INVESTIGATION OF DIATOM ENDEMISM AND SPECIES RESPONSE TO CLIMATE EVENTS USING EXAMPLES FROM THE GENERA CYCLOTELLA (LINDAVIA) AND SURIRELLA IN THE LAKE EL'GYGYTGYN SEDIMENT RECORD

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ABSTRACT

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Diatom assemblages from ancient lakes are a powerful proxy for recording past climatic events due to their high environmental sensitivity. A composite core drilled from Lake El’gygytgyn, northeastern Russian Arctic, contains an abundant diatom record extending to ~3.5 Ma. Preliminary research on the core has documented multiple shifts between the dominant planktonic genera. Declines in the plankton concentration have been associated with cold events. However, the nature of the lake’s ice cover during these events is still debated. To understand the connections between diatoms and climate in the lake, a systematic morphologic analysis was performed on examples of the planktonic genus Cyclotella (Lindavia) and the large benthic genus Surirella. Observations were made using light microscopy and scanning electron microscopy on samples from 1.2 Ma to recent. Cyclotella valves have large diameter and multiple morphologies during warm intervals and have smaller diameter and a single morphology during cold intervals. Major changes in morphology coincide with cold, low productivity events. These observations suggest that Cyclotella morphology is strongly climate driven. Large Surirella species occur throughout the 1.2 myr record, increasing in abundance from ~500 ka to recent. Abundance and morphological changes are less correlated with climatic variability suggesting that Surirella habitats are less influenced by events affecting the lake’s plankton.
This thesis is dedicated to my wonderful family. To my parents, Mary and Andy, and my siblings Anna, Eric, and Brian, I would not have gotten this far without your love and companionship.
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CHAPTER I: INTRODUCTION

In recent years, the scientific community has increasingly focused on the issue of human-induced climate change. Rapid warming within the 20th century has created interest at the rate of which global climate change occurs (Cunningham et al., 2013). Answers to these questions can be found through the use of paleoclimate data from various proxies. These proxies record shifts in climate over a variety of timescales. The Arctic is of particular importance climatically due to its involvement in complex feedback mechanisms related to the ocean, atmosphere, cryosphere, and tectonics (Vogel et al., 2013). The study of past climate changes in these areas provides insight into present and future changes.

Ancient lakes, with long continuous sedimentary records, present a unique setting for exploring climate history. One climate proxy is the relative abundance and composition of diatom assemblages. Diatoms are sensitive to changes in nutrient availability, pH, salinity, lake depth, temperature regimes, and light availability (Douglas & Smol, 2010). Diatom assemblages in lake-bottom sediments help evaluate the lake’s response to changing climate. Ancient lakes also have the potential for exploring patterns in evolution, biodiversity, and endemism (Albrecht & Wilke, 2008).

Studying diatom morphological diversity and productivity provides a basis for further understanding of ancient lakes, their reaction to climate changes, and how these factors influence the development of endemic species. Diatom assemblages in the Arctic typically respond to changes in paleoclimate, with diversity and production of diatom assemblages increasing during warm events and decreasing during cold events (Douglas & Smol, 2010). This response can be complicated by dynamics of lake-ice conditions.
LAKE EL’GYGTYGYN

The Lake El’gygytgyn is located in northeastern Russia (67°30’ N, 172°05’ E) about 100 km north of the Arctic Circle (Figure 1). The lake is situated inside a meteorite impact crater that is approximately 3.58±0.4 Ma (Layer, 2000). The impact crater is 18 km wide with a total watershed area of 293 km$^2$; the lake diameter is 12 km (Nolan & Brigham-Grette, 2007). The lake has a surface elevation of ~492 m a.s.l (Nolan & Brigham-Grette, 2007).

