rain could cause a rapid in-wash of soils and nutrients from the catchment (Cohen, 2003, Zuazo and Pleguezuelo, 2008), which also would explain high amounts of K and detrital minerals, low lake productivity (i.e. low diatom concentration and Ca/Ti ratio), as well as the sample devoid of diatoms. Further research is necessary to identify the causal mechanism, but the event is followed shortly afterwards by a complete compositional change of the diatom community towards a more eutrophic assemblage.

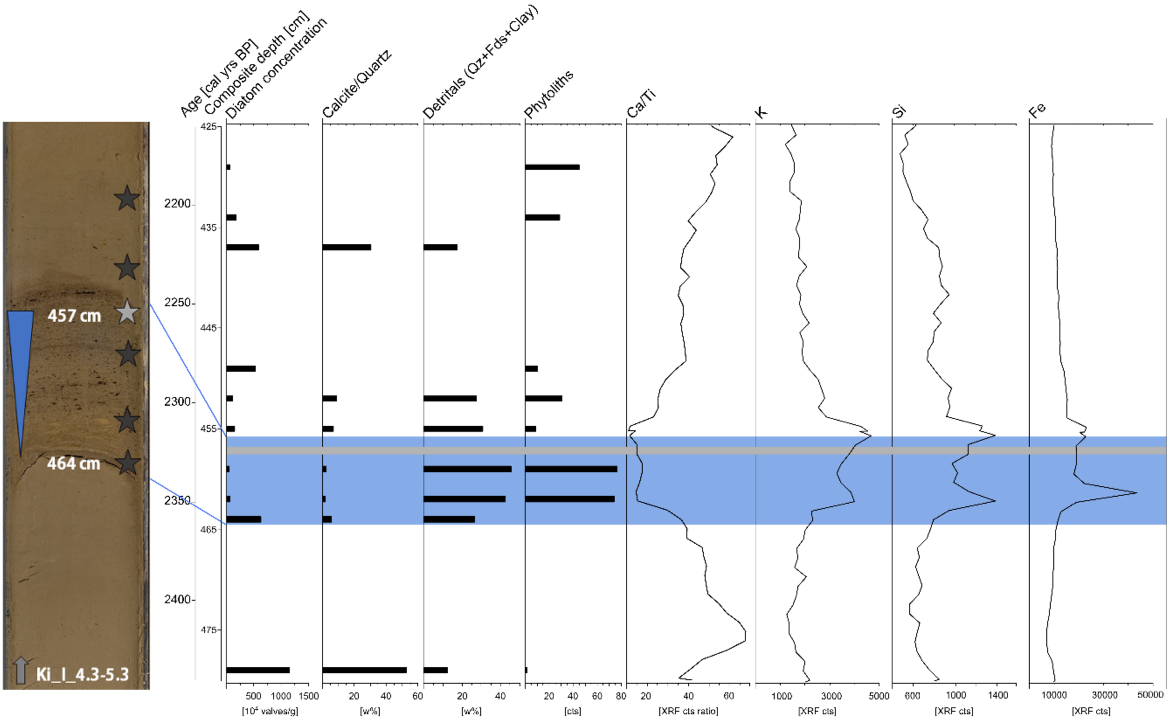

Figure 3.7 A putative event layer in core Ki_I_4.3-5.3 showing inverse grading and contrasting lithology compared to the rest of the record, correlating with marked shifts in geochemical and mineralogical indicators. Each star represents one sample. The light grey line denotes a sample containing no diatoms.

From 2,200 -1,600 cal yrs BP (DAZ-2, Hellenistic & Roman/Byzantine Period)

The onset of DAZ-2 (corresponding to the Hellenistic Period; around 2,200 cal yrs BP) is marked by a major reduction in the P/B-ratio and diatom concentration. A floral shift towards planktonic taxa such as *Aulacoseira granulata*, *Cyclotella polymorpha* and small *Stephanodiscus* (*S. minutulus/parvus and S. hantzschii*) strongly indicate a higher trophic state of the lake (Krammer and Lange-Bertalot, 1986, 1991a, 1988, 1991b, Stiller et al., 1984) and a possible reduction of lake level. *Cyclotella paleo-ocellata* and *S. galileensis* disappear completely from the record probably due to the increase in nutrient availability. Pollingher et al. (1984) made similar observations in diatom analysis of the sediment core KIND-4, taken close to station D in the southern part of Lake Kinneret at 23 m water depth, and inferred nutrient enrichment correlated to more dense human settlement and intensive agricultural activity around the lake during the Hellenistic-Roman period. The increase and diversification of *Pediastrum* spp. in this DAZ also supports an increase in trophic state (Pollingher, 1986).

The surprisingly low diatom concentration in DAZ-2 may be explained by the competitive advantage of green algae over diatoms (Stiller et al., 1984).

This interpretation is supported by the replacement of oak woodland by olive plantations (*Olea europaea*) in the catchment (Schiebel and Litt, 2017) and an inferred increase in terrigenous input indicated by mineralogy and phytolith data. Neumann et al. (2007) recognized deforestation activities during the same period in nearby Birkat Ram, a small maar lake in the northern Golan Heights. Rising population density, bigger urban societies and continuous agriculture activities are also well documented archaeologically in the Hellenistic and Roman/Byzantine time periods (Anderson, 1995, Dar, 1993, Chancey and Porter, 2001).

The clearance of the surrounding natural vegetation would enhance erosion of nutrients and terrestrial input to the lake, indicating that the shift from an oligotrophic to a more meso- to eutrophic lake system was induced by human activities rather than climate change.

Deforestation and intensive farming have led to marked changes in the nutrient balance of many lake systems during the mid- to Late Holocene, which is well reflected in many palaeolimnological records based on diatoms around the Mediterranean (e.g. Cvetkoska et al., 2014, Zhang et al., 2014).

The evidence for lake-level shallowing in the proxy data (slightly comparable to DAZ-4a/c) may be climatically induced, since this has also been recognised as a more arid, warmer phase by other researchers (Finné et al., 2011), but standing in contrast to colder and humid climate conditions reported for this region (Issar, 2003). A climate-induced shallower lake-level phase in Lake Kinneret is therefore unlikely and also stands in contrast to a high lake-level stand reported from the Dead Sea (figure 3.6, Kushnir and Stein, 2010). Woodbridge and Roberts (2011) have demonstrated in a palaeoclimate record from Nar Lake (Turkey) that anthropogenic changes in land use can lead to long-term shifts in the diatom response to climate variability through time and therefore highlight that diatom-inferred climate interpretations on Late Quaternary timescales should be considered with caution.

An alternative, non-climatically induced explanation for a lake-level reduction of Lake Kinneret could be human water abstraction associated with catchment vegetation management and irrigation. Major irrigation systems were introduced to this region in Hellenistic times and become common in the Roman era to ensure water-supply of bigger urban centres (Lemche, 2015), such as Tiberias, which were founded in the Roman period.

Overall, it can be concluded that human activities are strongly overprinting the climate signal of the multi-proxy record after the onset of the Hellenistic/Roman period. Shifts in the diatom assemblage or varying P/B-ratios in the following sections therefore reflect changes in the trophic state of the lake and its productivity, rather than being a reliable indicator for fluctuating lake levels.

From 1,600 – 900 cal yrs BP (DAZ-1c/-1b, Late Byzantine & Islamic Period)

In DAZ-1c/-1b (table 3.2) the recovery to an oligo-mesotrophic lake system is indicated by a decrease of initial dominance of *C. polymorpha* (DAZ-1c; mesotrophic) and the subsequent renewed dominance of *C. ocellata* (< 80 %; oligo-mesotrophic) in this subzone. The low abundance of *Aulacoseira* and *Stephanodiscus* taxa also support a shift to more oligo-mesotrophic conditions. This is not reflected in the geochemical data. Carbonate accumulation and S/Ti both increase, whereas detrital minerals are at their lowest values (< 15%). The consistent increase of pyrite concentration is indicative of an at least seasonally anoxic sediment surface, likely allowing sin-depositional pyrite concentration. This is a typical feature in eutrophic lakes, when increases in TOC production, and especially consumption, lead to anoxic conditions in the lower water column.

Schiebel and Litt (2017, Schiebel, 2013) report a period of woodland regeneration with the re-occupation of abandoned olive groves by evergreen oaks and pistachios in the palynological record of Lake Kinneret in this period. The recovery of the diatom flora as well as the regeneration of natural woodland can be reflecting a decrease in settlement activities and in economic structures as well as a decline of agriculture and population density reported in the southern Levant during the Islamic Period (Safrai, 1994).

From 900 cal yrs BP – present (DAZ-1a, Crusader Period till today)

DAZ-1a incorporates the species composition of the modern diatom flora of Lake Kinneret, which is now strongly influenced by the economic revival in this area, especially the development of industry and tourism. The subzone DAZ-1a is dominated by strongly eutrophic diatom taxa, which are also tolerant of general water pollution, including *Aulacoseira granulata*, *Cyclotella meneghiniana* and large *Fragilaria capucina* (Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b, Ehrlich, 1995, Lange-Bertalot, 2013). As noted above, the low diatom concentration in the modern flora is probably due to a marked increase in dominance of dinoflagellates and green algae (*Pyrrhophyta-Chlorophyta* assemblages) in the phytoplankton (Pollingher et al., 1984). The geochemical data exhibit an increase in detrital values and maximum pyrite values. The lack of shifts in other indicators compared to DAZ-1b suggest, that it was only recently that the annual pattern of lake mixing was established. This is also supported by the laminated sediment deposits only occurring in the upper most 25 cm of the sediment sequence.

Lake levels fluctuated markedly from 1,600 cal yrs BP until present, as indicated by shifts both in diatom concentration and the P/B-ratio. As noted above, lake levels can fluctuate by up to 4 m per year depending on precipitation/evaporation, but mostly on human water management control. Human-induced impacts (e.g. water abstraction, industry and agriculture) on the lake ecosystem and its watershed are well documented over the last > 40 years by the Lake Kinneret monitoring program (Sukenik et al., 2014).

3.7 Conclusions

Our study has greatly improved our understanding of Holocene climate variability in the Lake Kinneret area and across the southern Levant as a whole. The diatom data in particular provide a robust signal of lake-level response to shifts in moisture availability, although partly obscured in the later record by the impact of human activities. In the context of understanding palaeoclimate variability our major conclusions are:

1. Apart from lithological evidence for a possible disturbance event around 2,300 cal yrs BP, the Lake Kinneret sediment record provides an important continuous high-resolution Holocene sequence for the southern Levant.
2. Major shifts in the diatom community and especially in the P/B-ratio, during the Early and mid-Holocene are driven by changes in lake level and moisture availability rather than lake productivity or changes in trophic status.
3. During the Late Holocene, after 2,200 cal yrs BP, the climatic signal is overprinted by accelerated nutrient enrichment linked to intensification of human activities in the catchment area.
4. The new detailed lake-level reconstruction for Lake Kinneret based on the P/B-ratio of diatoms in combination with minero-geochemical analysis allows for the first time a detailed comparison between the two contrasting lake systems of the Dead Sea and Lake Kinneret. Following a phase of lake-level fluctuations in the Early Holocene linked to alternation between an arid and more humid climate in Lake Kinneret, diatoms indicate a prolonged stable deep lake phase throughout the mid-Holocene and the onset of the Late Holocene due to long-lasting humid climate conditions. Independent changes in the limnlogical behaviour of Lake Kinneret and the Dead Sea probably reflect the long-term existence of the strong north (humid) to south (arid) climate gradient which

operates today, coupled with the higher sensitivity to changing evaporation/precipitation conditions of the Dead Sea, as a closed basin system.

5. The presented diatom record shows similarities to palaeoclimate records studied around the Mediterranean. Lake ecosystems of these moderately deep, alkaline lakes seem to react in similar ways to larger scale climatic events during the Holocene such as the 8.2 k yrs event and the mid-Holocene humid period.

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4 Is the present the key to the past? Diversity and distribution of modern diatom communities in Lake Kinneret (Israel)

Chapter 4 is based on a publication in preparation, which will be submitted after performing some final analyses.

4.1 Abstract

Uniformitarianism is a key concept in palaeoecological research. Based on the assumption that ecological preferences remain constant, a better understanding of the modern lake environment can strongly improve palaeoenvironmental interpretation derived from analysis of fossil datasets preserved in lake sediment archives. In palaeolimnology, the analysis of modern diatom communities and their subfossil death assemblages is an example. This is the basis of the transfer function approach for quantitative palaeoenvironmental reconstruction of limnological variables, based on analysis of large regional datasets of modern diatom assemblages and water chemistry. Less often considered is the detailed limnological survey of a single lake system, which also can provide useful insights. Meso-eutrophic Lake Kinneret is the largest natural freshwater body in Israel and by water abstraction a major source of drinking and irrigation water for the whole region. Although the lake is currently the subject of extensive aquatic monitoring programmes, knowledge of the spatial distribution and habitat preferences of modern diatom assemblages is rather limited.

Twenty-eight surface sediment samples were collected from Lake Kinneret, covering a range of different water depths and habitat areas, to investigate the composition of diatom death assemblages and their distribution within the modern lake system. A quantitative diatom-inferred water-depth model based on simple linear regression between modern diatom assemblages and water depth is presented in this study, as a tool for semi-quantitative calibration of Holocene lake-level change. The new calibrated lake-level reconstruction fits well to palaeo-shoreline measurements and appears to display greater sensitivity to minor lake-level variation than a simple Plankton/Benthos-ratio approach. A close similarity between Lake Kinneret and the Dead Sea is observable, indicating that they were subject to similar regional fluctuations in moisture availability. Our results confirm that the investigation of modern diatom death assemblages can be helpful to understand and calibrate the limnological history of lakes. Approaches like this should be considered more often in future palaeoenvironmental studies.

Keywords: Holocene, modern diatom death assemblages, P/B-ratio, lake-level reconstruction

4.2 Introduction

Warm, monomictic Lake Kinneret lies 210 m below sea level (mbsl) and is located in the northern part of the East African Rift Valley. The lake is the largest natural freshwater body in Israel and plays an important role in the natural freshwater supply (50%) for the region. This has been the case since prehistory, and anthropogenic activities over time have had a marked effect on its ecosystem (Zohary et al., 2014a, Vossel et al., 2018), which has been well-monitored over the last ca. 50 years since the establishment of the Kinneret Limnological Laboratory in 1969.

The morphometry of a lake basin, i.e. shape and size, affects nearly all physical, chemical and biological parameters within a lake system. Lake morphometry (best described by a bathymetric map) and the geological substrates within the drainage area influence sediment-water interactions, the lake's productivity, water pH, and sediment grain-size characteristics (Wetzel, 2001). In general, a lake can be separated into the open-water pelagic zone (habitat zone of plankton) and the littoral zone (habitat zone of benthic organisms). The sediment area, which is free of vegetation lying below the pelagic zone, is referred as the profundal zone (figure 4.1).

Diatoms (single-celled siliceous algae; *Bacillariophyta*) are ecologically widespread, occurring in marine, freshwater and (semi-)terrestrial habitats worldwide (Mann, 1999). They are often an important component of the phytoplankton community inhabiting the pelagic zone of lakes and form diverse benthic communities in a range of shallow-water habitats. Due to their specific ecological preferences and the long-term preservation of their silica valves in (lake) sediments, diatoms are highly useful palaeoenvironmental indicators (Smol and Stoermer, 2010). As diatoms require light for photosynthesis processes, water clarity and the related light penetration depth are important limiting factors, both of which affect the available habitat for planktonic and benthic diatom growth (Stone and Fritz, 2004, figure 4.1).

