

Dynamic diatom response to changing climate 0–1.2 Ma

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Dynamic diatom response to changing climate 0–1.2 Ma at Lake El'gygytgyn, far east Russian Arctic

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Abstract

The Lake El'gygytyn sediment record contains an abundant diatom flora through most intervals of the lake's history providing a means to create and test hypotheses concerning the lake's response to changing climates. The 0–1.2 Ma core interval is characterized by shifts in the dominant planktonic genera and events of exceptional concentration and diversity. Warm interglacial intervals have enhanced concentration and diversity of the plankton. This response is most extreme during exceptional events corresponding to MIS 11 and 31. Diatom concentration and diversity also increases during some cold intervals (e.g. MIS 2), suggesting conditions of lake circulation and nutrient cycling promoting diatom production during these events. Short intervals of low plankton concentration accompanied by shifts in the dominant genus of the lake suggest conditions during certain cold events generate a severe impact on plankton production. The absence of these events during extended intervals of low summer insolation variability suggests a muted cold-event response of the lake system linked to regional climate.

1 Introduction

The sediment record from Lake El'gygytyn, far east Russian Arctic contains a unique archive of terrestrial paleoclimate spanning the last 3.6 million years (Melles et al., 2012). The majority of recovered sediment contains significant but variable biogenic silica (Meyer-Jacob et al., 2012) mostly in the form of diatom valves. Understanding the factors influencing the production and preservation of diatoms in the lake is one key to understanding many of the other proxy records used to unravel the response of the ancient lake system to changing climates. Diatom species assemblages also offer a powerful recorder of changes in the lake potentially linked to paleoclimate through ice conditions, circulation, nutrient delivery, and water chemistry (e.g. Smol, 1988; Douglas and Smol, 1999).

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Early research on the modern diatom flora in El'gygytgyn has focused on descriptions of extant taxa found in lake-bottom samples. These first studies describe many unique species, consistent with a long-lived lake system (Sechkina, 1956; Jouse and Sechkina, 1960; Kharitonov, 1980, 1993; Genkal and Kharitonov, 1996, 2005, 2006).

Prospects of the recovery of the complete sediment record have inspired a renewed interest in the modern diatom flora (Cremer and Wagner, 2003; Cremer et al., 2005; Cremer and van de Vijver, 2006; Stachura-Suchoples et al., 2008). However, because of its remote location, on-site studies have been only short duration, and the diatom response to inter-annual changes in the lake system is poorly constrained.

Previous diatom studies of sediment cores from Lake El'gygytgyn show a generally abundant, diverse, and variable flora. The core PG1351 record included 150 samples spanning the last 250 ka (Cherepanova et al., 2007, 2010). Although these initial investigations demonstrated the potential of these diatom records, the interpretations from these early core studies were complicated by the presence of turbidites and by taxonomic uncertainty, especially in the morphologically variable dominant planktonic diatom included in the *Cyclotella ocellata*-complex (sensu Cremer and Wagner, 2003).

This study utilizes samples from a more recent core Lz1024 (recovered in 2003 extending to 340 ka) and initial samples from the nearby deep drilling site (5011-1) to construct a continuous low-resolution composite record spanning the last 1.2 Ma. In addition, four intervals are analyzed in finer resolution to understand the diatom response to selected events. This study provides initial interpretations of these diatom records along with guidance and prospects for future investigation.

1.1 Setting

Lake El'gygytgyn (67°30' N, 172°5' E; Fig. 1) is situated in an impact crater dated 3.58 ± 0.04 Ma (Layer, 2000). The modern lake (12 km diameter and 175 m deep) is oligotrophic (Nolan and Brigham-Grette, 2007). In recent observed years, the lake is ice free during approximately July–October and completely mixes in summer. Weak sub-ice convection is also suggested by gas bubble patterns in the lake ice (Nolan

and Brigham-Grette, 2007). At the present lake level, a shallow shelf (less than 10 m deep) occupies approximately 11 % of the lake basin area (Nolan and Brigham-Grette, 2007). However, morphological evidence suggests higher and lower lake levels in the past, substantially impacting the area of shallow-water lake bottom (Fedorov et al., 2008; Juschus, et al., 2011). Additional details of the modern setting and limnology are described elsewhere (Nolan and Brigham-Grette, 2007; Fedorov et al., 2012; Nolan, 2012; Nolan et al., 2012; Wennrich et al., 2012).