Lake El’gygytgyn is cold, monomictic, and oligotrophic with the water temperature never exceeding 4°C (Nolan & Brigham-Grette, 2007). Fifty ephemeral streams drain into the lake, with only one major outflow to the Enmyvaam River (Melles et al., 2011). The mean annual air temperature recorded in 2002 was -10.3°C, and 70 mm of rain was recorded during the summer months (Nolan & Brigham-Grette, 2007). Ice covers the lake for 9 months of the year during which the lake is thermally stratified. It is only ice free during the months of July to October; complete mixing of the water column is achieved during these summer months (Nolan & Brigham-Grette, 2007). The low productivity of the lake combined with complete mixing of the water column in the summer leads to well oxygenated bottom waters (Melles et al., 2012).

The bathymetry of the lake is asymmetrical exhibiting shallow eastern and southern slopes, and steep western and northern slopes (Nolan & Brigham-Grette, 2007). The central portion of the lake is the deepest portion at ~175 m (Nolan & Brigham-Grette, 2007). Several shallow shelves or benches are present in the lake; these may be representative of paleo-shorelines as a result of differing lake levels (Nolan & Brigham-Grette, 2007; Juschus et al., 2011). Deep-water sediments on the shelf and raised shoreline features indicate higher than present day lake levels during a period of warmth in the Mid-Pleistocene (Juschus et al., 2011).
Figure 1: Location of Lake El’gygytgyn (from Snyder et al., 2013).
Drilling Project History

No evidence of glaciation in Lake El’gygytgyn has been documented (Schwamborn et al., 2012) which makes this ancient lake the longest continuous Arctic lake sediment record (Melles et al., 2011). To perform preliminary analyses, two early sediment cores were taken from the deepest part of the lake in 1998 and 2003 (PG1351 and Lz1024). Evaluation of these cores suggested that further drilling could recover a record of ~3.5 Myr of high Arctic paleoclimate (Koeberl et al., 2013).

To recover this sediment archive the El’gygytgyn Drilling Project was created. Two drilling sites were established, 5011-1 and 5011-3. 5011-3 was located on the western edge of the catchment in the area of permafrost (Melles et al., 2011). 5011-1 was located in the central area of the lake and three holes were drilled: 1A, 1B, and 1C (Melles et al., 2011). 1A and 1B were abandoned after twist offs at 143.7 m and 108.4 m respectively; 1C penetrated the rest of the lake sediments to 315 m, and into the impact rocks down to 517 m (Koeberl et al., 2013). A composite core was created from splices of parallel sediment cores recovered from 5011-1 and Lz1024.

Age Model

An age model was created for the sediment record using multiple methods including magnetic reversals, orbital tuning, and various others (Nowaczyk et al., 2013). Fourteen paleomagnetic polarity reversals were used to establish initial tie points (Nowaczyk et al., 2013). Stratigraphic parameters, including biogenic silica and magnetic susceptibility, reflective of conditions on the lake-bottom and catchment, were tuned to Northern Hemisphere spring-summer insolation and the marine oxygen isotope stack (MIS) (Nowaczyk et al., 2013). Eight
tephra layers deposited in the sediment have not yet provided age information (Nowackzyk et al., 2013). According to the age model, the upper ~160 m of sediment contains the last ~3.3 Myr, with sedimentation rates of 4-5 cm ka\(^{-1}\). The lower ~160 m contains the first ~0.3 Myr of the lake with sedimentation rates of ~45 cm ka\(^{-1}\) (Nowaczyk et al., 2013).

**BACKGROUND AND OBJECTIVES**

**Ancient Lakes**

Ancient lakes contain a unique sedimentary archive of past climatic conditions. These lakes are loosely defined as having a sedimentary record that spans a timescale since the last interglacial ~128 ka or further (Douglas & Smol, 2010). Distribution is not limited to one specific place; ancient lakes can be found on all continents and in varying climatic conditions. Grabens from active rift zones hold many of these ancient lakes such as Lake Baikal (Russia), Malawi Lakes (Malawi, Mozambique, Tanzania), and Lake Ohrid (Albania, Macedonia); others are found associated with volcanic activity (Lake Albano), karst landscapes (Lake Ioannina), and meteorite-impact craters (Lake El’gygytgyn and Lake Bosumtwi) (Douglas & Smol, 2010). Studies on ancient lakes have been multidisciplinary including geology, biology, and ecology. Ancient lakes are well known for their biodiversity and their endemism which greatly exceeds post-glacial or short-lived lakes (Albrecht & Wilke, 2008).