In modern Lake Kinneret the contribution of diatoms to total phytoplankton biomass volume has been described as irrelevant (Pollingher et al., 1984) and they are only represented by a limited number of species (less than 15) in the modern phytoplankton community (Zohary et al., 2014b). During the mixing period (December-March), when the concentration of nutrients is highest, a small peak of diatom biomass is observable in the annual records (Pollingher et al., 1984, Sukenik et al., 2014). In spite of this, planktonic diatom taxa tend to dominate over benthic taxa in the palaeolimnological record and are thus an important component of the diatom flora. In the benthic communities they play a more important role in regard to diversity, with more than 200 reported species (Round, 1978). The composition and fluctuations of the overall phyto- and zooplanktonic communities in correlation with the environmental conditions in Lake Kinneret are well documented and available for the past 50 years via the Kinneret Limnological Laboratory and its "Long-monitoring data centre" (http://www.ocean.org.il/eng/KineretDataCenter/ProfileDC.asp, Sukenik et al., 2014). However, our knowledge concerning habitat preferences, ecological tolerances, diatom community associations and dynamics in Lake Kinneret is still rather limited. Although anthropogenic influences have caused a shift in the modern diatom composition compared to the fossil one (Vossel et al., 2018), the modern flora still contains many of the taxa present in the fossil record.

The concept of uniformitarianism ("the present is the key to the past"; in *Principles of Geology* after Lyell, 1830) is fundamental to palaeoecological reconstruction in Quaternary research (e.g. Saros, 2009, Woodbridge and Roberts, 2010, Seddon et al., 2014), allowing interpretation of fossil assemblages based on the premise that ecological preferences remain constant over time. The diatom-based 'transfer function' approach for quantitative reconstruction of limnological variables, based on analysis of large regional datasets (or 'training sets') of modern ecological and water chemistry data, is a prime example (Battarbee et al., 2001). Transfer functions have primarily been developed for the key parameters of salinity, pH and total phosphorus (e.g. Reed et al., 2001, Cumming et al., 2012, Birks, 2003). While diatom-based salinity, lake-level and thus palaeoclimate reconstruction has been common in studies of Mediterranean closed-basin lakes (e.g. Reed et al., 1999, Roberts et al., 2008), the approach is not applicable to open-freshwater Lake Kinneret. Vossel et al. (2018) showed that Holocene lake-level changes in Lake Kinneret cannot be linked to major changes in salinity, as the subfossil diatom assemblage analysed in a 18 m sediment sequence, does not contain a significant number of halophilious diatom species and therefore demonstrated that the lake has remained fresh throughout the record. Geochemical analyses also did not reveal salinity variations during the Holocene.

Instead, the greatest potential for reconstruction of shifts in moisture availability in a freshwater lake is that of physical reconstruction of lake-level change. Shifts in the water level of a lake system can give insights into changing hydrological conditions in its catchment area, which often reflect regional changes in effective moisture (precipitation minus evapotranspiration). The ratio of planktonic-to-benthic diatoms, derived from stratigraphic diatom death assemblage analysis of freshwater lake sediment records, has been used in many palaeolimnological studies as an indicator for past lake-level changes and thus to gain insights into regional climatic shifts in moisture availability (e.g. Wolin and Stone, 2010, and references therein, Jones et al., 2013; Cvetkoska et al.; 2014). Those studies are most robust when they are supported by multi-proxy analysis, e.g. sediment stratigraphy or geochemical analysis. The use of the “simple” P/B-ratio for lake-level reconstructions to infer climate shifts during the Holocene for Lake Kinneret is already discussed in detail in Vossel et al. (2018, see Chapter 3).

In modern limnological research to exploit the value of the present environment as a key to the past, the detailed limnological survey of a single lake system rather than collection of a regional dataset has received relatively little attention. This study investigates the distribution of modern diatom death assemblages in Lake Kinneret with the aim of improving understanding of diatoms as proxies for past environmental change by quantification of water-depth change over time. A few studies have developed quantitative diatom-inferred depth models, which rely on simple linear or multiple regression analysis to determine possible correlations between diatoms and water depth (e.g. Barker et al., 1994, Yang and Duthie, 1995). Diatoms were assigned to growth-habit categories in these studies (i.e. planktonic, facultative planktonic or benthic) based on the literature. Since the assignation of a single growth-habitat classification for each taxon is rather subjective and to some extent artificial, this approach can be problematic (Wolin and Stone, 2010).

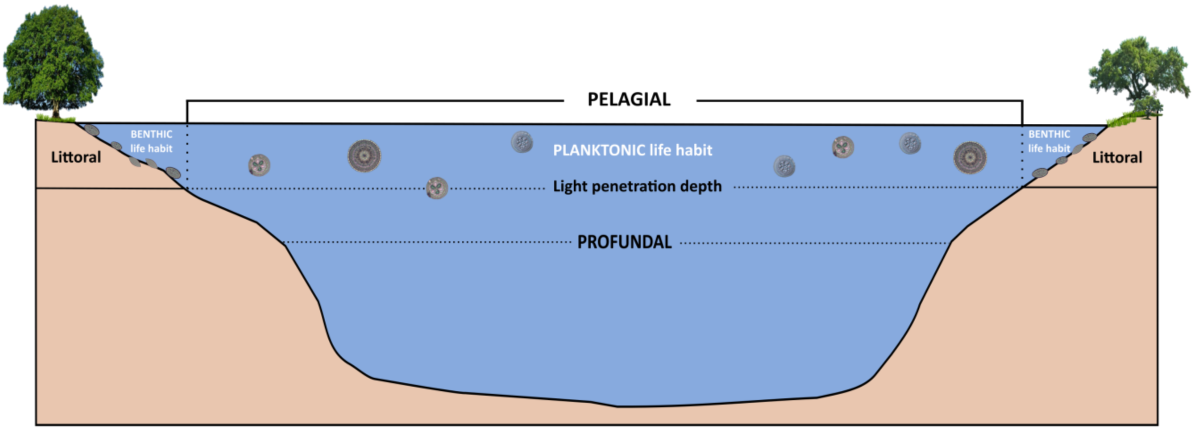

Figure 4.1 Classical lake zonation into different habitat areas of planktonic and benthic organisms.

To provide a comprehensive data-set of modern diatom communities for analysis of diatom habitat preferences and distribution at different water depths, 27 sediment surface samples of Lake Kinneret were taken from across the lake bed (including the profundal and littoral zone as well as saline springs and a variety of benthic habitats). A quantitative diatom-inferred depth model based on simple linear regression between diatom distribution and water depth was then developed. The ultimate aim was to develop a tool for calibration of lake-level changes from fossil diatom data generated by analysis of a ca. 18 long sediment core (taken in 2010; Vossel et al., 2018) to provide a quantitative index of water levels over the last 9,000 years.

4.3 Study site

Lake Kinneret (Sea of Galilee or Lake Tiberias) is, with a surface elevation of 210 mbsl, the lowest-lying freshwater lake on Earth. The lake is located in the north of Israel in the northern part of the Jordan Rift Valley (32°48’08.12’’ N, 35°35’20.62’’ E; figure 4.2), which is filled with alluvial and lacustrine sediments of Neogene and Pleistocene age. The Holocene Sea of Galilee has evolved from ancient water bodies (such as former Lake Lisan) that filled the Kinnarot tectonic depression during the Late Pleistocene (Hazan et al., 2004). The lake basin itself was partly shaped by tectonic movements associated with the tectonically active Dead Sea transform fault system (Ben-Avraham et al., 2014). The surrounding lake catchment is mainly composed of Cretaceous to Eocene carbonate rocks (limestones, dolostones, chalks and marls) with extensive karst and Neogene and Pleistocene basalts, which form escarpments of up to 500 m in height, especially on the eastern shore of the lake (Sneh et al., 1998).

The lake is the largest natural freshwater body in Israel (22 x 12 km; 167 km^2) and by water abstraction is a major source of drinking and irrigation water for the whole region. The lake is around 41.7 m deep at its central basin and its catchment area encompasses around 2730 km^2 (Berman et al., 2014). Total annual water inflow is about 629 x 10^6 m^3 comprising the inflow of the Jordan River (main freshwater input with 434 x 10^6 m^3/year), direct catchment runoff, saline springs, direct precipitation and other water sources (Rimmer and Givati, 2014). Modern lake level can fluctuate by up to 4 m a year depending on precipitation, evaporation (230 x 10^6 m^3/year) and water use for human consumption and agriculture (Rimmer and Givati, 2014, National Water Carrier, personal communication). The lake is also fed by several saline springs (e.g. Tabgha; sample LK_12_65), which influence its salinity and geochemical composition (Stiller et al., 2009, Stein, 2014, Kolodny et al., 1999, Nishri et al., 1999).

The Kinneret region is currently characterized by a typical semi-arid Mediterranean climate (Baruch, 1986), with an average annual precipitation of 400 mm and a mean annual temperature of 21 °C. 90 % of the precipitation in northern Israel originates from the Mediterranean Sea and is brought to this region by west winds generated from mid-latitude (Cyprus) lows (Ziv et al., 2014). The mean annual precipitation and temperature vary considerably from northern to southern Israel, partly as a function of topography. Maximum precipitation occurs further north, on Mt. Hermon (Golan Heights), with an average of 1600 mm/year. In the Jordan Valley precipitation varies from 700 mm/year in the Hula basin to 300 mm in the Beth-Shean region (Langgut et al., 2016). There is a sharp transition to a fully arid climate in the south. Annual temperatures increase approximately linearly with decreasing precipitation.

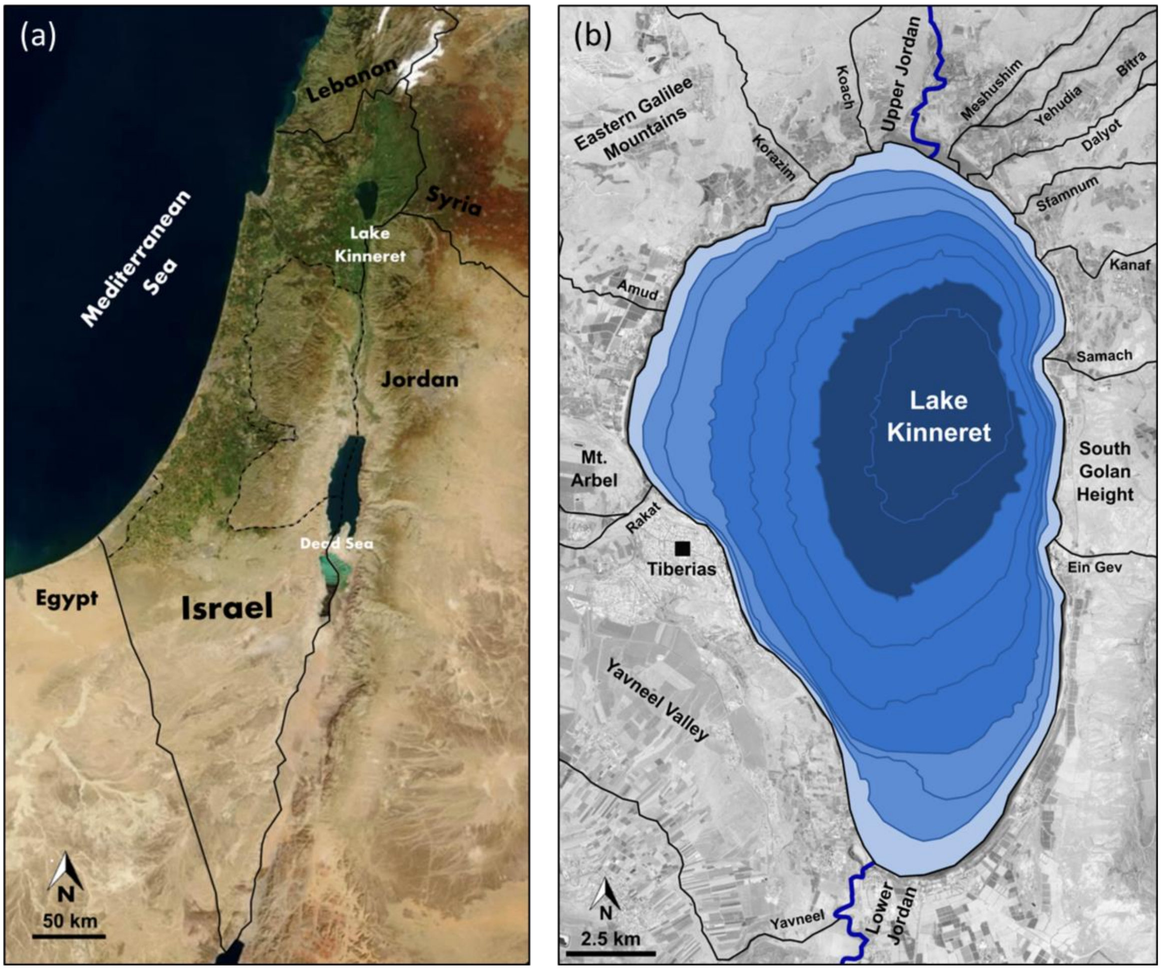

Figure 4.2 (a) Regional setting of Lake Kinneret in the Jordan Rift Valley in the northern part of Israel. (b) Bathymetry (10 m intervals) of Lake Kinneret. All inflows of the catchment area are displayed; major in- and outflow is the Jordan River (backgrounds for (a) and (b) after NASA).

Lake Kinneret is a meso-eutrophic, warm monomictic lake, being stratified with an anoxic hypolimnion from May to December and fully mixed from December to April (Gophen, 2003, Katz and Nishri, 2013). In modern Lake Kinneret the phytoplankton flora is dominated by dinoflagellates, with a low proportion of diatoms, cyanobacteria and chlorophytes. In older literature the seasonal dynamics of the phytoplankton community in Lake Kinneret were described as an annual succession at species level (four stages described in detail by Pollingher (1981)) with distinctive spring blooms of the dinoflagellate *Peridinium gatunense* that repeated every year with only minor deviations. More recent studies reveal that the Kinneret phytoplankton record can be split into two major periods (Zohary, 2004, Zohary et al., 2014b): (1) 1969-1993 – a period of distinct stability with typical dinoflagellate spring blooms occurring every year. (2) 1993-ongoing – the loss of this annual pattern, with "bloom years" and "no-bloom years" combined with e.g. an intensification of winter diatom blooms (i.e. *Aulacoseira granulata*) or occurrences of cyanobacteria in summer with increased values in total biomass volume.

The most common planktonic diatom taxa in Lake Kinneret are *Cyclotella* (newly *"Pantocsekiella"*) spp., *Stephanodiscus* spp. and *Aulacoseira granulata,* which are often accompanied by the periphytic *Brachysira* spp. The most common benthic taxa are *Amphora pediculus*, *Achnanthes* sensu lato spp., *Navicula* spp., *Synedra ulna* and *Rhoicosphenia curvata*. A detailed species list is provided in (Zohary et al., 2014b).

4.4 Material and Methods

4.4.1 Surface samples

Around 50 freeze dried sediment surface samples from Lake Kinneret were provided by Dr. Ahuva Almogi-Labin from the Geological Survey of Israel for detailed diatom analyses. Sediments were taken during a sampling survey in January 2012 within a project aiming to improve understanding of faunal associations (ostracods and molluscs) during the un-stratified season of Lake Kinneret. Samples were taken from different water depth and different habitat areas within the lake. 27 of those 50 samples were selected and included in this study (figure 4.3). The sediment surface samples, taken with an Ekman grab, were sampled along the following transects: a major transect from North to South; transects near hot, saline springs and one near the Jordan River delta (figure 4.3). All areas within the lake are covered by the chosen samples, except from water-depth intervals covering 1-8 m and 12-16 m. Due to limited sample sizes and availability, those areas are lacking data points, e.g. the western intermediate water depth. Palynological analyses of the same sample material have been carried out by Böttcher (2016).