2 Methods

Diatom samples were prepared from a measured mass of freeze-dried sediment, treated with boiling 30 % H₂O₂. Systematic diatom counts were conducted at 1000× magnification with a Leica DMLB light microscope with differential interference contrast. At least 500 valves were counted in all but a few sparse samples. Quantitative diatom concentrations were calculated using measured transect areas on slides prepared from a measured sediment mass and added calibrated microspheres settled through a water column onto a microscope cover slip (modified from Battarbee et al., 2001; Scherer, 1994).

Counted diatoms were identified to species level, wherever possible, using a wide variety of taxonomic references. Taxonomy of the dominant diatoms was confirmed by scanning electron microscopy of selected samples. Names assigned to the taxa are generally those used by previous El'gygytgyn investigators (e.g. Sechkina, 1956; Cremer and Wagner, 2003; Cherepanova et al., 2007; Stachura-Suchoples et al., 2008). Presentation and discussion of planktonic diatoms in this study focusses on genus-level variations. In most cases, each genus is dominated by a single species as noted in the text. *Cyclotella* contains multiple morphotypes which, with further taxonomic work, will warrant further subdivision. Here they are lumped with the *Cyclotella ocellata*-complex (Cremer and Wagner, 2003) because of the difficulty to distinguish these taxa in routine counts. *Aulacoseira subarctica* (O. Müller) Haworth is the dominant member of its

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genus. Minor occurrences of other *Aulacoseira* species also occur and are excluded from the *Aulacoseira* plots. Genus-level diversity in the plankton was estimated utilizing the Shannon Index (e.g. van Dam, 1982). Further observations of periphyton assemblage, valve size and preservation were noted and quantified in certain cases.

The age model for the Lz1024 core is provided by methods described elsewhere (e.g. Juschus et al., 2007). Below 340 ka, the chronology is based on the detailed age model derived primarily from paleomagnetic reversal and orbital tuning (Haltia-Hovi and Nowaczyk, 2012; Nowaczyk et al., 2012) and correlation to the base of the Lz1024 record. The initial analysis interval presented here provides an approximately a 4–5 kyr average resolution for the 0–1.2 Ma record and 1 kyr resolution for the intervals analyzed in more detail. Short term variations in sediment accumulation rate are insufficiently known to adjust diatom concentrations in individual samples (valves g^{-1}) for diatom accumulation rates (valves $\text{cm}^{-2} \text{kyr}^{-1}$), but these variations are not anticipated to significantly affect the interpretations presented for this interval of the El'gygytgyn record.

3 Results

3.1 The composite record 0–1.2 Ma

The 0–1.2 Ma record presented here preserves a complex cyclicity in the lake's diatoms, reflected in the concentration, preservation, valve size, and species assemblage (Fig. 2). Because of the great differences in size, silica content, and valve concentration in dominant planktonic diatoms and the sporadic occurrence of some other planktonic taxa, absolute concentrations, rather than percentage within an assemblage, are presented for comparison. Numerical valve counts of total diatoms show a broadly similar trend to the biogenic silica record (Frank et al., 2012). Subtle differences in these trends may be attributed to minor variation in valve size and preservation observed in these intervals and by contributions from larger, less numerically abundant taxa.

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The most notable down-core changes are shifts in the dominant genera. *Pliocaenicus seczkiniae* Stachura-Suchoples, Genkal et Khursevich, previously observed to emerge since 15 ka, has a long complex history in El'gygytgyn, exhibiting substantial morphological variability. *Cyclotella* likewise becomes a minor component of the plankton during certain intervals. During other times, both diatoms co-exist, as in the Holocene.

One clear aspect of the 0–1.2 Ma diatom record is the occurrence of intervals of exceptional diatom concentration that correspond to inferred warm intervals (yellow in Fig. 2). Both plankton and periphyton concentrations increase, and the valves exhibit better preservation. Other planktonic taxa including *Stephanodiscus* cf. *minutulus* (Kützing) Cleve & Möller also occur during some of these events. *A. subarctica* occurs in abundance during some of these events prior to 550 ka, and is the numerically most abundant taxa during particular intervals from 800–1200 ka. The most extreme of these exceptional events correspond to MIS 11 and MIS 31. Here periphyton abundance is at its highest, and an exceptional diversity of planktonic diatoms occurs. Many of the high diatom concentration events are characterized by temporary size increases in the morphologically plastic planktonic genera (especially *Cyclotella* and *Pliocaenicus*). For example, during MIS 11 the initial cell diameter of *Cyclotella* is 25–30 μm compared to 15–20 μm before and after this event. During MIS 31 the initial cell diameter of *Pliocaenicus* increases to 35–50 μm from less than 30 μm before this event.