**Diatom Records from Ancient Lakes**

Diatom records found in ancient lake sediments serve as a powerful proxy for environmental change on glacial-interglacial scales. These organisms exhibit patterns of biodiversity, endemism, and adaptation (Douglas & Smol, 2010). Assemblages are susceptible to change under certain conditions such as changes in ice cover, duration of growing seasons,
nutrient availability, pH, conductivity, and temperature (Douglas & Smol, 2010). Shifts in climate affect diversity of diatom genera (Snyder et al., 2013) and are associated with differences in valve morphology and size (Genkal & Kiss, 1993; Hausmann & Lotter, 2001; Cherepanova et al., 2010; Genkal et al., 2013; Phillips, 2013). High environmental sensitivity causes different genera to thrive under specific environmental parameters at both generic and specific levels. Nutrient availability and incubation depths play an important role in these changes. Alteration in light availability affects water clarity, lake trophic state, water column stability, and nutrient concentrations such as nitrogen, phosphorus, or silica (Saros et al., 2014). These mechanisms among others must be considered when interpreting changes in small centric diatom abundance.

Lake Baikal provides an excellent example of both diatom endemism and response to paleoclimate. Drilling revealed a ~7500 m long sedimentary record that extends back ~20 Ma (Williams et al., 2001), containing an exceptional record of diatoms as a proxy for paleoclimate (Khursevich et al., 2001). Analyses of diatom evolution over the last 0.8 Ma linked diatom speciation to insolation changes (Khursevich et al., 2001). Shifts in dominance between *Aulacoseira baicalensis* (Meyer) Simonsen, *Cyclorella minuta* (Skv.) Antipova, and *Stephanodiscus incospicuus* Makarova & Pomazkina occur throughout the assemblage (Bangs et al., 2000). Diatom assemblage changes occur uniformly across the lake which indicates that external variables are the cause (Bangs et al., 2000).

Drilling at Lake Ohrid, located between Albania and Macedonia, yielded a composite of 1,075 cm, recording ~1.2 Ma (Wagner et al., 2014). Diatom assemblages were used as a proxy for paleoclimate. Low concentrations and diatom assemblages consisting of *Pseudostaurosira*, *Staurosira*, and *Staurosirella* were associated with cold glacial intervals (Wagner et al., 2009). Increasing abundances of planktonic diatoms and diversity indicated a temperature increase
across the Pleistocene-Holocene boundary, which would increase the growing season and reduce ice cover (Wagner et al., 2009). A higher resolution study was performed on the diatom morphological response of the dominant planktonic taxa at the species level to glacial-interglacial cycles. *Cyclotella fottii* Hustedt (syn. *C. hustedtii*) dominance was associated with cold intervals, while *Cyclotella ocellata* Pantocsek represented warm intervals (Reed et al., 2010). However, this analysis highlights the importance of further research on distinguishing between evolutionary pressures causing assemblage changes and external forces.

**Lake El’gygytgyn Diatoms**

The modern diatom community is documented from studies of core tops, bottom grabs, and sediment traps. The planktonic community is numerically dominated by the *C. ocellata*-complex (sensu Cremer & Wagner et al., 2003). Also important within the planktonic community is *Pliocaenicus Sechkinae* Stachura-Suchoples, Genkal & Khursevich (syn. with *Pliocaenicus costatus* (Lupikina)) (Cherepanova et al., 2007). Although *Pliocaenicus* is found in less abundance, they generally have a larger valve diameter. Additional minor species are also reported from the following genera: *Cyclostephanos*, *Aulacoseira*, *Cyclotella* (*Lindavia*), *Discostella* and *Stephanodiscus* (Kharitonov & Genkal, 2010). Within the benthic community both cosmopolitan species and species described only from Lake El’gygytgyn occur, most notably within the genera *Surirella* and *Navicula* (sensu lato) (Sechkina, 1956). Three distinct species have been noted from the genus *Surirella*, known for its endemism, including *S. robusta* var. *ovalis* Sechkina, *S. capronii* var. *anadyrensis* Sechkina, and *S. gravei* Sechkina (Sechkina, 1956).