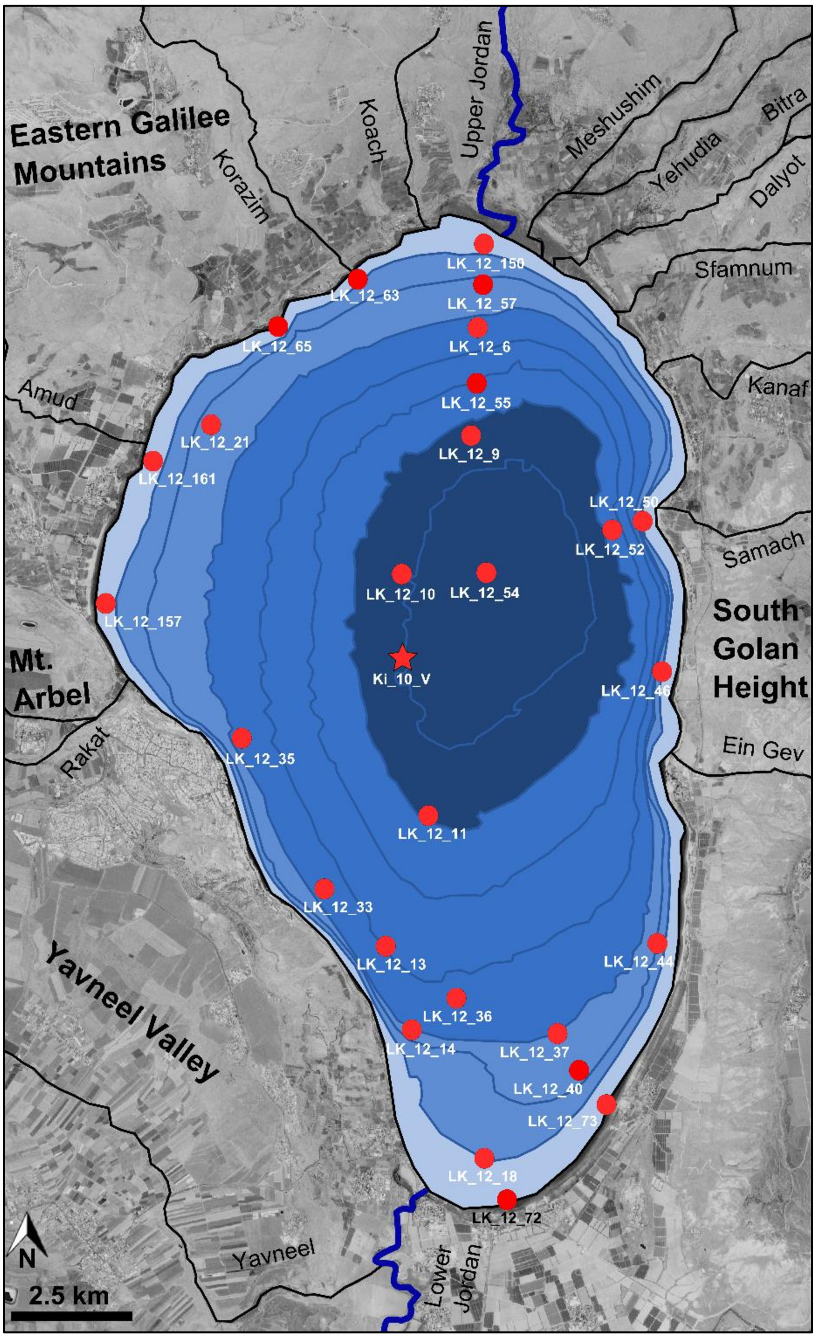

Figure 4.3 Overview of sampling sites of 27 analysed sediment surface samples (red dots) taken in 2012, including the drilling site (star) of the core Ki_10 (taken in 2010) at the deepest part of the lake.

4.4.2 Core material

For comparison purposes the top layer of a sediment core (Ki10_V1_top; 0-1 cm sampled in composite depth profile) recovered from a water depth of 38.8 m at the central, deepest part of the lake basin, was also analysed. These sediment cores were recovered during a coring campaign in March 2010, which formed a part of the Collaborative Research Centre (CRC) 806 “Our Way to Europe” (http://www.sfb806.uni-koeln.de). Core chronology is presented in full detail in Schiebel and Litt (2018).

Lake-level reconstructions inferred from shifts in the fossil diatom assemblages (Plankton/Benthos (P/B)-ratio) analysed from the complete ca. 18 m long sediment record taken in 2010 (Vossel et al., 2018) are calibrated within this study following the approach of Barker et al. (1994), with minor modifications. The results of lake-level calibration are compared with the results of analysis of palaeo-shoreline measurements conducted by Hazan et al. (2005) and (for regional palaeoclimate comparison) with inferred lake-level data for the Dead Sea, which were compiled for the Holocene by Kushnir and Stein (2010).

4.4.3 Diatom slide preparation and counting

For diatom analysis subsamples of 27 sediment surface samples and one core sample were prepared for light microscopy (LM) observation. All samples were prepared using standard techniques (Battarbee, 1986): 0.1 g of the freeze dried material was cleaned by adding H_2O_2 (30 %) and heated on a hot plate for 2 to 3 hours to oxidize organic matter. Afterwards a few drops of concentrated HCl (35 %) were added to the hot sample residual to remove carbonates. Samples were washed with distilled water and centrifuged (1200 rpm for 7 min/5-7 times) to eliminate the acid residual and avoid dissolution during storage. To allow the calculation of diatom concentrations (valves/g), known quantities of microspheres were added to each sample after chemical treatment and before dilution. Cleaned, organic-free diatom material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides and was dried on microscope coverslips overnight. Samples were mounted in Naphrax™ for permanent slide preparation.

In each samples 500 diatom valves were identified and enumerated on random transects using a Zeiss Axio Lab.A1 LM at x1000 magnification under oil immersion. Diatom taxonomy and nomenclature follow Krammer and Bertalot (1986, 1988, 1991a, 1991b), Lange-Bertalot (2013) and the Diatom Flora of Israel (Ehrlich, 1995). Current changes in nomenclature are modified following the Catalogue of Diatom Names (Fourtanier and Kociolek, 2009).

Diatoms were classified according to the three common habitat groups: planktonic, facultative planktonic (tychoplanktonic) and littoral based on data provided in the available ecological literature. Littoral taxa in this study include all periphytic (i.e. epiphytic, epilithic, epipsammic and epipelic) and shallow-water benthic life forms.

4.4.4 Data analysis

Diatom counts were converted to percentage data and Tilia version 1.7.16 (© 1991-2011 Eric C. Grimm) was used to display stratigraphic diatom data. The summary diagram (figure 4.4) shows selected diatom taxa (with abundance > 5 %); some of the rarer benthic taxa are grouped together at genus level (e.g. *Amphora* spp., *Achnanthes* sensu lato spp., *Cocconeis* spp., *Naviculoid* spp.).

Multivariate numerical analyses were applied to summarise and interpret the diatom data. Firstly, stratigraphically unconstrained cluster analysis using square root transformation was applied using CONISS (Grimm, 1987) to define different diatom assemblages. All taxa present at more than 5 % of the total diatom sum were included in this cluster analysis. Samples were re-ordered in accordance with the results of this cluster analysis (figure 4.4 and 4.5). Secondly, linear regression analyses were conducted with Microsoft Excel 2016 and the Add-on *XLstats* to evaluate the relationship between various parameters (i.e. the plankton-to-benthos-ratio, diatom diversity and relative abundance of diatoms) and water depth. Diagrams were created using the software OriginPro 8.

4.5 Results and discussion

4.5.1 Modern diatom assemblages of Lake Kinneret

A total of 108 diatom taxa were identified within the sediment surface samples of Lake Kinneret. The modern diatom flora still contains many of the taxa present in the fossil record (Vossel et al., 2018), although anthropogenic influences have caused slight changes in the composition of modern diatom assemblages compared to the fossil one. A detailed list of modern diatom species identified in the sediment surface samples of Lake Kinneret is provided in the appendix of this chapter.

Figures 4.4 and 4.5 show the results of the unconstrained cluster analysis, which revealed five major diatom assemblages for modern Lake Kinneret, which can each be correlated to specific water-depth intervals. Samples covering the water-depth intervals from 1-8 m and 12-16 m, were not provided and therefore not implemented in the cluster analysis.

Diatom assemblage of the littoral zone (0-1 m water depth)

The diatom flora of the littoral zone is dominated (up to 90 %) by benthic species such as *Amphora coffeaeformis*, *A. pediculus*, *Planothidium lanceolatum*, *Navicula cryptotenella*, *Nitzschia constricta*, *N. frustulum* and *Rhoicosphenia curvata*. Diatom concentration is low in all samples of the littoral zone. The proportion of facultative planktonic taxa is low (less than 5 %). One sample contains some valves of planktonic *Pantocsekiella ocellata*.

Sample LK_12_65 taken from Tabgha, one of the largest saline brines, contains some typical salt-tolerant diatom species such as *Amphora coffeaeformis, Nitzschia constricta, N. frustulum* and *N. granulata*.

The common taxa of the littoral zone cannot be found in any of the diatom death assemblages of the profundal zone, so that a wash-in of littoral taxa to the central area of the lake basin can be excluded. We therefore can assume a shallowing in lake levels, when common taxa of the littoral zone increase in number in quantitative analysis of the core material.
The unconstrained cluster analysis did not reveal differences in habitat preferences (e.g. epilithic, epipelic, epiphytic, epipsammic or periphytic) of the benthic diatom assemblages of the littoral zone. Anyhow, a much larger dataset of samples from different areas/substrates within the littoral is needed to investigate such preferences in more detail in the future. This result underlines that depth (and for the saline spring sample LK_12_65 salinity) is the main driver of differences in assemblage composition in the provided diatom dataset.

Diatom assemblage of the intermediate zone I (8-12 m water depth)

The diatom assemblage of the intermediate zone I is characterised by planktonic diatom species, especially *Pantocsekiella ocellata* (up to 80% abundance). *Aulacoseira granulata* and a few facultative planktonic taxa such as *Fragilaria construens* var. *venter*, *Pseudostaurosira brevistriata* and *Staurosirella pinnata* are present in low amounts. Diatom concentration is low in sediment surface samples of the intermediate zone I.

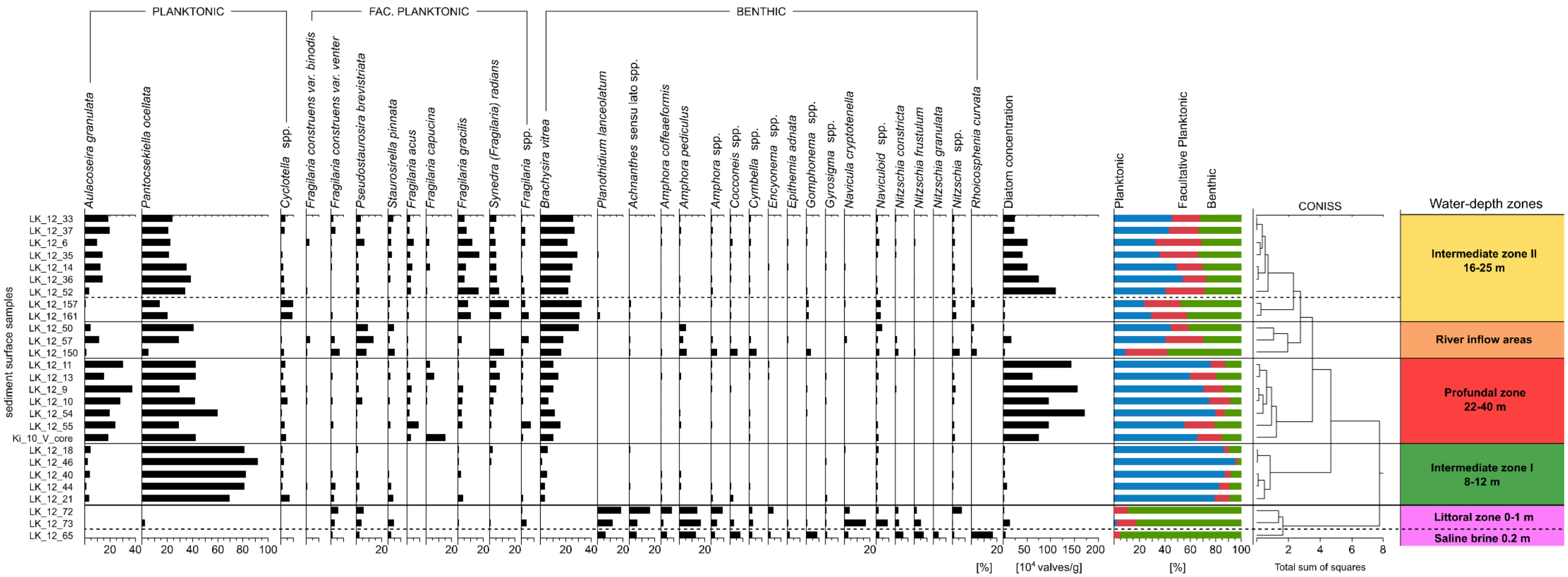

Figure 4.4 Summary diatom diagram from sediment surface sample analyses from Lake Kinneret showing selected taxa present at > 5 % abundance. The diagram also includes the division into different water depth zones based on the outcome of the unconstrained CONISS cluster analysis. Percentage portions of planktonic, facultative planktonic and benthic taxa for each sample are also displayed as well as diatom concentration.

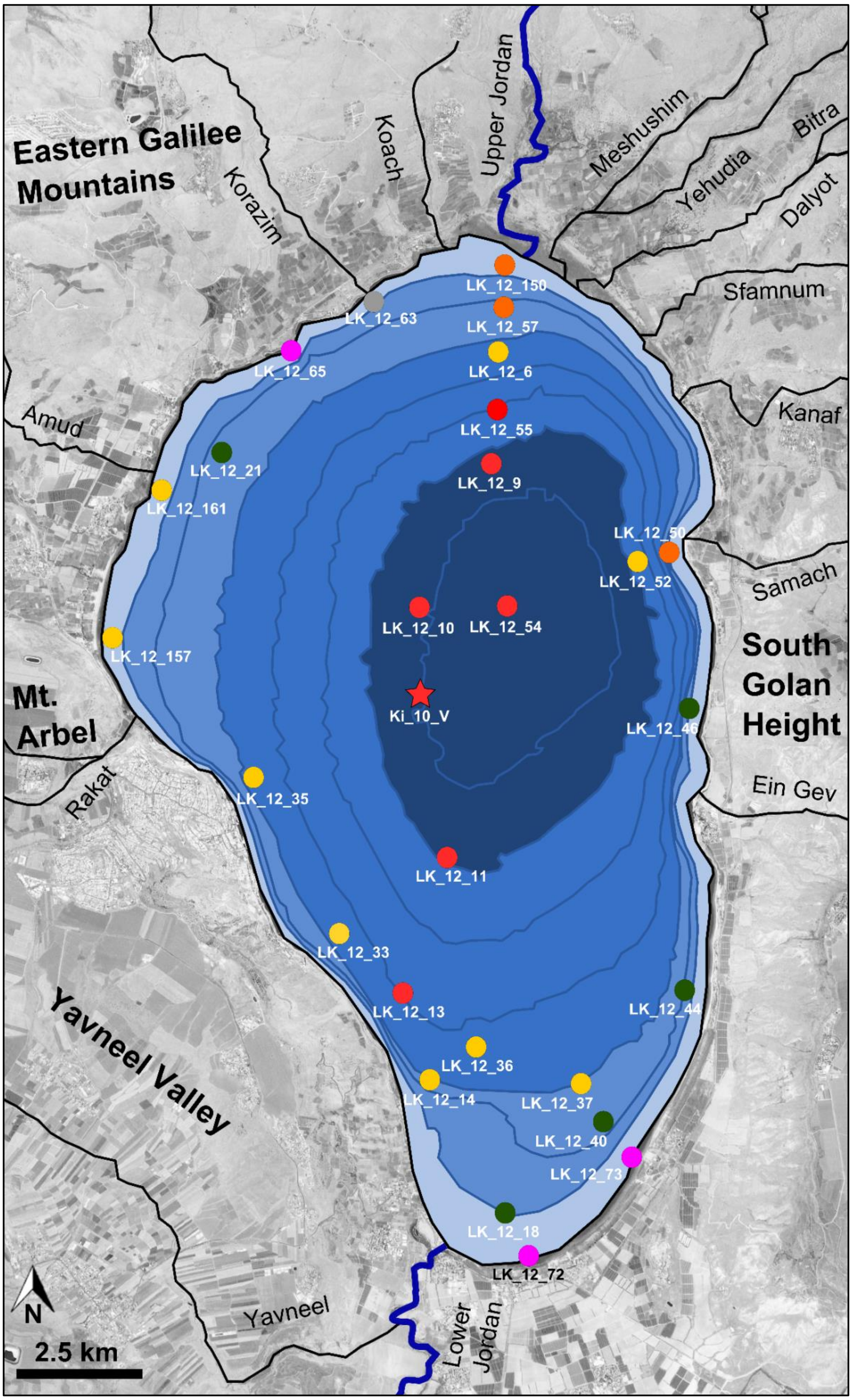

Figure 4.5 Outcome of the unconstrained CONISS cluster analysis in relation to the distribution of sample sites and related water-depth zones. Pink = Littoral zone (0-1 m); green = intermediate zone I (8-12 m); yellow = intermediate zone II (16-25 m); red = profundal zone (22-40 m); orange = samples in river-inflow areas/estuary; grey = sample with no diatom preservation.