A few intervals of increased plankton and periphyton abundance correspond to apparently cold intervals (purple in Fig. 2). These are distinguished by their distinctive periphyton assemblage, particularly the absence of species found in inferred warm intervals, especially *Achnantheidium kriegeri* (Krasske) Hamilton, Antoniadou et Siver and *Cocconeis placentula* Ehrenberg (see Sect. 3.2). None of these intervals is characterized by significant concentration of *Pliocaenicus*.

Short (< 20 cm) intervals of low plankton abundance also occur in the diatom record. Seven of the 234 samples systematically analyzed for this study contain less than 10^7 valves g^{-1} total planktonic diatoms (green in Fig. 2). Many of these zones have

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persisting moderate concentrations of well preserved periphyton. These intervals, in many cases, correspond to shifts in the dominant plankton in the lake. For example at 924 ka, *Pliocaenicus* replaces *Cyclotella*. One such zone occurs at 225 ka. Although *Cyclotella* persists, this interval corresponds to an abrupt decline in a morphotype of the *Cyclotella ocellata*-complex (Cherepanova et al., 2010) which dominates the plankton 225–550 ka. This long-term dominance and abrupt decline may justify the establishment of this morphotype as a separate distinct species.

3.2 MIS 1 and 2 (0–34 ka)

The genus *Cyclotella* dominates the sediment record of the last 30 ka (Fig. 3). Minor and sporadic planktonic diatoms vary dramatically across this portion of the record. The 20–25 ka interval exhibits the greatest diversity in plankton with peaks in *Fragilaria* cf. *nanana* Lange-Bertalot, *S.* cf. *minutulus*, and *Asterionella formosa* Hassal often associated with higher nutrient concentrations (e.g. Lotter et al., 1998; Bennion et al., 2004). This interval corresponds to the highest biogenic silica concentrations in the last 30 ka, some intervals exceeding 30 %. The comparatively large, heavily silicified *Pliocaenicus* occurs in abundance only since 15 ka, although a few individual valves are observed on slides from earlier samples.

The periphyton species assemblage also changes with comparable timing. Small Achnantheaceae are numerically the most abundant valves in most samples. *A. kriegeri* and *Achnantheidium minutissimum* (Kützing) Czarnecki occur in greatest abundance since 15 ka. In contrast, *Planothidium oestrupii* (Cleve-Euler) Round et Bukhtiyarova peaks from 19–24 ka. Diatoms with valves greater than 75 µm length vary more irregularly. However, *Frustulia rhomboides* var. *amphipleuroides* (Grunow) DeToni is almost exclusively observed 15–25 ka, and *Eunotia pseudopectinalis* Hustedt is more characteristic of the interval since 15 ka.

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3.3 MIS 5e (111–135 ka)

The genus *Cyclotella* also dominates the 111–135 ka core interval (Fig. 4). Sparse *Pliocaenicus* and planktonic *Fragilaria* occur in a few samples. The inferred peak warmth of MIS 5e corresponds to an approximate doubling of the diatom concentration driven mostly by *Cyclotella*. Calculated genus-level plankton diversity does not significantly increase in this interval. This index may underestimate the true plankton diversity in this interval because the dominant *Cyclotella* contains at least two morphotypes with significantly different diameter. The peak in diatoms seen at 135 ka corresponds to the preceding cold productive mode (Fig. 2).

3.4 MIS 11 (360–4340 ka)

The interval corresponding to MIS 11 exhibits the greatest peak in diatom concentration driven mostly by *Cyclotella* (Fig. 5). During the first part of this interval (411–416 ka) peak abundance corresponds to numerically abundant but small diameter *Cyclotella* and *Stephanodiscus*. From 411 to 499 ka, *Cyclotella* occurs in lower abundance but increased size. Diversity also increases significantly in this interval, especially 401–403 ka, where *Fragilaria* and *Asterionella* peak.

3.5 MIS 31 (1057–1113 ka)

The interval corresponding to MIS 31 peak warmth contains a diatom abundance second only to MIS 11 in the 0–1.2 Ma record (Fig. 6). *Aulacoseira* is the most consistent and numerically abundant member of the plankton assemblage. The robust *Pliocaenicus*, although numerically less abundant, is also a significant and consistent part of the assemblage. Similar to MIS 11, additional genera occur in the more recent portion, in this case *Stephanodiscus* and *Asterionella* occur 1067–1076 ka. The diatom concentration increases well before the inferred MIS 31 peak warmth; however, conditions in the interval preceding this event already exceed Holocene warmth according

to pollen analysis (Melles et al., 2012). Above this interval is a low abundance zone corresponding to the extirpation of *Pliocaenicus* and return of *Cyclotella* to dominance in the lake. These low abundance samples are missed in the 0–1.2 Ma record because of the lower sample resolution, although they are suggested by the observed shift in dominant genus.