The Lake El’gygytgyn sediment record contains an archive of diatoms for most of the lake’s history. These diatoms record differences between glacial-interglacial cycles showing
variation in abundance, species assemblages, and preservation. Planktonic diatoms are present in low diversity with high abundance, while benthic diatoms are present in higher diversity, but in lower abundance.

Preliminary studies of the El’gygytgyn core record document shifts in the dominant planktonic genera multiple times in the lake’s history (Figure 2). Since 18 ka, *Cyclotella* and *Pliocaenicus* co-occur. From 550 ka to 18 ka, *Cyclotella* dominates with only occasional observations of other genera (Snyder et al., 2013). At other times additional planktonic genera such as *Aulacoseira* and *Stephanodiscus*, occur, for example during peak warmth associated with MIS 11 and MIS 31 (Snyder et al., 2013). Shifts in dominance occur during cold intervals suggesting extended ice cover, reducing plankton abundance (Snyder et al., 2013). However, there are also long intervals with stable plankton assemblages suggesting some cold intervals are more extreme. Uncertainty remains in determining how climate-driven changes in the lake system drive these shifts.
Figure 2: The Lake El’gygytgyn diatom record spanning the last 1.2 Ma (from Snyder et al., 2013).
OBJECTIVES

Previous analyses demonstrate changes in the planktonic and periphytic diatom assemblages that correspond to climatic events. This study explores diatom species response to climatic events to better understand the linkage between climate and diatoms in the Lake El’gygytgyn record. For example, one hypothesis for extremely low productivity intervals is extended complete ice cover, limiting the light availability. These events may affect different habitats differently depending on the nature of the ice extent.

To further explore the diatom-climate connection, a systematic investigation of diatoms in different habitats spanning the last 1.2 Ma was performed. Two genera, planktonic *Cyclotella* and benthic *Surirella* were used as examples. *Cyclotella* is the most consistently dominant planktonic genus since 1.2 Ma. Some examples of *Surirella* from the lake are extremely large (commonly exceeding 100 µm) making it easier to find within the relatively low abundance, high diversity benthic fauna. The results of this research contribute to a greater understanding of the El’gygytgyn climate record, and provide a unique data set for understanding diatom evolution and endemism in lake systems.

This thesis is organized into four main chapters, with chapters II &III intended as stand-alone publications. Chapter II focuses on the planktonic genus *Cyclotella*. Chapter III focuses on the large *Surirella*. The final chapter discusses the two genera in relationship to one another, the Lake El’gygytgyn paleoclimate record, and to other diatom morphological analyses.
CHAPTER II: CYCLOTELLA

INTRODUCTION

Diatoms within lakes serve as a powerful proxy for paleoclimatic reconstructions due to their environmental sensitivity (Douglas & Smol, 2010). Arctic lakes are particularly sensitive to climate changes, and extensive or long-lived diatom records within these lakes are rare. The majority of diatom based studies performed in the Arctic are limited to the last few centuries or millennia of environmental change (Douglas & Smol, 2010). Arctic diatom records before the Late Pleistocene are scarce because of multiple glaciations (Douglas & Smol, 2010).