Diatom assemblage of the intermediate zone II (16-25 m water depth)

The diatom assemblage of the intermediate zone II is mainly composed of two planktonic species *Pantocsekiella ocellata* (up to 40 %) and *Aulacoseira granulata* (up to 20 %); the presence (between 10 to 30 %) of several facultative planktonic species such as *Fragilaria acus*, *F. gracilis* and *Synedra radians* and the occurrence of the benthic species *Brachysira vitrea* (with up to 30 %) in large numbers. The diatom concentration is moderate to high in most samples.

Diatom assemblage of the profundal zone (22-40 m water depth)

The diatom flora of the profundal zone is dominated by the dominance of the two planktonic taxa *Pantocsekiella ocellata (30-60 %)* and *Aulacoseira granulata (15-40 %).* Beside these two dominant species, several *Fragilaria* taxa and the species *Brachysira vitrea* are also present in low amounts. Diatom concentration is high in all samples belonging to this zone and typical littoral taxa are not present in the diatom composition of the profundal zone.

The six analysed sediment surface samples taken from the deepest parts of the lake contain a similar diatom composition compared to the sample taken from the upper part of the sediment core Ki_10_V (analysed and interpreted in detail in Chapter 3 of this thesis). All of these samples were grouped together by the unconstrained cluster analysis (figure 4.4 and 4.5). Therefore, we are able to conclude, that the chosen coring site is reliable and suitable for palaeoecological analysis, as it is well reflecting the unaffected sediment deposition at the centre of the lake.

Diatom assemblage of river inflow areas

The cluster analysis defined a group of samples, which were taken in river inflow areas (figure 4.4 and 4.5). Samples LK_12_150 and LK_12_57 were taken from the Jordan River inflow and sample LK_12_50 was taken in an area where the ephemeral stream ‘Samach’ is water-bearing and drains into Lake Kinneret during the winter season of peak precipitation. The diatom assemblages found in these samples reflect a mixture of all four above described communities: planktonic species such as *Pantocsekiella ocellata* and *Aulacoseira granulata* are present beside typical littoral genera such as *Amphora* spp., *Cocconeis* spp., *Naviculoid* spp., *Nitzschia* spp. and *Rhoicosphenia* spp. The diatom concentration in these samples is low.

4.5.2 Diatom diversity related to water depth

Diatom diversity is decreasing with increasing water depth (figure 4.6): Samples from the littoral, mainly dominated by benthic taxa, show a higher species richness than samples taken from the deeper lake, mainly dominated by planktonic species. This may be partly explained by the limitation of available habit space for phytoplankton to grow. In modern Lake Kinneret especially, the phytoplankton community is dominated by dinoflagellates, cyanobacteria and chlorophytes, which are highly competitive for space to grow and nutrient availability (Zohary, 2004; Zohary et al., 2014b). As already mentioned in the introduction, the contribution of diatoms to total phytoplankton biomass has been described as irrelevant (Pollingher et al., 1984), but in the benthic communities they play a more important role. (Round, 1978) also recognized, with more than 200 reported taxa, a species enrichment in the littoral zone of the lake.

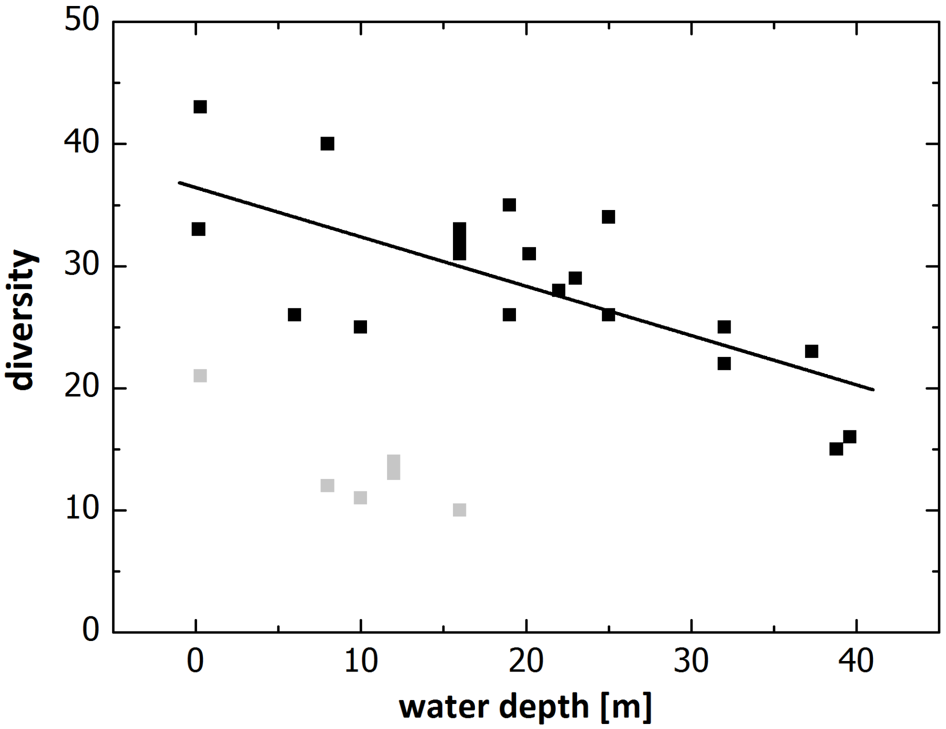

Figure 4.6 Diatom diversity (number of counted taxa in each sample) in relation to measured water depth during sampling. Light grey squares present the excluded samples from the intermediate water depth and the sample LK_12_65 from the saline spring. A linear fit is given with an r2-value of 0.70.

4.5.3 Diatom preservation, diatom concentration and its relation to water depth

Diatom preservation was good in nearly all samples as the preserved valves did not show any signs of dissolution. Only one sample (LK_12_63) did not contain any diatoms. Figure 4.8 gives insights into changes of diatom concentration at different lake areas and water depth. Diatom concentration is highest in the centre of the lake and low in samples taken close to the shore. When the lake is fully mixed, highly turbulent and enriched in nutrients between December and February (Pollingher, 1981), a small increase in total phytoplankton biomass volume due to the occurrence of larger diatom algal blooms is normally observable in January at Lake Kinneret. Therefore, we would expect a higher diatom concentration than observed for all our samples, which were taken in January during this bloom period. However, datasets (from 2011 to 2013; figure 4.9) from the monitoring program conducted by the Kinneret Limnological Laboratory, show that the typical diatom algal bloom was strongly reduced (around 10 gr/m^2) compared to the multi-annual averages (around 35 gr/m^2) for three following years including 2012, when samples were taken. Interestingly, strongly increased values (35 gr/m^2, clearly above the annual averages (around 5 g/m^2) of Cyanobacteria occurred in January 2012 (KLL monitoring program; Sukenik et al., 2014). January 2012 was reported as a month with high wind speeds, high nitrogen (0.6 mg/l) and phosphate (0.3 mg/l) values, which might have favoured a bloom of Cyanobacteria instead of diatoms, which is possibly another explanation for the observed reduced diatom concentration.

Figure 4.7 Sediment supply into Lake Kinneret from the Jordan River delta in March 2012 after a winter with higher precipitation values.

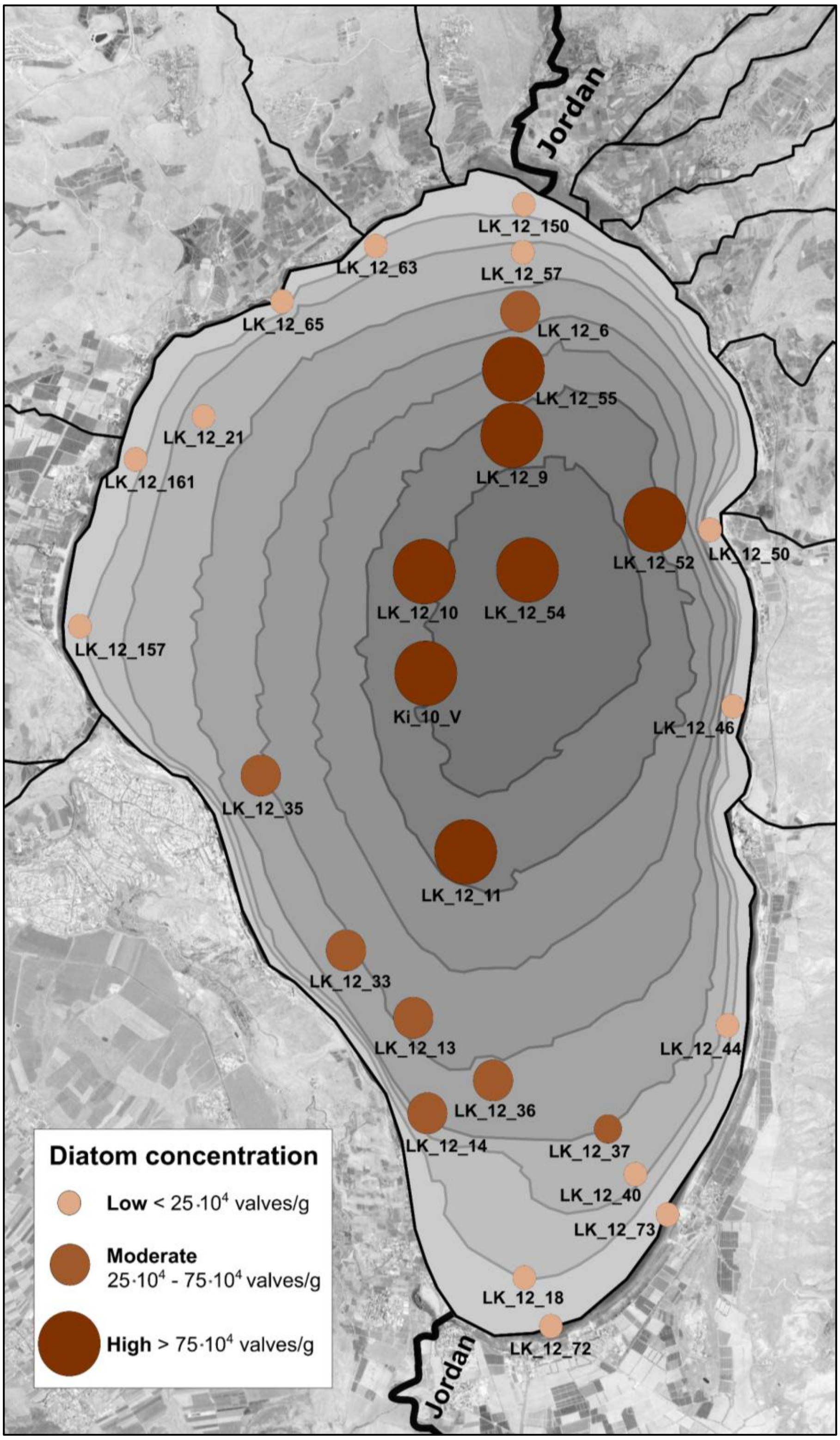

Figure 4.8 Distribution of diatom concentration for each analysed sediment surface sample across the lake assigned in three different categories: low, moderate and high.

Additionally, our observed results are possibly also influenced by the fact that samples were collected in early January, a month where Lake Kinneret receives strong sediment supply from the catchment area via Jordan River and several small inflows. A high sediment discharge, supported by high precipitation values recorded for 2012 (meteorological data provided from the Israel Meteorological Service (IMS, personal communication); figure 4.7) can simply dilute the diatom concentration, which here seems to be most likely, as preserved valves do not show signs of dissolution. Due to different depositional areas of Jordan River sediment load, the sedimentation rate is much lower in the central part of the lake compared to the shallower lake areas (Koren and Klein, 2000). Bathymetry and shape of the lake basin are also influenced by this. Therefore, it is not surprising that diatom concentrations are higher at the central part, where less sediment particles are deposited together with diatom valves sinking to the lake bed.

A comparison between diatom, green algae and pollen grain concentration is given in figure 4.10. Results show a similar distribution of concentrations for all counted proxies. Concentrations are highest in the deeper lake basin and low in samples located closer to the shore, which is strengthen the argument of strong sediment supply from the catchment into the lake causing dilution of concentration.

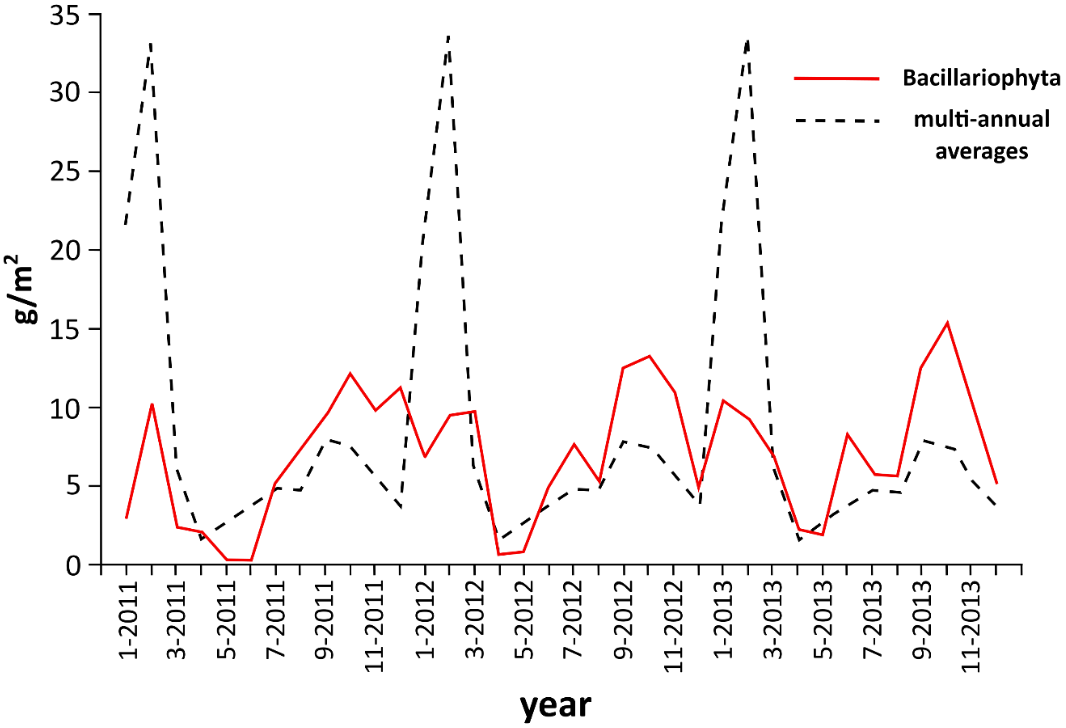

Figure 4.9 Total biomass volume of *Bacillariophyta* (given in gr/m^{-2}) in comparison with multi-annual averages of *Bacillariophyta* biomass volume recorded by the Kinneret Limnological Laboratory for January 2011 till December 2013 (Sukenik et al., 2014). Typical diatom algal bloom is strongly below multi-annual average values for the recorded years.