4 Discussion

4.1 Peak warmth intervals

Using the Holocene and other identified interglacial intervals from the composite core record, a clear pattern in diatom response is apparent. Concentration increases in both periphyton and plankton. Genus-level diversity increases in the plankton. Valves are generally well preserved with only minor dissolution noted. The occurrence of certain periphytic taxa also characterizes each of these intervals, especially *A. kriegeri* and *C. placentula*. These taxa also occur in the deeper record, even as the dominant plankton varies. In general, the diatom response is consistent with a relatively favorable environment for diatom growth that might be anticipated from enhanced nutrient delivery, prolonged open-water growing season, and expanded diversity in habitats in the lake and its catchment.

The emergence of *Pliocaenicus* since 15 ka may be a response to warming and enhance open-water conditions. Little is known about the ecological tolerance of this taxon. Flower et al. (1998) speculate the similar *Pliocaenicus costatus* var. *sibiricus* (Skabitch.) Round et Håkansson responded favorably to 20th-century warming in Lake Bolshoe, Siberia. The appearance of *Pliocaenicus* in El'gygytgyn at 15 ka may also partially reflect the elimination of a competitive exclusion from larger members of the *Cyclotella ocellata*-complex. These forms disappear from the record during an inferred cold, diatom-poor interval at ca. 70 ka. Thus, favorable conditions for this large, heavily

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silicified *Pliocaenicus* may first recur after 15 ka, allowing expansion into this vacated niche in the phytoplankton.

Although not yet quantified in detail, the observed size increase in *Pliocaenicus* or *Cyclotella*, particularly in MIS 11 and 31, may also be a response to conditions during these times. Diatom size control may vary with conditions of a specific lake (e.g. Finkel et al., 2009). In a nutrient-limited lake system, higher nutrients (including silica) may favor larger plankton. Further, larger plankton could be an adaptation to greater mixing/turbulence due to more open water, allowing larger diatoms to remain in the photic zone without sinking.

Observed interglacials within the 0–1.2 Ma record are highly variable in the magnitude of their diatom response. MIS 11 and 31 are exceptional events both in diatoms and other proxies (Melles et al., 2012). Both intervals have peaks in species usually associated with enhanced nutrient status. The occurrence of these assemblages corresponds to sediments Facies C, sensu Melles et al. (2012), characterized by reddish-brown finely laminated silt, explained by high productivity in the growing season and anoxic bottom waters during winter. The unique diatom response may result from enhanced nutrient delivery from the catchment or a threshold in lake-water oxygenation and circulation, altering the nature and timing of nutrient cycling in the lake (e.g. Rippey et al., 1997; Brüchman and Nedendank, 2004). This exceptional diatom production and accumulation plays an important role in the formation of this sediment facies, ranging between 20 and 50 % biogenic silica during these peaks.

The distribution of *A. subarctica*, a widespread diatom preferring intermediate nutrient conditions (Gibson et al., 2003), illustrates some of the complexity of comparing particular interglacials. This diatom, occurring almost exclusively in identified interglacial intervals, is a minor component since 550 ka but dominates in some intervals between 830 and 1150 ka. This species is also abundant in Lake Baikal during approximately this same time, peaking ca. 850, 1150, and 1190 ka (Grachev et al., 1998), suggesting a broader biogeographic influence on its occurrence and distribution.

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4.2 Cold productive intervals

The unexpected occurrence of high biogenic silica (20–35 %) and diatom concentration during MIS 2 may help to decipher the environment of the lake during this interval and to understand the dynamics of the lake system and its response to changing climate.

5 The substantially different overall assemblage, including blooms of delicate planktonic taxa, generally favoring higher nutrient status and not observed in substantial quantities in the Holocene, suggests that this trend is more than a preservation effect or lack of dilution from other inputs. More likely, the environment in the lake was similarly favorable for diatom production compared to the recent lake. Yet other proxies, such as
10 pollen, sediment facies, and diatom isotopes suggest at least 4 °C colder summer air temperatures compared to modern (Melles et al., 2012; Chaplignin et al., 2012).