One of the most important members of the freshwater Arctic and subarctic diatom flora is the planktonic genus *Cyclotella* (Schlegel & Scheffler, 1999; Cremer et al., 2005; Cherepanova et al., 2007; Genkal et al., 2008; Cherepanova et al., 2010; Genkal et al., 2010; Genkal & Popovskaya, 2011; Snyder et al., 2013). At species level, there is considerable morphological variability, making it difficult and often controversial to determine taxonomic placement. Morphological studies have been performed on multiple species, for example *Cyclotella atomus* Hustedt (Genkal & Kiss, 1993), *Cyclotella comensis* Grunow (Hausmann & Lotter, 2001), *Cyclotella ocellata* Pantocsek (Cherepanova et al., 2010), and *Cyclotella bodanica* Eulenstein (Genkal et al., 2013). Species variations are sometimes referred to as “morphotypes” or “morphs”; however, determining whether there are multiple morphotypes of a species, or a different singular species has been argued. Specifically, the *C. ocellata*-complex has been scrutinized. One argument separates *C. ocellata*, *Cyclotella rossii* Håkansson, and *Cyclotella krammeri* Håkansson into individual species, while the other places *C. rossii* and *C. krammeri* into the *C. ocellata* complex (Cremer et al., 2005). This variability needs to be studied further in order to clarify taxonomic placements and evolutionary trends.
Changes in the species assemblage and morphological variability within species can occur due to sensitivities in light availability, nutrient availability, seasonal ice cover, temperature, and pH. For example, a study performed by Saros & Anderson (2015), from two lakes in the Kengerlussuaq, analyzes the effects of light availability and incubation depth on *Puncticulata radiosa* (Grunow) and *Discostella stelligaria* (Cleve & Grunow). The study reveals that *P. radiosa* is found more abundantly in shallow incubation depths, while *D. stelligaria* responds more strongly to nutrient increases (Saros & Anderson, 2015). This observation suggests that light availability and nutrient conditions are both potentially important in regulation of the growth of small centric diatoms in Arctic lakes (Saros & Anderson, 2015).

This idea is further supported by Rühland et al. (2008) who performed a meta-analysis of ~140 sites containing *Cyclotella*. The widespread increase of this genus within the northern hemisphere is attributed to warmer temperatures regionally and longer ice-free periods, which increases the amount of light available (Saros & Anderson, 2015).

Lake El’gygytgyn, in its recent history, has a planktonic diatom population dominated numerically by *Cyclotella* (Snyder et al., 2013). In the modern community, multiple species of *Cyclotella* are recorded including *C. ocellata*, *Cyclotella tripartita* Håkansson, *Cyclotella arctica* Genkal & Kharitonov, and *Cyclotella dubius* Fricke (Cremer & Wagner, 2003; Cremer et al., 2005; Kharitonov & Genkal, 2010). Prior to ~1.2 ka, *Cyclotella* is observed only sporadically within the core record. Multiple morphologies and species shifts occur from core sediments spanning the last 1.2 Ma (Cherepanova et al., 2010). Lake El’gygytgyn provides a unique data set for studying the morphological variability of *Cyclotella* species due to its long continuous record (1.2 Ma) and low levels of dissolution.
This study focuses on the genus *Cyclotella* in core sediment samples extending to 1.2 Ma. Core intervals with abundant *Cyclotella* observed in preliminary light microscope investigations are analyzed in detail using scanning electron microscopy and light microscopy for morphology and ultrastructure. These observations provide a unique record of *Cyclotella* variation in a long-lived lake and are used to better understand the Lake El’gygytgyn paleoclimate record.

**TAXONOMIC BACKGROUND**

The genus *Cyclotella* (Kützing) Brébisson is one of three members of the family Stephanodiscaceae Glezer & Makarova (see Round et al., 1990). Recently, some species previously within the *Cyclotella* genus, specifically the *Cyclotella comta* Kützing group and those with *C. ocellata* characteristics, have been transferred to the genus *Lindavia* (Nakov et al., 2015). These species have been transferred to *Lindavia* based on the characteristic of having one or more rimoportula on the valve face (Nakov et al., 2015). The present study refers to the species as members of the *Cyclotella* genus, but the *Lindavia* classification may be substituted (see Appendix A for list of synonyms).

Morphological variability within the genus *Cyclotella* creates taxonomic controversy at the species level. Disputes occur over whether certain claimed species are variations or part of a morphological continuum of one or two species. The following section analyzes some *Cyclotella* species that have been recorded within the Lake El’gygytgyn record, as well as some that have been regarded as part of a morphological continuum within the species *C. ocellata* Pantocsek.