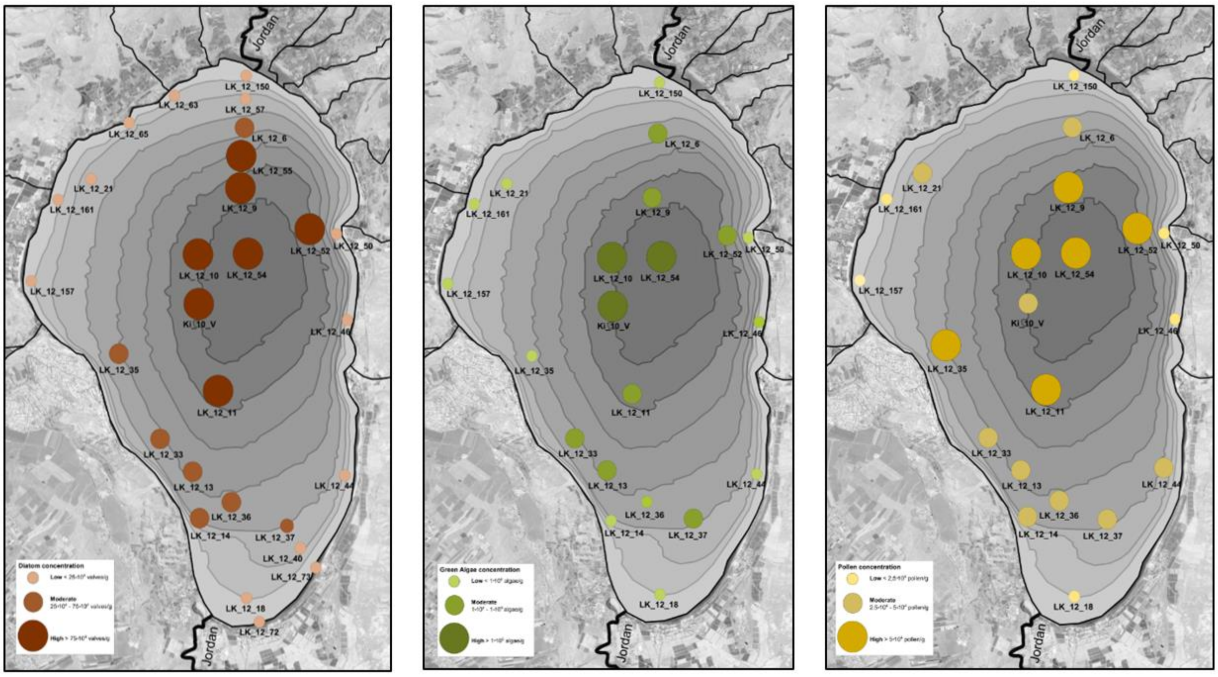

Figure 4.10 Estimated diatom concentration (brown) in comparison with estimated values of green algae (green, Böttcher, 2016) and pollen concentration (yellow, Böttcher, 2016). Each concentration was estimated from the same analysed sample. Concentrations were highest in the centre of the lake and lowest closer to the shoreline.

4.5.4 Influence of water depth on modern diatom distribution

Figures 4.11 and 4.12 show the relative abundance of planktonic, facultative planktonic and benthic species in relation to the measured water depth during sampling. Both figures show that shallower parts of the lake are dominated by benthic taxa communities, the intermediate water depth show a mixture of all, and the deeper lake basin is dominated by a fully planktonic species assemblage. Total diatom abundance increases markedly with increasing water depth, in line with the increasing relative abundance of planktonic taxa at the expense of benthic taxa. Facultative planktonic diatoms show highest abundances in the intermediate water depth zone. These results show that the composition of the modern diatom assemblages is closely related to water depth and that it is possible to distinguish clearly between littoral and profundal diatom death assemblages. Assumptions for diatom death assemblages from the intermediate water depth should be considered with more caution, due to the missing sample points in those areas.

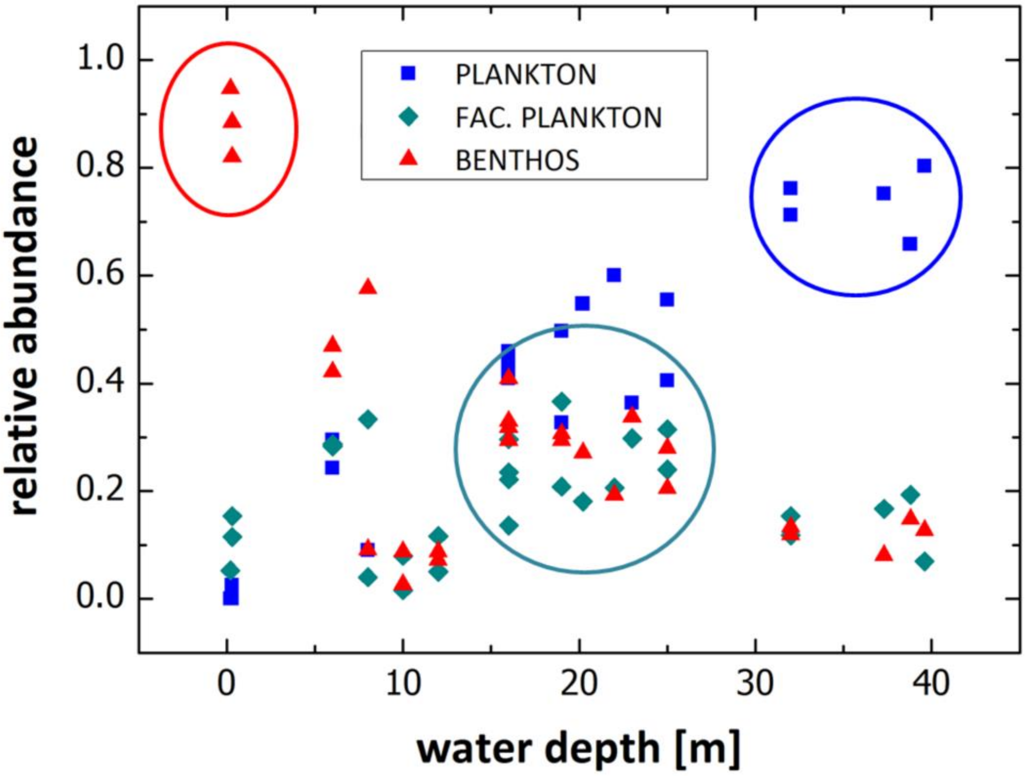

Figure 4.11 Relative abundance of planktonic, facultative planktonic and benthic diatoms in relation to water depth given for all analysed sediment surface samples.

This is an important result for using the plankton-to-benthos ratio of diatoms for lake-level reconstructions, which is based on the assumption that the variability in the P/B-ratio can be interpreted as a response to varying basin morphology as lake level fluctuates (Jones et al., 2013). For example, as the lake shallows, benthic habitats may increasingly disperse into regions that were previously dominated by sedimentation of planktonic diatoms, thereby changing the P/B-ratio. Effectively, decreasing lake level shortens the transport distance from littoral habitats to the deepest region of the lake (the favoured coring site), coupled with a reduction in area suitably deep for planktonic diatoms (Stone and Fritz, 2004). In addition, those results prove the reliability of the chosen coring site for palaeoenvironmental studies. Samples of the profundal zone clearly reflect the floral composition of the deeper lake basin, which seems not to be influenced either by the inflow of the Jordan River or the in-wash of littoral taxa and/or larger sediment transport. These observations confirm the results of Koren and Klein (2000), who measured the sedimentation rate in Lake Kinneret over several years by using sediment traps situated at seven different locations all over the lake. They found out that sedimentation rate is lowest at the centre of the lake nearby station A, which represents the location of the analysed coring site, and that most sediment deposits are of authigenic origin. Highest sedimentation rate occurs in spring during bloom periods of the dinoflagellate

Peridinium gatunense, favouring the precipitation of calcite accumulation in the lake due to intensive photosynthesis processes (Koren and Klein, 2000). However, the presence of facultative planktonic and benthic diatom taxa at very low abundances in the profundal samples are indicating some sort of sediment transportation, e.g. sediment focussing, which is present to some extend in every lake system (Blais and Kalff, 1995, Håkanson, 2012).

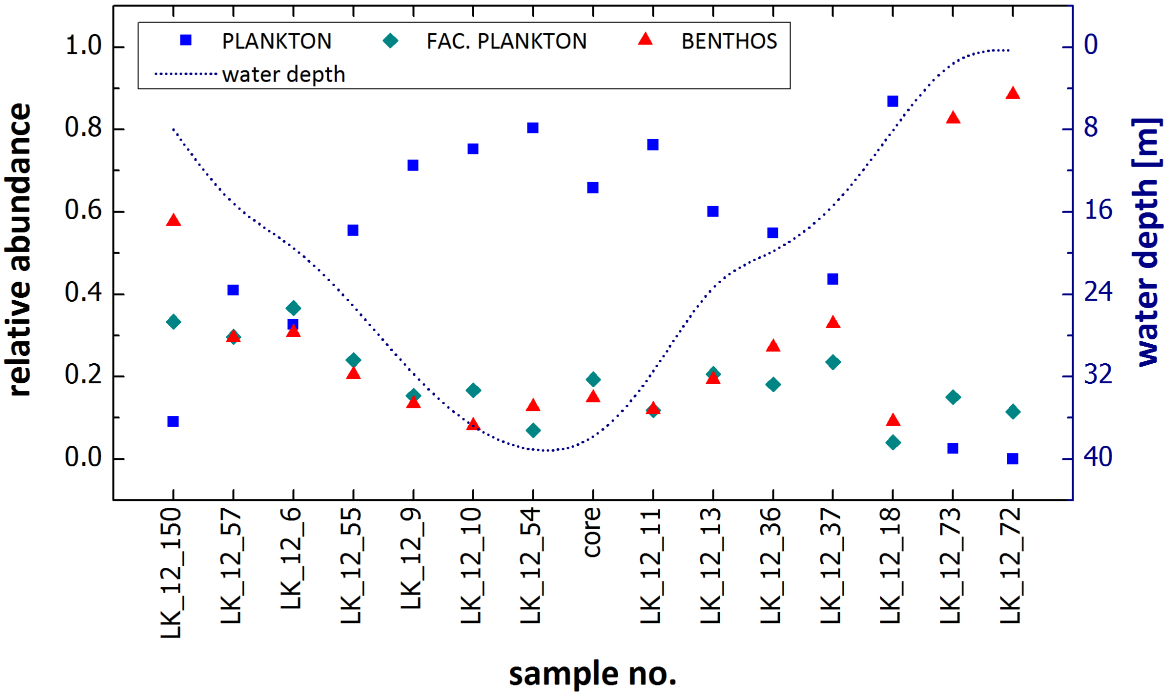

Figure 4.12 Relative abundance of planktonic, facultative planktonic and benthic diatoms in relation to water depth given for selected samples on a North (LK_12_150) to South (LK_12_72) transect through Lake Kinneret. The profundal diatom death assemblages are clearly dominated by planktonic ones and the littoral assemblages are dominated by benthic species.

4.5.5 Holocene lake-level calibration based on the distribution of modern diatom death assemblages

As already explained in the introduction, the variations in diatom habitat groups (here the plankton-to-benthos ratio of diatoms) are used in the case of Lake Kinneret to infer lake-level changes during the Holocene. The use of diatom habitat groups as an indicator for lake-level shifts in development of a quantitative diatom-inferred depth model depends on several assumption (supplemented to Barker et al., 1994): (1) changes in the nutrient status of the lake do not affect the diatom composition and the balance between planktonic and benthic diatom productivity, even if overall abundance has changed markedly. (2) Reworking of marginal sediment has not led to an influx of fossil littoral diatoms to the coring site. (3) Diatom species can be clearly allocated to either a benthic or planktonic life habit classification. The classification of diatom species which have a facultative planktonic life habit can be problematic, as lake-level estimations can vary depending on the group to which they have been assigned; the uniformitarian principle that their predominant affiliation is constant over time also applies. This will be analysed and discussed in more detail below. (4) Depositional processes (of diatom frustules) observed in the modern lake system remain constant and also occurred in a similar way in the past, i.e. the concept of uniformitarianism. Nevertheless, all assumptions considering the past have an element of uncertainty, as they are based on theoretical concepts and probabilities.

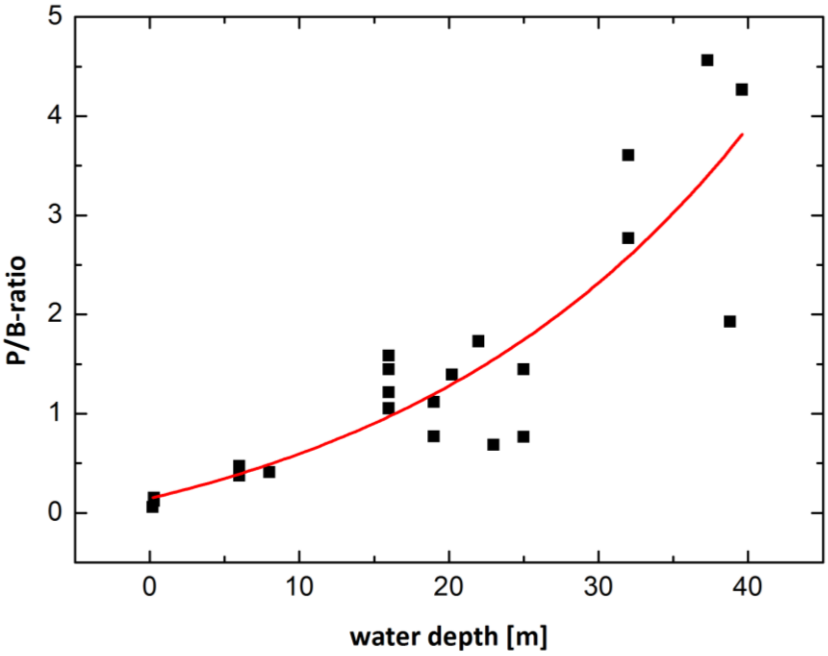

Figure 4.13 Exponential relationship between the ratio of planktonic-to-benthic diatoms and measured water depth. Red line describes the exponential function.

Our results (figure 4.11, 4.12 and 4.13) show that the composition of modern diatom assemblages in Lake Kinneret is closely related to water depth. Additionally, an exponential relationship between water depth and the ratio of planktonic-to-benthic (P/B-ratio) diatoms can be observed (figure 4.13). For the following analyses, the P/B-ratio is converted into a logarithmic function to better display its linear relationship to water depth. This relationship and its statistical significance depends on

(1) The clear allocation of the facultative planktonic diatoms to (a) an either planktonic or benthic habitat classification or (b) excluding them completely from the analysis.

(2) five samples from the intermediate water depth I (8-12 m), where the diatom assemblage consist of 80 % or more of the species *Pantocsekiella ocellata*, which is known to have very broad ecological preferences. Those samples were excluded from further analysis as a statistical significance was not given ($r^2 = 0.2$ or smaller).

According to these uncertainties, three versions of linear regression lines have been modelled, which best describe the logarithmic P/B-ratio in relation to water depth:

(1) the facultative planktonic diatom species are classified as full-planktonic
(2) the facultative planktonic diatom species are excluded from the analysis and calculations
(3) following the allocation of Pollingher et al. (1984), facultative planktonic taxa are assigned as benthic (i.e. littoral) taxa

Regression equations describing the modern logarithmic distribution of the P/B-ratio against water depth for each of these three versions of the P/B-model and their statistical significance are given in table 4.1. Model version 1 is, with an r^2-value of 0.80, the most reliable one of all three. Figure 4.14 shows the regression line of this model within its confidence limits.