To explain the occurrence of these taxa also observed to occur during peak warmth intervals, one must consider the timeframe represented by sediment samples and the potential diatom community responses and their timeframe. Individual diatom samples
15 may span over two centuries of sediment deposition. The general dominance of *Cyclotella* or *Pliocaenicus* may represent a competitive exclusion of other taxa during the typical range of conditions (e.g. Stoermer and Edlund, 1999). Periodic expansion in plankton diversity may reflect adaptation of the dominant species to a more limited range of conditions or periodic changes in nutrient resource distribution (e.g. Kilham et
20 al., 1996). The particular occurrence of these nutrient-favoring phytoplankton species during MIS 2 may indicate conditions providing seasonal to extra-seasonal pulses of nutrients to the plankton, allowing for a temporary increase in the population of these widespread taxa. Periodic circulation of a mostly-ice-covered lake may generate such conditions. Circulation-induced seasonal nutrient pulses timed to persistent transpar-
25 ent ice cover may also promote the expansion of these otherwise sporadically occurring taxa. Such a scenario may also be consistent with the lack of significant *Pliocaenicus*, perhaps requiring more extensive open water conditions. Melles et al. (2012) also suggest the sediment facies indicates more extensive ice cover leading to oxygen depleted

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bottom waters, but sufficient melting of the lake's margins to allow some fluvial input. However, this sediment Facies A does not always correspond to the diatom response observed in MIS 2.

The periphyton assemblage also changes during this same interval suggesting environmental changes across all diatom habitats. Their abundance suggests at least periodic melting sufficient in the lake margins to promote the diversity and abundance of the lake's periphyton community. The periphyton may respond directly to climate induced shallow water habitat changes, or indirectly to suggested nutrient conditions and lowered lake level during MIS 2 (Juschus et al., 2011). However, the uncertain tolerance ranges of the dominant *El'gygytgyn* periphyton make a specific interpretation of these changes difficult.

Additional short productive intervals (*sensu* MIS 2) lacking the characteristic interglacial periphyton suggests the potential recurrence of conditions favorable to diatoms during some cold events. Similar to MIS 2, several of these intervals correspond to low insolation and heavy marine oxygen isotopes in the tuned chronology. Thus, interpretations of biogenic silica and diatom concentration in the deeper record may be complicated by additional such events, requiring confirmation with other proxy records.

4.3 Sparse plankton events

Events in which plankton dramatically decreases in abundance and subsequently re-emerges with a different character may help to constrain the nature of these intervals of the lake's history. These observations imply that phytoplankton in the lake is stressed such that competitive exclusion is eliminated for some time. However, the recurrence of apparently unique *El'gygytgyn*-adapted species over the long history of the lake implies that minimal populations are sustained through these events. Given the correlation of these events to relatively cold intervals, these extreme declines in the lake's plankton are most easily explained by a prolonged light limitation from extended summer ice and snow cover on the lake. The role of changing lake level in these events cannot be excluded based on the diatom observations. The persistence of well-preserved

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near-typical periphyton concentration across some of these intervals suggests some shallow water habitats are maintained during these times.

The low-plankton events are not evenly distributed through the lake record. None has yet been observed from 550–225 ka in the low-resolution sampling completed, and none is anticipated based on the apparent stability of the dominant *Cyclotella*. The interval 680–920 ka also lacks low-plankton zones with a consistent dominance of *Pliocaenicus*. These intervals both corresponds to a time of lower-amplitude summer insolation variability (e.g. Laskar et al., 2004), suggesting that these events may be triggered by conditions unique to summer insolation lows. This observation is similar to the interval of sustained high diatom concentration in the Lake Baikal record 580–370 ka (Prokopenko et al., 2002). The lake system and the regional climate are sensitive to intervals of extreme insolation lows, perhaps inducing extended periods of light limitation in planktonic habitats. Careful observations of diatom assemblages provide clues the nature of exceptional cold events only subtly expressed in other proxies.

5 Conclusions

From 0–1.2 Ma, diatoms in the Lake El'gygytgyn sediment record vary dramatically in plankton and periphyton species assemblage and abundance. These variations correlate to climate conditions inferred from other proxies in the lake. Observed diatom changes suggest climate-induced reorganization of the lake system related to ice conditions and the timing and nature nutrient delivery to the photic zone. Higher resolution diatom studies, including additional quantification of diatom size, preservation and periphyton assemblages, through key intervals of the lake's history, combined with other proxy measures and modeling of the lake system, will help to develop linkages between specific climate conditions and the observed lake response. The El'gygytgyn diatom record further provides a unique setting to observe diatom evolution linked to changing climate in this relatively isolated environment.