*C. ocellata* Pantocsek demonstrates an extremely wide range of morphological variability (Håkansson, 1993; Schlegel & Scheffler, 1999; Knie & Hübener, 2007; Cherepanova et al.,
The characteristics of this species are similar to several other species (Table 1). *C. ocellata* has a circular valve with a diameter of 5-22 µm with fine striae of 14-20/10 µm that are often of unequal lengths (Houk et al., 2010). Marginal fultoportulae are found every 2-5 costae accompanied by two satellite pores; there are 1-4(5) central fultoportulae also accompanied by two or three satellite pores (Houk et al., 2010). Usually one rimoportula is located within the marginal area of the valve with a sessile labium, a relatively short slit, and oblique to radially oriented (Houk et al., 2010). The central area pattern externally smooth to colliculate, with 3-6 large depressions; ornamentation may be present in the form of ball-like granules (Houk et al., 2010). Many other species have been classified as a variation, “morphotype” or “morph” of *C. ocellata*, and are referenced as the *C. ocellata*-complex.

Cherepanova et al. (2010) performed a morphological analysis of the *C. ocellata*-complex within Lake El’gygytgyn spanning the last ~250 ka. This study included *C. tripartita*, *Cyclotella kuetzingiana* Thwaites, and *C. arctica* as a complex that developed from phenotypic selection. The *C. ocellata kuetzingiana*-morphotype was gradually replaced by the *ocellata*-morphotype, which was replaced by the *arctica* morphotype (Cherepanova et al., 2010). The *tripartita*-morphotype was also found, although the authors did not include this in the phenotypic continuum. Similarly, Genkal & Popovskaya (2011) performed an analysis on *Cyclotella* morphology within Lake Khubsugul, Mongolia. The study concluded that there were several morphotypes present within the population dominated by the *ocellata* morphotype, and they further concluded that all of the morphologies present were part of the *C. ocellata* species.

The morphotypes discussed by Cherepanova et al. (2010) and Genkal & Popovskaya (2011) all have differences and similarities with *C. ocellata*. *C. tripartita* differs from *C.
ocellata in that it has a smaller valve diameter (2-18 µm), a larger number of striae per 10/µm, marginal fultoportulae every 3-5(7) costae, and (1)2-3 central fultoportulae (Houk et al., 2010). However, the most distinctive characteristic of C. tripartita is the central area pattern, which is strongly radially undulate divided into 6 sections (3 elevations, 3 depressions) with fultoportulae situated within the depressions (Houk et al., 2010). C. kuetzingiana differs greatly in the maximum range of valve diameter (8-45 µm), while the striae/10 µm and the marginal fultoportulae placement, and central fultoportulae are similar. The central area pattern in C. kuetzingiana is also similar; however, the depressions are shallow and may be arranged in radial rows (Houk et al., 2010). Finally, C. arctica has a much smaller valve diameter (3-11 µm) than C. ocellata, and has a larger number of striae/10 µm (24-32), with marginal fultoportulae every 4-8 costae, and a smaller number of central fultoportulae (Houk et al., 2010). All three of these morphotypes have similarities and overlaps, but contain at least one distinct difference from C. ocellata (sensu stricto).

Duleba et al. (2015) further complicate the taxonomy of Cyclotella species by including C. comensis within the morphological spectrum of the C. ocellata morphology. Their study includes morphs of ‘ocellata’, ‘trichonidea’, ‘comensis’, pseudocomensis’, and ‘costei’ as distinguished through morphometric and molecular analysis (Duleba et al., 2015). A sixth group is also distinguished as transitional forms between the above constituted morphs (Duleba et al., 2015). The study concludes that, along with the recent majority of morphological analyses, the C. ocellata complex consists of diverse related species of C. ocellata, C. rossii, C. tripartita, C. kuetzingiana, and Cyclotella polymorpha Meyer & Håkansson. A distinction is drawn between C. ocellata and C. comensis based on the morphometric parameters used, and the slight
molecular phylogenetic separation (Duleba et al., 2015), indicating closely related species with a recent evolutionary divergence (Duleba et al., 2015).