Table 4.1 Regression equations describing the relationship between water depth (D) and three versions of LOG_{10}(P/B-ratio). Simple linear regression was used such that $\log_{10}(P \cdot B^{-1}) = m \cdot D - n$. Coefficients for the gradient of the regression line (m) and the intercept (n) are given for each version as well as the r^2-values and adjusted r^2-values for statistical significance.

	version	**m**	**n**	**r^2**	**adj. r^2**	**F-test (p-value)**
1	(P+FP)/B	0.036	-0.726	0.80	0.78	0.0016
2	P/B	0.029	-0.594	0.53	0.51	0.0021
3	P/(FP+B)	0.029	-0.641	0.52	0.50	0.0021

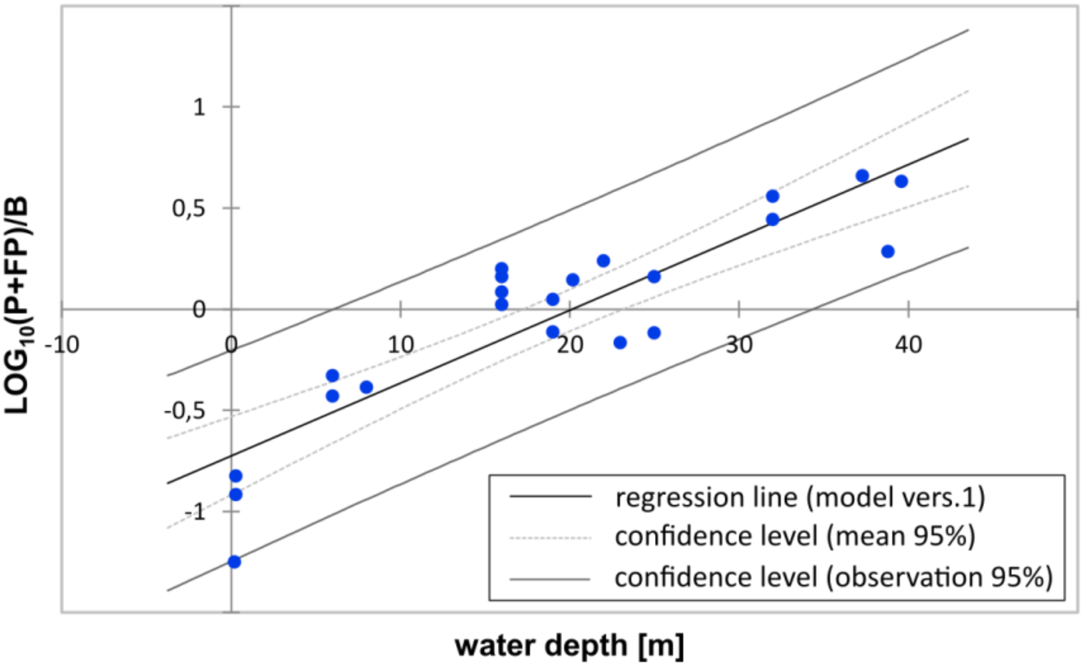

Figure 4.14 Regression of LOG_{10} (P+FP)/B and water depth for model version 1 of the P/B-ratio. The regression line is defined as: $\log_{10}\left((P+PF)\cdot B^{-1}\right) = 0.036 \cdot D - 0.726$ with $r^2 = 0.80$.

In a next step, down-core variations observed in the P/B-ratio of diatoms during Holocene palaeoenvironmental reconstructions of Lake Kinneret (Vossel et al., 2018) can be quantified in terms of water depth using the three models describing the diatom-depth relationship calculated from the modern surface samples, allowing more direct comparison with palaeo-shoreline measurements conducted by Hazan et al. (2005). Figure 4.15 summarizes the results of the calibrated lake-level variations derived from the three different P/B-models. The calculated error ranges between 20 to 25 % for all model runs. All models are in accordance concerning relative changes in water depth, except from shifts observable for the Early Holocene. Here, models 2 and 3 show "negative" water depth, which makes those models highly unlikely, as sediments from the recovered core show no signs (e.g. desiccation cracks or crusts) for a full desiccation of the lake at any time during the last 9,000 years (Langgut et al., 2015, Schiebel and Litt, 2018). Model version 1 (figures 4.15 and 4.16), which includes the facultative planktonic diatom species as full-planktonic, shows the highest statistical significance for its linear regression (table 4.1) and the most realistic lake-level reconstruction compared to the measured palaeo-shorelines and archaeological observations (figure 4.15, 4.16 and 4.17; table 4.1). It also gives an estimate close to the value of the modern lake level at around 212 mbsl. Therefore, the following interpretations, comparisons and assumptions (see section 4.5.6) are based on the calibrated lake-level reconstruction for model version 1 (figure

4.16). A smoothed curve (five point average) is given as well as the corresponding lake-level elevations in meters sea level [msl] for Lake Kinneret for a better comparison with the wider literature.

Why do all models show similar trends (except from the Early Holocene), but show different amplitudes?

All model versions are based on the calculated Plankton/Benthos-ratio of diatoms, which has been estimated for the sediment record of Lake Kinneret covering the last 9,000 cal yrs BP by Vossel et al. (2018). Therefore, it is not surprising that all model versions show similar trends for lake-level shifts as they are based on the same output-dataset. Nevertheless, models show variations in the strength of their amplitudes (which here equal calculated lake levels), especially in the Early Holocene. These variations in amplitude can be explained by (a) the allocation of facultative planktonic diatoms to either planktonic or benthic diatom habit group or the complete exclusion and/or (b) by the dominance of facultative planktonic diatoms in the fossil dataset. Especially in the Early Holocene, small facultative planktonic diatoms such as *Pseudostaurosira brevistriata*, *Staurosira venter* and *Staurosirella pinnata* dominate the fossil diatom flora with varying occurrences between 40-80% of the total diatom abundance (Vossel et al., 2018). This explains, for example, why values for the lake-level calculation in model 3 (blue curve in figure 4.15), went clearly below zero between 9,000-8,500 cal yrs BP, and in general shows the lowest amplitudes of all models.

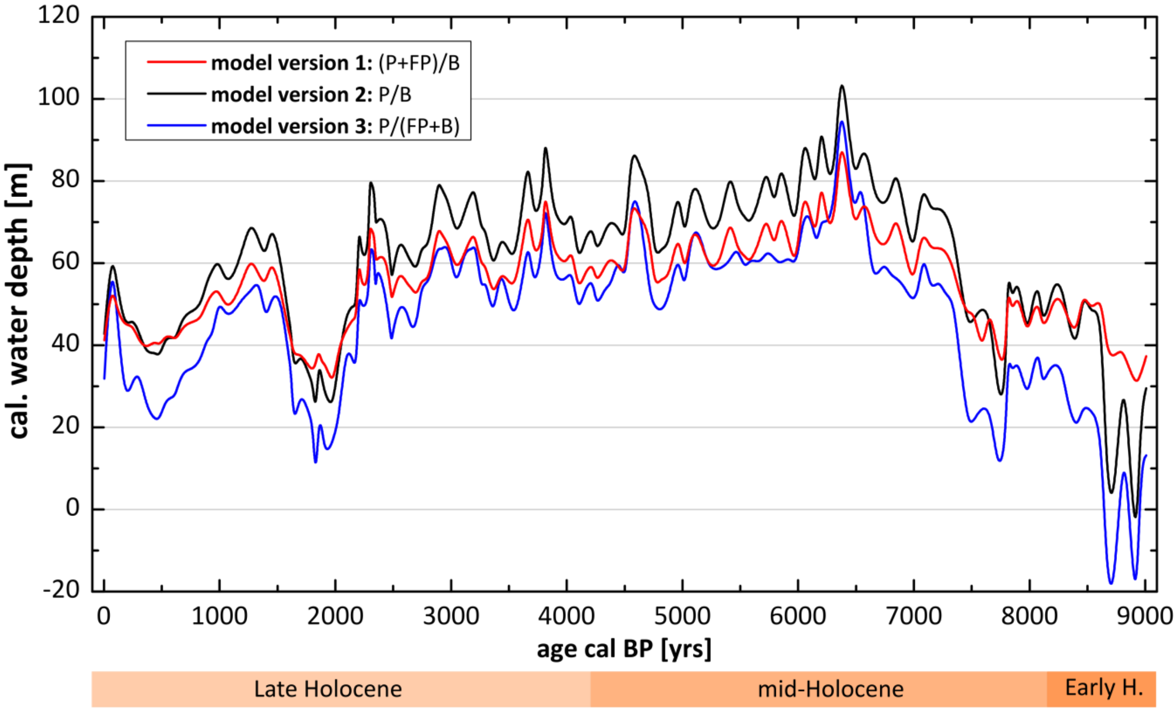

Figure 4.15 Results of the calibrated and modelled lake-level calculation [m] in relation to ages [yrs] determined from cores Ki_10_I and Ki_10_II.

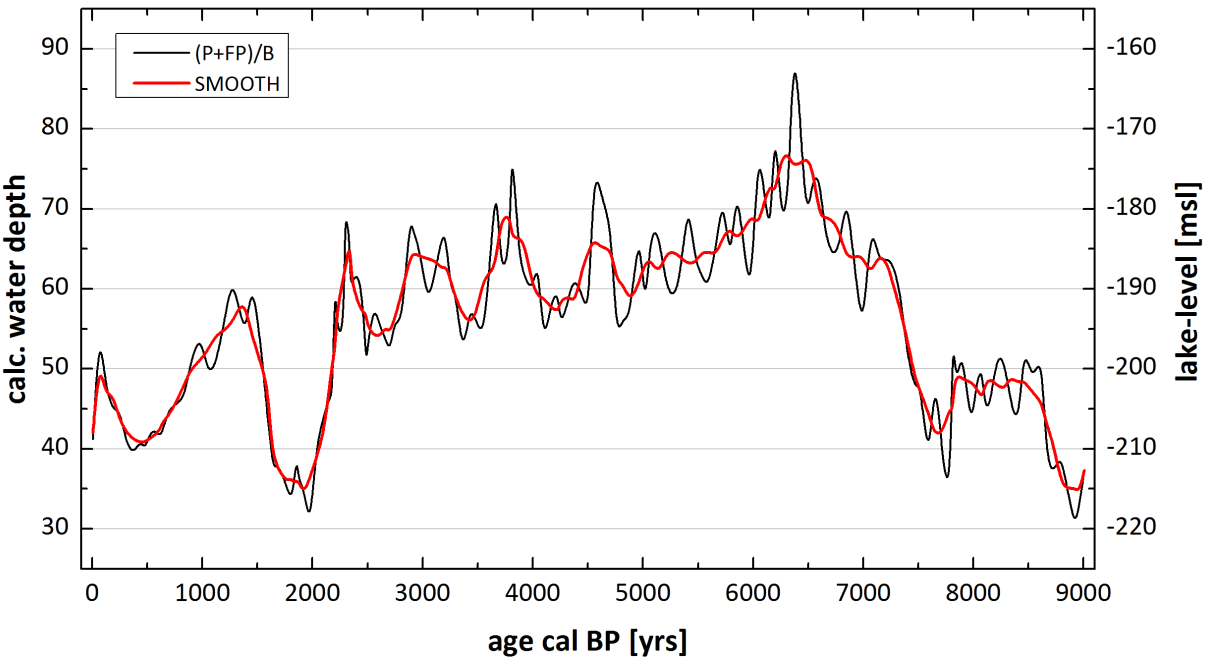

Figure 4.16 Modelled lake-level calculation for model version 1 ((P+FP)/B) in relation to ages determined from cores Ki_10_I and Ki_10_II in more detail. A smoothed curve (red line; five point average) is given as well as the corresponding lake-level elevations in [msl].

4.5.6 Comparison with palaeo-shoreline measurements (Hazan et al., 2005) and lake-level reconstruction from the Dead Sea (Kushnir and Stein, 2010)

General remarks

Figure 4.17 shows a comparison of different lake-level reconstructions from Lake Kinneret, which are based on different methods:

The current, most accepted lake-level curve, covering the last 44 cal kyrs BP, was reconstructed by Hazan et al. (2005) and is based on the identification of radiocarbon-dated palaeo-shorelines and surveying elevations from several exposed sections and archaeological sites, which are located close to the lake. Nevertheless, for the Holocene this curve only offers a fragmentary reconstruction.

A more recent lake-level reconstruction covering the last 9,000 cal yrs BP was published by Vossel et al. (2018), based on the Plankton/Benthos-ratio of diatoms and the assumption that the variability in the P/B-ratio can be interpreted as a response to varying basin morphology as lake level fluctuates (Jones et al., 2013). This lake-level reconstruction is used as basis for the calibrated lake-level curve presented in this study.

Additionally, lake-level variations from the Dead Sea are also compared to the new dataset, as a similar response to regional changing climatic-hydrological conditions is presumed for those two lake systems (Stein, 2014). Lake-level reconstructions from the Dead Sea are based on a combination of absolute lake-level curves (based on palaeo-shorelines and knowledge of their age and original elevation) and relative lake-level curves (based on estimates of relative water depth identified by lithological changes in sediment cores).

Figure 4.17 shows that slight chronological discrepancies occur in the correlation between the Dead Sea record and Lake Kinneret. Those can result from (a) the large observed reservoir offset in the age-depth model from Lake Kinneret ranging from 800 to ca. 1,600 yrs, especially in the lower core section (Schiebel and Litt, 2018, Vossel et al., 2018), and/or (b) the uncertainties/error ranges within the radiocarbon dating method itself, which was applied for both lake chronologies.

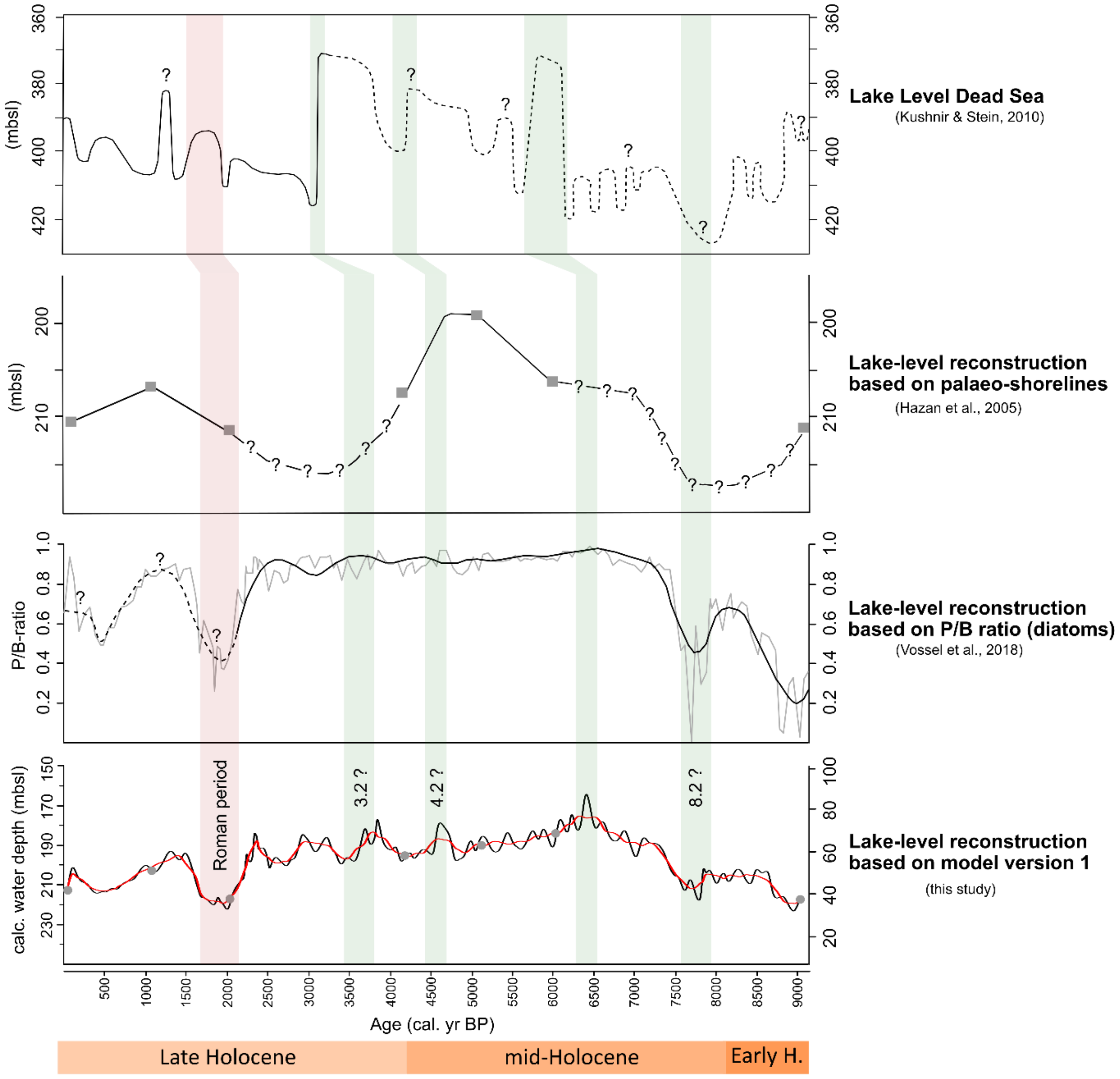

Figure 4.17 Comparison of currently known, fragmentary Holocene lake-level reconstructions from the Dead Sea (Kushnir and Stein, 2010) and Lake Kinneret (Hazan et al., 2005, Vossel et al., 2018) compared to the modelled and calibrated lake-level curve inferred from model version 1 (black curve shows water depth calculation in high resolution; red curve is a 5 point average). Grey squares and dots represent comparison points between palaeo-shoreline measurements and calculated elevations, which are summarised in table 4.2. Assumed correlations between the Dead Sea and Lake Kinneret curves are marked for a better comparison (green=good correlation, red=problematic correlation).