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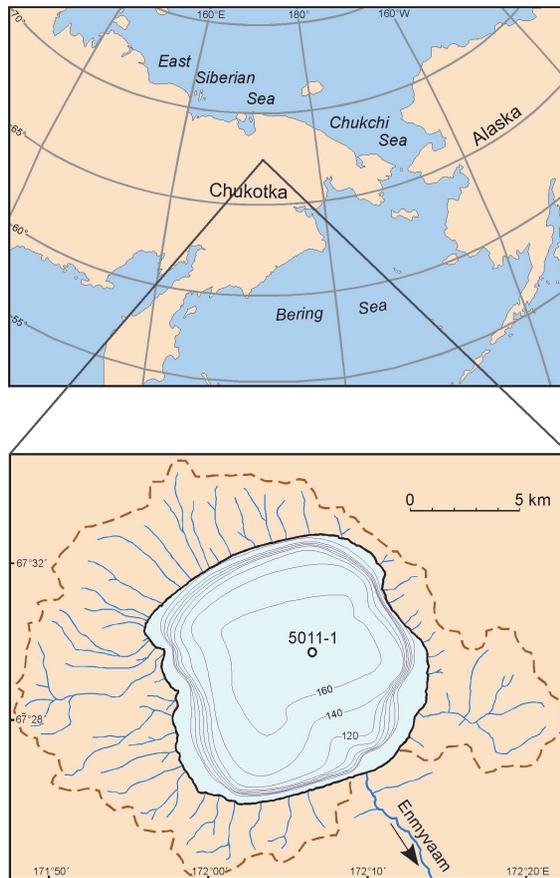


Fig. 1. Location map of Lake El'gygytyn and its catchment. Bathymetry (20-m contour interval) and stream network are modified from Nolan and Brigham-Grette (2007).

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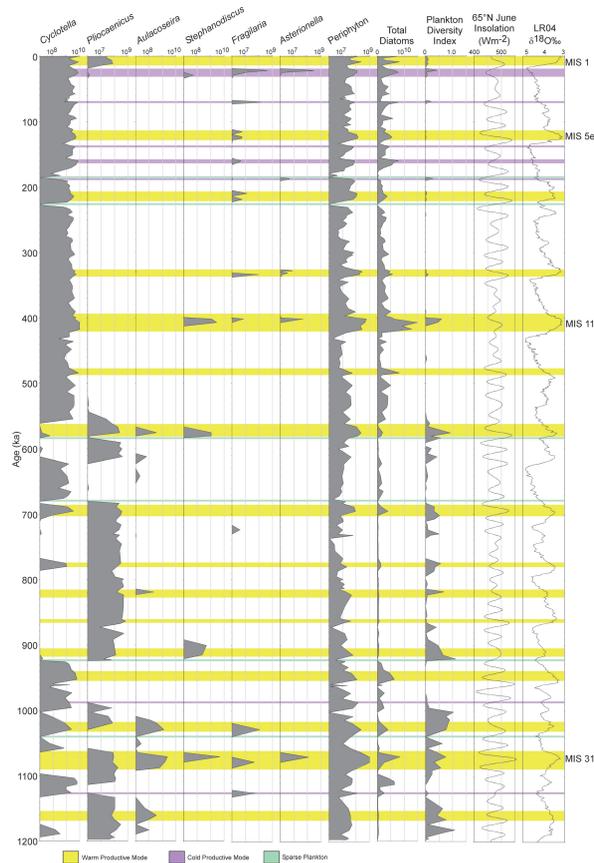


Fig. 2. Concentration (values g^{-1}) of planktonic species, total periphyton, total diatoms, and plankton diversity (Shannon Index) from 0–1.2 Ma. Exceptional events are indicated by colored intervals. Diatom concentrations, except total diatoms, are plotted on a log scale with range appropriate to the observed variation in the core record. For comparison, the marine isotope stack (Lisiecki and Raymo, 2005) and 65° N June insolation (Laskar et al., 2004) are also plotted.