Although *C. comensis* and *C. ocellata* are treated separately, their morphology is similar. The valve diameter (4-15 µm), the striae (16-22/10 µm), and the marginal fultoportulae (every 2-4 costae) are similar to *C. ocellata* (Houk et al., 2010). The central area pattern exhibits the largest difference between the two. The central area is transversally undulate, with radially positioned bulges or bumps creating an irregular star shape, and it has distinct large depressions of unequal size between the lobes (Houk et al., 2010). *C. comensis* tends to have a single central fultoportula situated on the external concave undulation, while *C. ocellata* may have more central fultoportulae that exhibit no distinct orientation.

*Cyclotella pseudocomensis* Scheffler and *Cyclotella costei* Druart & Straub have an uncertain species status in relationship to *C. comensis*. These species have been referred to as part of the same complex (Kistenich et al., 2014). They most likely each express a smaller portion of a morphological spectrum within a single species (*C. comensis*) (Kistenich et al., 2014). Morphometric and molecular analyses have also been performed on this morphological complex, showing *C. comensis* is a closely related species to *C. ocellata* (Duleba et al., 2015).

*C. comensis*, *C. pseudocomensis*, and *C. costei* all have valve diameters and the number of central fultoportulae in common. The striae/10 µm is larger in both *C. pseudocomensis* and *C. costei* (20-26 and 20 respectively) in comparison to *C. comensis*. A distinguishing feature of *C. pseudocomensis* is the larger distance between marginal fultoportulae at every 3-6(9) costae, while *C. comensis* and *C. costei* lie within a similar range.
Table 1: Characteristics of *Cyclotella* species of controversial taxonomy as described in Houk et al. (2010) and Genkal & Popovskaya (2011)

<table>
<thead>
<tr>
<th><em>Cyclotella</em> Species</th>
<th>Valve Diameter (µm)</th>
<th>Striae in 10 µm</th>
<th>Marginal Fultoportulae (MF)</th>
<th>Central Area Pattern</th>
<th>Central Fultoportulae (CF)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. ocellata</em></td>
<td>5-22</td>
<td>14-20</td>
<td>2-5 costae</td>
<td>Flat to colliculate with 3 to 6 large depressions</td>
<td>1 to 4(5)</td>
</tr>
<tr>
<td><em>C. kuetzingiana</em></td>
<td>8-45</td>
<td>12-18</td>
<td>2-4(5) costae</td>
<td>Transversally undulate to nearly flat with short radial rows of depressions</td>
<td>1-5(7)</td>
</tr>
<tr>
<td><em>C. polymorpha</em></td>
<td>4.5-45</td>
<td>(16)-18-20(24)</td>
<td>2-5 costae</td>
<td>Variable from radial rows of depressions to 1-5 large depressions</td>
<td>1-5(7) radially scattered</td>
</tr>
<tr>
<td><em>C. tripartita</em></td>
<td>2-18</td>
<td>19-22</td>
<td>3-5(7) costae</td>
<td>Colliculate, radially undulate divided into 3 elevations and 3 depressions</td>
<td>(1)2-3 situated in depressions</td>
</tr>
<tr>
<td><em>C. rossii</em></td>
<td>5-18</td>
<td>16-18</td>
<td>2-3(5) costae</td>
<td>Flat to colliculate with 2-8 radial rows of puncta</td>
<td>2-3(5)</td>
</tr>
<tr>
<td><em>C. arctica</em></td>
<td>3-11</td>
<td>24-32</td>
<td>4-8 costae</td>
<td>Several large depressions or radially divergent ribs, sometimes pitted or tubercular</td>
<td>2</td>
</tr>
<tr>
<td>Cyclotella Species</td>
<td>Valve Diameter (µm)</td>
<td>Striae in 10 µm</td>
<td>Marginal Fultoportulae (MF)</td>
<td>Central Area Pattern</td>
<td>Central Fultoportulae (CF)</td>
</tr>
<tr>
<td>-------------------</td>
<td>---------------------</td>
<td>----------------</td>
<td>-----------------------------</td>
<td>---------------------</td>
<td>---------------------------</td>
</tr>
<tr>
<td>C. comensis</td>
<td>4-15</td>
<td>16-22</td>
<td>2-4(5) costae</td>
<td>Transversal with radially positioned large bumps and depressions</td>
<td>1-2</td>
</tr>
<tr>
<td>C. pseudocomensis</td>
<td>4-15</td>
<td>20-26</td>
<td>3-6(9) costae</td>
<td>Transversally undulate, colliculate, with depressions of unequal size and scattered in radial rows</td>
<td>1-2</td>
</tr>
<tr>
<td>C. costei</td>
<td>4-17</td>
<td>20</td>
<td>2-5(7) costae</td>
<td>Nearly flat, externally smooth or colliculate</td>
<td>(0)1-2</td>
</tr>
</tbody>
</table>
METHODS