Comparison with palaeo-shorelines:

The comparison between lake-level reconstructions based on palaeo-shorelines with the calibrated lake-level reconstruction based on the modelled Plankton/Benthos-ratio (figure 4.17 and table 4.2) results in a number of good correlations. Five out of seven measured palaeo-shorelines by Hazan et al. (2005) fit to the calculated water depth based on model version 1 within an error of +/- 2m. Therefore, the new reconstruction can be seen as a good supplement to the existing lake-level curve for Lake Kinneret, particularly for missing sections. The greatest discrepancy between the reconstructions occurs at around 4,250 and 6,105 cal yrs BP: at both times, the modelled lake-level reconstruction indicates a clearly deeper lake system (10-16 m) than does the measured palaeo-shoreline. Possible causes could be (a) uncertainties of the age-depth model of the cores recovered from the lake, as well as uncertainties in radiocarbon dating of *Melanopsis* shells used for chronology of the sedimentary sections; (b) the correct allocation of the diatom taxa to a specific growth-habitat classification; (c) the strong dominance of planktonic diatoms in the fossil diatom death assemblage (=high P/B-ratio; figure 4.17) within those time intervals and the possible ability from diatoms to buffer smaller lake-level shifts; (d) the clear and correct identification of the elevation of a palaeo-shoreline, which also can be affected by tectonic activities (Marco et al., 2003, Hazan et al., 2004).

Table 4.2 Comparison of palaeo-shoreline elevation measurements (Hazan et al., 2005) with calculated water depth based on calibrated lake-level reconstruction of model version 1.

Age [cal yrs BP]	**water depth [msl] palaeo-shorelines/archaeology** (Hazan et al., 2005)	**calculated water depth [msl] diatoms** (this study)
present	-212	-212
1300	-208	-208
2000	-212	-210
4250	-208	-198
5230	-197 to -200	-195 to -198
6105	-206	-190
9540	-212	-212

Comparison with the Dead Sea record

Both diatom-based lake-level reconstructions presented for Lake Kinneret revealed several rises and declines for the past 9,000 cal yrs BP, which can be correlated in most cases with larger rises and declines observable in the Dead Sea record (figure 4.17). This observation confirms the assumptions made by Hazan et al. (2004, 2005), Marco et al. (2003) and Stein (2014), postulating that Lake Kinneret and the Dead Sea are reacting in similar ways to changing hydrological conditions in the catchment area, e.g. due to climate variability. Especially the new generated, calibrated lake-level curve allows a more detailed comparison with the Dead Sea than the “simple” lake-level curve based on the P/B-ratio of diatoms provided by Vossel et al. (2018), as it displays smaller variations in more detail (figure 4.17). Good examples are the major declines presumed for the Dead Sea record, occurring at around 6.0, 4.2 and 3.2 cal kyrs BP, which were not visible in the “simple” P/B-ratio reconstruction, but now can be observed as possible drops in Lake Kinneret as well. Beside the assumed lake-level decline at around 4.5 cal kyrs BP, it was also problematic, to see those relations in the palaeo-shoreline based lake-level reconstruction provided by Hazan et al. (2005).

The newly modelled lake-level curve from Lake Kinneret allows for the first time a direct comparison of water-level fluctuations in meters. In general, the Dead Sea often seems to react with higher amplitudes to changing moisture availability than Lake Kinneret. Presumed declines inferred from the Dead Sea lake-level curve (Kushnir and Stein, 2010) are often twice as high as the estimated declines for Lake Kinneret. This observation can be possibly explained by the fact that Lake Kinneret and the Dead Sea lie on a chained limnological system and that both lakes are fed by similar water sources in a shared catchment area: Lake Kinneret represents the fresh-water flow-through water body and the southern Dead Sea represents the terminal hypersaline lake system in this chain (Hazan et al., 2004). The Dead Sea therefore reacts more sensitively to changing moisture availability than Lake Kinneret. Another important aspect is the strong north to south climate gradient, which was already established during the Late Pleistocene (Enzel et al., 2008), active throughout the Holocene (Vossel et al., 2018) and can still be observed till today. This gradient implies that the northern Kinneret basin receives more annual precipitation than the southern Dead Sea and that evaporation processes are less strong in Lake Kinneret, as annual temperatures are lower in the North than in the South. Therefore, Lake Kinneret would naturally receive a higher water budget than the Dead Sea basin. Nevertheless, both lake systems are connected via the Jordan Rift Valley and a close interaction between both systems regarding their water levels is therefore not surprising. A third important aspect to consider is the existence of the Yarmouk sill located at 200 mbsl southward from Lake Kinneret, which acts as a natural, topographic spillway of the lake (Hazan et al., 2005, Stein, 2014).

Well-dated palaeoclimate records from many different locations and archives show that the Holocene climate was punctuated by several so called rapid climate changes (RCCs) and was not as climatological stable as presumed (Dansgaard et al., 1993). Some of them occur synchronously across the globe and are triggered by different climatic forcing functions and their interaction (Mayewski et al., 2004). Some of the most prominent RCCs occurred at around 8,200 cal yrs BP (the so-called 8.2 event), at around 4,200 cal yrs BP (the 4.2 event) and at around 3,200 cal yrs BP (the 3.2 event). A rapid change towards cooler and more arid climate conditions during those events is recognizable around the globe, including the Eastern Mediterranean (Alley et al., 1997, Mayewski et al., 2004, Kaniewski et al., 2010). The “simple” P/B-ratio based lake-level reconstruction already indicated shifts in moisture towards more arid climate conditions around 7,900 cal yrs BP for Lake Kinneret and was supposed to coincide with the so-called 8.2 kyr cold (arid) event; the most prominent RCC during the Holocene (Vossel et al., 2018). Other proxies (e.g. XRF-data) supported this interpretation and other archive data (e.g. of speleothems (Bar-Matthews et al., 1999, Verheyden et al., 2008) and lake-level reconstructions of the Dead Sea (Kushnir and Stein, 2010) indicated a region-wide response to this event. No shifts in lake levels (i.e. climate) could be observed in the P/B-ratio based reconstruction during the other two prominent RCCs, which was surprising, because the Dead Sea clearly showed a reaction by remarkable drops in its lake level. The new calibrated lake-level reconstruction presented for Lake Kinneret in this study (figure 4.17), however, seems to reveal a possible reaction of the lake system to all those three prominent RCCs by declined lake levels. Especially for the 4.2 cal kyrs BP drought event, comparable drops in lake levels of around 15-25 m can now be observed for the Dead Sea, the exposed palaeo-shorelines at Lake Kinneret and the new calibrated reconstruction (figure 4.17). Similar observations can be made for the 8.2 event and the highly discussed 3.2 event, where clear drops in lake levels of both lakes indicate a shift towards more arid climate conditions and presume a regional-wide reaction to those Holocene RCCs. Those results confirm again the close interaction between those two lake systems as they show similar responds to changing climatic-hydrological conditions during the Holocene. Furthermore, there is evidence related to drought events in the pollen record of Lake Kinneret (i.e. two slight decreases in the oak pollen curve) occurring at around 4,000 and 3,200 cal yrs BP (Langgut et al., 2013, Schiebel and Litt, 2018) and in the Dead Sea pollen records from Ein Gedi (Litt et al., 2012) and from the Ze’elim beach ridge (Langgut et al., 2014) at least for the 3,200 cal yrs BP drought event. Neugebauer et al. (2015) observed sedimentological changes in the Ein Gedi Dead Sea record, interpreted as a larger lake-level decline and therefore a dry period between ca. 3,500 and 3,300 cal yrs BP. This observation is correlating well with the new calibrated diatom lake-level reconstruction indicating a lake-level decline between 3,600 and 3,400 cal yrs BP at Lake Kinneret (figure 4.17).

Beside the good correlation with the Holocene RCCs, it is remarkable, that the new water-depth model-based reconstruction also shows a good correlation with one of the largest lake-level rises of the Dead Sea occurring at around 6,000 cal yrs BP. Based on our model, this was the highest water level reached in Lake Kinneret (here observed at around 6,500 cal yrs BP) during the entire Holocene. There is also sedimentological evidence that Lake Kinneret rose above the Yarmouk sill at ca. 6,000 cal yrs BP, which is indicative for a lake-level rise to 200 mbsl or more and covered the prehistorical site “Tel Bet Yerach” (located at the south-eastern shoreline of Lake Kinneret) with a coarse sand layer containing shells of the freshwater snail *Melanopsis* (Hazan et al., 2005, Stein, 2014). Those observations are also well reflected by the expansion of the Mediterranean woodland components in the Kinneret area and around the Dead Sea at the same time, possibly caused by an increased precipitation to evaporation value (Litt et al., 2012, Schiebel and Litt, 2018). Floodwater farming and horticulture were invented during this time, e.g. olive and date palm cultivation, also indicating a more humid mid-Holocene period (Litt et al., 2012). Biome models based on pollen data assume precipitation values up to 650 mm/a for the Dead Sea region, long lasting rain intervals and lower temperatures (Litt et al., 2012), which is well reflected by lake-level high stands in all provided reconstructions (figure 4.17).

Beside a number of good correlations observable between the Lake Kinneret and the Dead Sea lake-level reconstructions, one major discrepancy occurs at the Roman time period between 2,200 and 1,700 cal yrs BP (see figure 4.17): During this time, the diatom-based reconstructions indicate a major decline in lake levels for Lake Kinneret, whereas the reconstruction from the Dead Sea record shows a rise in lake level. Vossel et al. (2018, Chapter 3 of this thesis) discussed this observation already in detail and suggested that a climate-induced shallower lake-level phase for Lake Kinneret is unlikely, as other proxies also indicating more humid climate conditions for the southern Levant for this period (e.g. Issar, 2003, and refereces therein, Litt et al., 2012). Additionally, studies from Schiebel and Litt (2018) and Vossel et al. (2018) demonstrated that the climate signal inferred from the diatom-based and palynological record is strongly overprinted by human impact from the Hellenistic period onwards and therefore should not be derived from lake-level variations. Marco et al. (2003) and Hazan et al. (2004) also reported deviations between the Dead Sea and Lake Kinneret lake-level reconstructions during the Late Holocene and speculated, that tectonic subsidence, e.g. of one of the measured palaeo-shorelines, could be responsible for those observations.

The modelled lake-level curve shows several other possible rises and declines in the lake level of Lake Kinneret, which are not discussed in scope of this publication. It has to be clarified within future research whether those signals can be linked to additional possible climate variations occurring during the Holocene or reflect natural and/or human induced lake-level variations. Changes in the Plankton/Benthos-ratio od diatoms in general have to be interpreted with caution as they can be indicative for either shifts in lake level and/or changes in productivity (Battarbee, 1986). Therefore, it is always advisable to gain supporting evidence for lake-level changes from multi-proxy analysis.

4.6 Conclusions, critical considerations and future perspectives

1. Five major diatom death assemblages can be observed in the sediment surface of Lake Kinneret. Each of those assemblages can be correlated to specific water-depth areas in the lake.
2. The strong sediment supply by the Jordan River during winter month is affecting the diatom concentration and also depositional processes of the lake. However, our results show, that the deeper lake basin seems not to be influenced by the inflow of the Jordan River nor the in-wash of littoral diatom taxa from the shoreline or massive sediment deposits. This proves, on one hand, the reliability of the chosen coring site of Ki_10_I and Ki_10_II for meaningful palaeoenvironmental reconstructions. On the other hand, this supports the usage of the Plankton/Benthos-ratio in Lake Kinneret as indicator for possible lake-level changes.
3. Our study highlights, that a systematic sediment surface sampling of modern diatom death assemblages are helpful to understand and calibrate the limnological history of lakes, which are used for palaeoenvironmental reconstructions. Modern datasets should be included more often in future studies and interpretations, especially in those lake systems, where commonly used indicators, e.g. for changes in water depth (such as salinity), are not available.
4. A quantitative diatom-inferred water-depth model based on simple linear regression between modern diatom assemblages and water depth is presented in this study and was used to calibrate Holocene lake-level reconstructions of Lake Kinneret. This method might not be applicable in other lake basins, as it is site specific: individual mixing processes of each analysed lake system lead to unique fossil diatom death assemblages (Barker et al., 1994).
5. The new calibrated lake-level reconstruction fits well to palaeo-shoreline measurements and displays smaller variations more sensitive. Our results highlight a close interaction between Lake Kinneret and the Dead Sea as they often show a similar response to changing hydrological conditions in the catchment, e.g. due to changing climatic conditions during the Holocene.

6. Presented lake-level reconstructions of this study are based on a linear relationship of diatom assemblages and their relation to water depth, which was measured during sampling in January 2012. Water depth and diatom assemblage composition can vary over a one-year cycle and therefore might lead to different results, if samples were taken in the summer month. Nevertheless, we assume that the composition of analysed diatom death assemblages probably shows a mixture of the last three to five years and present a reliable picture of distribution and depositional processes. For a better understanding of those processes and also human induced ecosystem changes, future studies should analyse annual shifts of the living diatom flora and its death assemblage deposition in relation to chemical parameters (not considered in the presented study) and modern lake-level changes, e.g. by the usage of sediment traps.
7. A three-dimensional modelling of the morphometry of Lake Kinneret should be applied in future, as it would allow the calculation of the lake volume, planar and basin surface areas. Those are the critical components of a conceptual model, which could explain how planktonic and benthic habitat areas might have changed with varying lake levels (Stone and Fritz, 2004).

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4.9 **Appendix*:*** Lake Kinneret diatom species list from modern sediment surface samples

Centrales

Aulacoseira ambigua
Aulacoseira granulata
Cyclostephanos dubius
Cyclotella distinguenda
Cyclotella meneghiniana
Discostella stelligera
Discostella spp.
Pantocsekiella ocellata
Pantocsekiella polymorpha
Stephanodiscus hantzschii
Stephanodiscus medius
Stephanodiscus minutulus
Stephanodiscus rotula

Pennales

Achnanthes clevi
Achnanthes delicatula
Achnanthes kolbei
Achnanthes lanceolata
Achnanthes minutissima
Achnanthes spp.
Amphora acutiuscula
Amphora coffeaeformis
Amphora libyca
Amphora ovalis
Amphora pediculus
Amphora veneta
Aneumastus stroesei
Anomoeoneis vitrea
Caloneis permagna
Caloneis schumanniana
Cocconeis disculus
Cocconeis neodiminuta
Cocconeis neothumensis
Cocconeis placentula var. lineata
Cratucula halophila
Cymatopleura elliptica
Cymatopleura solea
Cymbella affinis
Cymbella cymbiformis
Cymbella helvetica
Cymbella muelleri
Cymbella spp.
Cymbella tumida
Encyonema spp.