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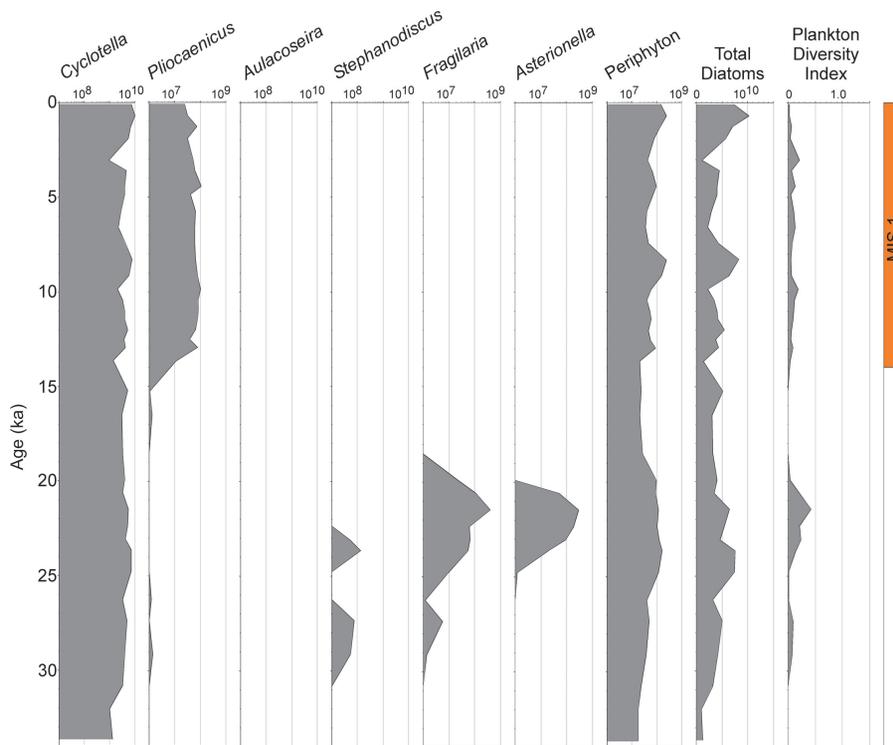


Fig. 3. Concentration (valves g^{-1}) of planktonic species, total periphyton, total diatoms, and plankton diversity (Shannon Index) from 0–34 ka. Peak MIS 1 warmth indicated by other proxies (Melles et al., 2012) is also shown.

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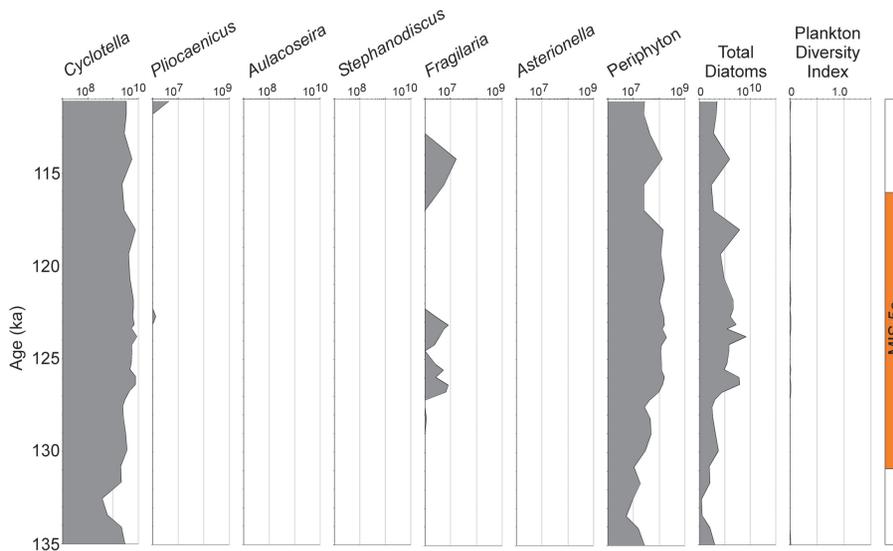


Fig. 4. Concentration (valves g^{-1}) of planktonic species, total periphyton, total diatoms, and plankton diversity (Shannon Index) from 111–135 ka. Peak MIS 5e warmth indicated by other proxies (Melles et al., 2012) is also shown.