Pennales

Epithemia adnata
Epithemia spp.
Eunotia spp.
Fragilaria acus
Fragilaria capucina
Fragilaria construens var. binodis
Fragilaria construens var. construenses
Fragilaria construens var. venter
Fragilaria delicatisima
Fragilaria gracilis
Fragilaria lapponica
Fragilaria nanana
Fragilaria rumpens
Fragilaria ulna
Fragilaria vaucherie
Gomphonema affine
Gomphonema clevei
Gomphonema gracile
Gomphonema insigne cf
Gomphonema parvulum
Gomphonema spp.
Gyrosigma attenuatum
Gyrosigma nodiferum
Gyrosigma spp.
Hanitzschia amphioxys cf.
Mastogloia elliptica
Mastogloia smithii
Navicula (sub-)rotunda
Navicula capitata
Navicula clementis
Navicula cryptotenella
Navicula meniscul us
Navicula placentula
Navicula porifera
Navicula pupula
Navicula pusilla cf.
Navicula reinhardtii
Navicula scutelloides
Navicula signatoides
Navicula tusculus/pseudotusculus
Navicula veneta
Naviculoide
Nitzischia palea
Nitzschia amphibia

Pennales

Nitzschia constricta
Nitzschia frustulum
Nitzschia gracilis
Nitzschia granulata
Nitzschia levidensis
Nitzschia linearis
Nitzschia paleacea
Nitzschia sigma
Nitzschia spp.
Opephora martyi
Pinnularia borealis
Pinnularia spp.
Pleurosigma elongatum
Pseudostaurosira brevistriata
Reimeria (Cymbella) sinuata
Rhoicosphenia curvata
Rhopalodia gibba
Staurosira pinnata
Surirella linearis
Surirella spp.
Synedra (Fragilaria) radians
Tabellaria flocculosa

5 Synthesis

5.1 General remarks

The main aim of this PhD thesis was to investigate and understand the potential of diatoms as palaeoenvironmental and palaeoclimate indicators in Eastern Mediterranean Quaternary research, by the analysis of modern and subfossil diatom assemblages in Lake Kinneret, Israel. The Levantine region is located in the transition belt between two climate zones, the Saharo-Arabian desert belt and the subtropical Mediterranean climate zone, which makes this area ideal to investigate climate changes. Furthermore, the study area represents an ideal area for investigating the complex relationship between climatic, environmental and social changes, as it is part of the Fertile Crescent, which has a long history of human occupation (Frumkin et al., 2011, Issar and Zohar, 2004, Richter et al., 2012).

To achieve the main goals of this thesis, diatom assemblages were analysed from modern sediment surface samples and, for palaeoenvironmental reconstruction, from an 18 m long sediment sequence recovered from Lake Kinneret in 2010, covering the last 9,000 cal yrs BP. As part of the study, the formal description of a new diatom species found in the lake sediment core was achieved, adding a taxonomic focus to the research. The following paragraphs present a summary of major conclusions of the presented PhD thesis in the context of the project's aims and objectives.

In reading the thesis, it should be noted that the age-depth model was improved in 2016 by the addition of a new series of dates. The publication, Vossel et al. (2015, Chapter 2) is based on the earlier age model, as presented in the thesis of Schiebel (2013). This model gave an age estimate of 8,200 cal yrs BP for the 17.8 m long sediment section recovered from Lake Kinneret; since the work is already published, the chronology for this section has not been updated. Dates referred to in Chapters 3 (Vossel et al., 2018) and 4 (Hartung et al., in prep) of this thesis are based on the new age-depth model published in detail in Schiebel and Litt (2018), which gives an age of 9,000 cal yrs BP for the recovered core. The content of the publication "*Cyclotella paleo-ocellata*, a new centric diatom (Bacillariophyta) from Lake Kinneret (Israel)" (Vossel et al., 2015, Chapter 2) is unaffected by those modifications.

5.2 Diatom flora of Lake Kinneret

This thesis provides detailed information about modern and subfossil diatom death assemblages and their distribution in Lake Kinneret. As they only constitute a minor component of the recent phytoplankton community of Lake Kinneret, diatoms have not been a major research focus during the last 30 years. The presented analyses in this thesis revealed that anthropogenic influences have caused a shift in the modern diatom composition compared to the fossil one. However, the modern flora still contains many of the taxa present in the fossil record. The most common planktonic diatom species present in Lake Kinneret are from the genera *Cyclotella (*recently reclassified as *"Pantocsekiella")* and *Stephanodiscus*, plus the species, *Aulacoseira granulata.* These taxa are often accompanied by the periphytic *Brachysira* spp. The most common benthic taxa are *Amphora pediculus, Achnanthes* sensu lato spp., *Navicula* spp., *Synedra ulna* and *Rhoicosphenia curvata*.

Large, subfossil populations of an unknown centric, planktonic diatom were observed during palaeoenvironmental diatom analyses conducted on the sediment cores from Lake Kinneret. In the scope of this thesis, this species was described as C*yclotella paleo-ocellata* sp. nov. VOSSEL AND VAN DE VIJVER (Chapter 2). The new taxon belongs to the *Cyclotella ocellata* species complex and was described and separated from other similar taxa based on morphological characters. As *C. paleo-ocellata* is at present only known from the subfossil bottom sediments of Lake Kinneret, DNA- analysis could not be conducted to reveal its molecular fingerprint and genetic relationship to the *Cyclotella-ocellata* complex. Assumed ecological preferences (i.e. oligotrophic conditions with low tolerances of nutrient enrichment; deep turbulent open water) were inferred from the associated diatom flora.

5.3 Applicability of diatoms as palaeoecological indicators

This thesis underlines the value of diatom analyses in long (decadal to millennial timescale) terrestrial, sedimentary records. Across the circum-Mediterranean, and the southern Levant in particular, there has been surprising little Quaternary diatom research to date. In this PhD thesis a high-resolution diatom dataset (sample/50 yrs) based on a robust chronology was created for Lake Kinneret (Israel). The results confirm that diatoms provide a powerful tool for Holocene palaeoenvironmental and climatological reconstructions in the southern Levant region, especially if they are interpreted in combination with multi-proxy datasets (as carried out in Chapter 3). In this thesis, the diatom data in particular provides a robust signal

(a) of lake-level changes in Lake Kinneret, and therefore climate variability during the Holocene.

(b) of the changing trophic status of Lake Kinneret, and therefore indicates the initiation and subsequent pattern of anthropogenic impact on the lake's ecosystem.

This thesis demonstrates clearly,

(a) that diatom data should be interpreted, if possible, in combination with multi-proxy datasets, e.g. pollen, which reveals the catchment vegetation and palaeoclimate history, and/or limnological mineralogy and geochemistry data such as XRF-data, giving useful insights into soil erosion processes and terrestrial input.
(b) that a systematic sediment surface sampling of modern diatom death assemblages is helpful to understand, interpret and calibrate fossil diatom assemblages, which are used for palaeoenvironmental reconstructions.
(c) that depositional processes occurring within the investigated lake basin (e.g. sediment supply from the catchment by river inflow) can strongly influence the composition of the analysed diatom death assemblage and its concentration, which can affect interpretation.

5.3.1 Lake-level reconstructions based on diatoms at Lake Kinneret and its implications for palaeoclimate reconstruction in the southern Levant

The results of the research confirmed that the lake basin has remained fresh (i.e. hydrologically open) throughout the Holocene, such that lake-level changes in Lake Kinneret cannot be derived from diatom-inferred salinity as a proxy indicator, as applied in closed-basin saline lake studies across the Mediterranean climate zone (Reed et al., 1999, Roberts et al., 2008). Instead, variation in diatom habitat groups (here the plankton-to-benthos ratio of diatoms) is used in this study, to provide a physical rather than chemical indicator of lake-level change. The applicability of this approach was discussed in detail in Chapter 3 and 4 of this thesis. Two different methods were used:

Lake-level reconstruction presented within the publication “Lake Kinneret (Israel): New insights into Holocene regional palaeoclimate variability based on high-resolution multi-proxy analysis” (Vossel et al., 2018, Chapter 3) is based on the calculation of a “simple” Plankton/Benthos-ratio (P/B-ratio). Lake-level reconstruction presented in Chapter 4 (Hartung et al., in prep) “Is the present the key to the past? Diversity and distribution of modern diatom communities in Lake Kinneret (Israel)” is based on a linear regression model derived from analysis of the modern dataset, which was applied in a second step to the subfossil dataset.

Both lake-level reconstructions draw similar conclusions for possible palaeoclimate variation during the Holocene. The Early Holocene was characterised by fluctuating lake levels, which can be linked to alternation between an arid and more humid climate at Lake Kinneret. Diatoms indicated a prolonged stable deep lake phase throughout the mid-Holocene and the onset of the Late Holocene due to a long-lasting humid climate. During the Late Holocene, shifts in lake-level, and therefore the climate signal, cannot be derived from variations in the P/B-ratio. Those signals are overprinted by accelerating nutrient enrichment linked to intensified human activities in the catchment area.

The two reconstructions differ in detail and the model appears to be more sensitive to minor fluctuations in lake level. This calibrated lake-level reconstruction (presented in Chapter 4) fits most closely to the pattern inferred from palaeo-shoreline measurements by Hazan et al. (2005) and displays smaller variations in water level, and, by implication, is more sensitive to palaeoclimate variation. Similarities between Dead Sea and Lake Kinneret lake-level fluctuations during the Holocene could be recognized and linked tentatively to the known rapid climate change (RCC-) events. The 8.2 ka BP cold event, for example, is the most prominent RCC at northern latitudes during the Holocene (Johnsen et al., 2001, Pross et al., 2009). Its influence on terrestrial records from the Eastern Mediterranean is strongly debated (Robinson et al., 2006), as several of those records show phases with reduced precipitation, but which lasted longer than the short-lived 8.2 event described from northern high latitude sites (e.g. Staubwasser and Weiss, 2006, Weninger et al., 2009). It is remarkable, that the diatom record from Lake Kinneret showed a strong response at around 7,900-7,400 cal yrs BP (assumed 8.2 event within age-to-depth error range), indicating low lake levels and more arid conditions, whereas no marked changes in the palynological dataset, i.e. impact on catchment vegetation, is recognized during the entire Early Holocene. This again highlights the importance of diatom analysis in the southern Levant region and its useful contribution to ongoing palaeoclimate debates. The response of diatom assemblages and geochemical data of Lake Kinneret show similarities to palaeoclimate records studied around the Mediterranean (e.g. Ariztegui et al., 2001, Cvetkoska et al., 2014). Another good example for this, is the prolonged stable deep lake-level phase of Lake Kinneret indicated by the diatom data throughout the mid-Holocene. Other diatom records in the Eastern Mediterranean are in accord with this result, e.g. Lake Ioannina (Jones et al., 2013), Lake Prespa (Cvetkoska et al., 2014) and Lake Dojran (Zhang et al., 2014).

The newly presented lake-level reconstruction within this PhD thesis (Chapters 3 and 4) allowed for the first time a detailed comparison between the two contrasting lake systems of Lake Kinneret (as an open lake basin with an in-and outflow) and the Dead Sea (as a closed lake basin). This is important, as a similar response to regional changing climatic-hydrological conditions is presumed for those two lake systems in literature (e.g. Kushnir and Stein, 2010, Stein, 2014). Although similar, the results of this thesis also demonstrated that the two lake systems have sometimes exhibited contrasting responses. Possible explanations could be (a) the higher sensitivity of the Dead Sea to changing moisture availability or (b) the long-term existence of the strong North (humid) to South (arid) climate gradient which operates in Israel today. Nevertheless, the results of the calibrated lake-level reconstruction in particular (Chapter 4) highlight the close similarity between Lake Kinneret and the Dead Sea, indicating that the two systems have been subject to similar regional palaeoclimate forcing during the Holocene.

5.3.2 Human impact on the ecosystem of Lake Kinneret

Major shifts in the diatom community during the Early and mid-Holocene were driven by changes in lake-level and moisture availability rather than changes in the trophic status of the lake. The diatom data indicate that fluctuating human settlement size and activities around Lake Kinneret during those time periods (Langgut et al., 2013, 2015, Schiebel and Litt, 2018) seems not to have a remarkable impact on the lake's ecosystem and its tropic state.

Intensive human occupation phases during the Hellenistic/Roman period around Lake Kinneret (Dar, 1993, Anderson, 1995, Chancey and Porter, 2001) showed the first effects on the lake's ecosystem. This is well recognizable in the diatom data as well as in the multi-proxy datasets (e.g. pollen, mineralogy, green algae, archaeology). The disappearance of two diatom species *Stephanodiscus galileensis* HÅKANSSON & EHRLICH and *Cyclotella paleo-ocellata* VOSSEL & VAN DE VIJVER (both firstly described in bottom sediments from Lake Kinneret) at around 2,300 cal yrs BP possibly marks the beginning of this human-induced impact and the turnover from an oligotrophic fossil to a meso-to eutrophic modern diatom assemblage. Intensive agriculture activities, e.g. the replacement of oak woodland by olive plantations (Schiebel and Litt, 2018) or the establishment of major irrigation systems (Lemche, 2015) led to intensive nutrient enrichment in the lake. This favoured an increase in dinoflagellates and green algae in the phytoplankton biomass volume of Lake Kinneret (Pollingher et al., 1984) and led to the permanent replacement of the "typical" diatom flora.

5.4 Future perspectives

This thesis confirm that diatoms provide a powerful tool for Holocene palaeoenvironmental reconstructions in the southern Levant region. Therefore, the results emphasize the need for further analysis of long, terrestrial diatom records with robust age-control, both in this region and across the circum-Mediterranean. It would also be valuable to retrieve a longer sequence from Lake Kinneret spanning the Last Glacial and Holocene/Pleistocene transition, since this represents the phase during which Lake Kinneret was merged with the Dead Sea to form the former, more extensive, Lake Lisan.

The investigation of Holocene sediments of the Dead Sea or laminated sediment sections (no halite deposits) of the Samra formation (Fm) and Lisan Fm could be promising for future diatom analysis as well. Preliminary observations showed that diatoms are preserved in those intervals (Begin et al., 1974). Freshwater diatom taxa can be distinguished from brackish ones and therefore could be used as indicators for palaeo-salinity reconstructions.

As part of the research for this thesis (not reported), investigations of sediment cores from Birkat Ram (a small maar lake in the Golan Heights) revealed that diatoms were not preserved in the Holocene section, which made detailed quantitative analysis impossible. Therefore, I strongly would advise against future diatom research on sediments from Birkat Ram covering this time period. As Birkat Ram represents the only other potential, natural freshwater lake system in the region, future research potential is constrained by the availability of other suitable study sites.

The concept of the Plankton/Benthos-ratio used for lake-level reconstructions is a simple method, which turned out to be applicable for Lake Kinneret. However, a three-dimensional modelling of the morphometry of Lake Kinneret could be a valuable extension of this approach, as it would allow the calculation of the lake volume, planar and basin surface areas. Those are the critical components of a conceptual model, which could better explain how planktonic and benthic habitat areas might have changed with varying lake levels (Stone and Fritz, 2004).

The composition of diatom death assemblages (analysed in all investigated samples of this thesis) probably shows a mixture of three to five depositional years. For a better understanding of those depositional processes and also modern human induced ecosystem changes, future studies should analyse annual shifts of the living diatom flora and its death assemblage deposition in relation to chemical parameters and modern lake-level changes, e.g. by the usage of sediment traps.

5.5 References

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