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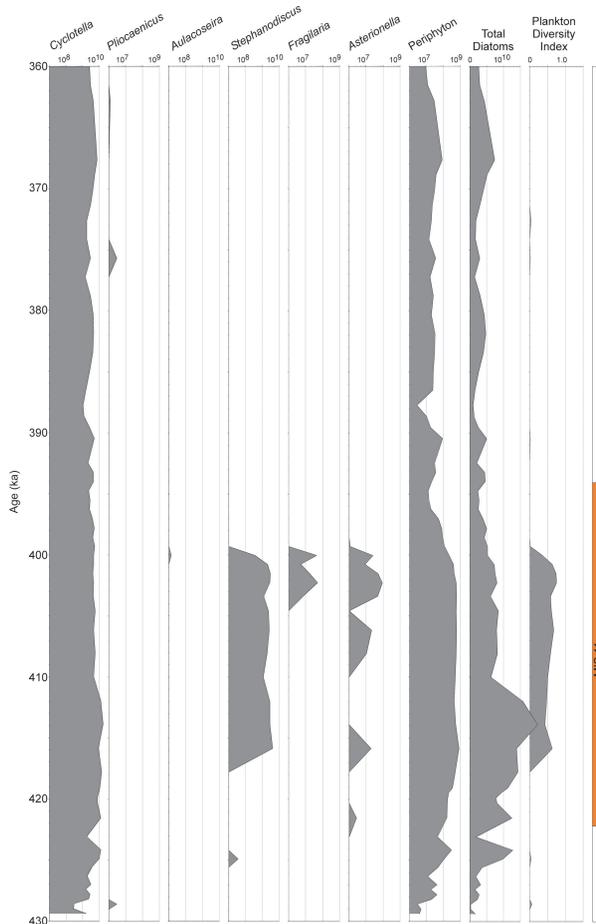


Fig. 5. Concentration (valves g^{-1}) of planktonic species, total periphyton, total diatoms, and plankton diversity (Shannon Index) from 360–430 ka. Peak MIS 11 warmth indicated by other proxies (Melles et al., 2012) is also shown.

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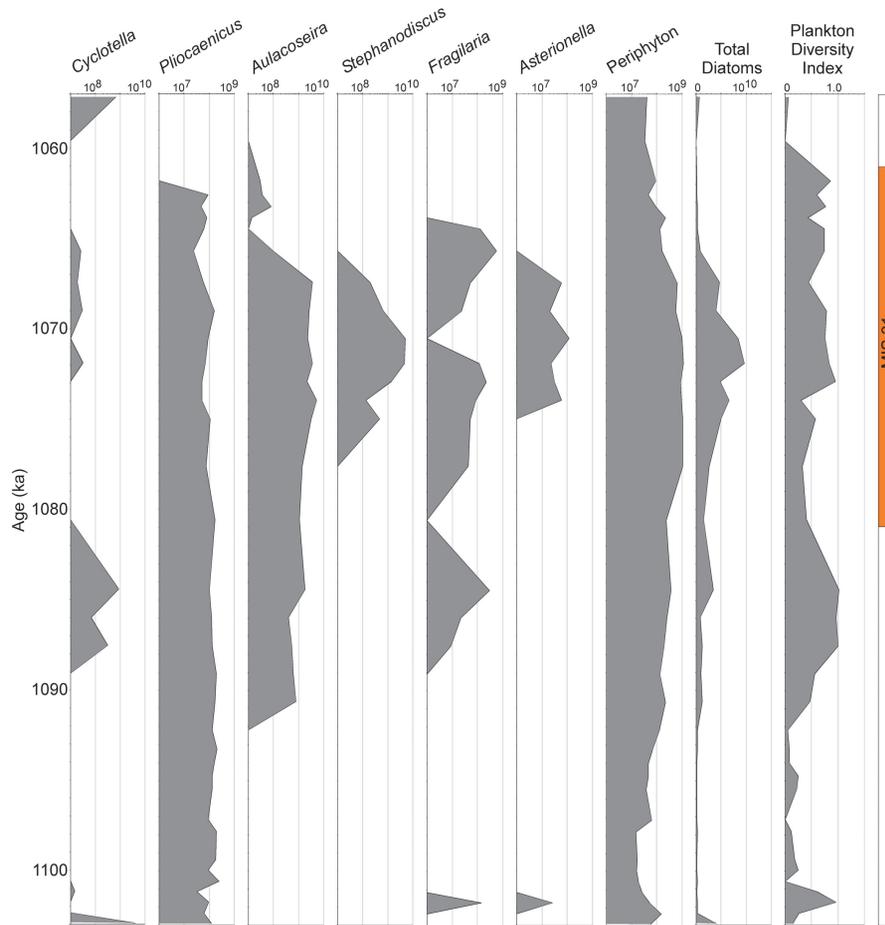


Fig. 6. Concentration (values g^{-1}) of planktonic species, total periphyton, total diatoms, and plankton diversity (Shannon Index) from 1057–1103 ka. Peak MIS 31 warmth indicated by other proxies (Melles et al., 2012) is also shown.

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