A systematic analysis of *Cyclotella* valves spanning the last ~1.2 Ma (composite core depths 0.005 m to 51.017 m) was performed using light microscopy (LM) and scanning electron microscopy (SEM). Sample pretreatments for microscope analyses followed standard procedures developed for the Lake El’gygytgyn sediments (Battarbee, 1974; Scherer, 1994) (see Appendix A). SEM cover slips were sputter coated with gold palladium. LM analyses were performed using a Leica DMLB, with differential interference contrast, and a DFC 425 digital camera was used to take images and measurements. SEM analyses were performed at the University of Toledo using the Hitachi S-4800; SEM measurements were taken using the tpsDig program.

A total of 234 slides were viewed in LM. Thirty-six of these samples were selected for detailed analysis on the basis of preliminary observations of high abundance and observed morphological variation. Morphometric features were observed using both SEM and LM (Table 2, Figure 3). Quantitative morphological features analyzed in LM included total valve diameter, central area diameter, and striae per 10 µm. A total of 50 valve diameter and central area diameter measurements and 25 striae counts were taken along a slide transect. SEM images (20 for each interval) were taken of both the internal (10) and external (10) valves. Observed features of the external valves included measurements of total valve diameter and central area diameter, striae per 10 µm, number/pattern of orbiculi depressi, number of central fultoportulae, rimoportulae placement, and central area undulation. Observed features of the internal valves included measurements of total valve diameter, number of central fultoportulae, number/placement of marginal fultoportulae, number of costae, and placement/orientation of rimoportula. These features were used to divide the record into intervals based on the dominant
“type” or “types” of *Cyclotella* observed. Microsoft Excel and PAST (Paleontological Statistics) were used for statistical analyses.
Table 2: Summary of morphological characteristics recorded LM, SEM external valve, and SEM internal valve images

<table>
<thead>
<tr>
<th></th>
<th>LM</th>
<th>SEM External</th>
<th>SEM Internal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Valve Diameter</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Central Area Diameter</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Central Area Undulation</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Orbiculi Depressi</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Striae/10 µm</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Number of Costae</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Number of Central Fultoportulae</td>
<td></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Number of Marginal Fultoportulae</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Rimoprtula Orientation/Placement</td>
<td></td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>
Figure 3: *Cyclotella* morphological features of interest (A: total valve diameter, B: central area diameter, C: striae, D: orbiculi depressi, E: central fultoportulae, F: rimoportula, G: costae, H: marginal fultoportulae).
RESULTS

The *Cyclotella* population within the samples varies throughout the last ~1.2 Ma (Table 3 & 4). Observed valve diameter ranges from a minimum of 1.3 µm to a maximum of 31.2 µm with sample mean values ranging from a minimum of 6.7 µm to a maximum of 12.7 µm (Appendix B, Table B1). The central area diameter ranges from 1.3 µm to 16.4 µm with sample mean values ranging from 2.8 µm to 6.7 µm. The ratio of these two values ranges from 0.2 to 0.8 with mean values ranging from 0.4 to 0.7. The following sections present the eight intervals defined by observed morphological features, organized from the first abundant occurrence of *Cyclotella* to the recent record (Figure 4).
Figure 4: *Cyclotella* concentration (valves/gram) (Snyder et al., 2013), plotted with 65°N June insolation (Laskar et al., 2004), and the marine isotope stack (Lisiecki & Raymo, 2005); Blue lines and capital letters designate time intervals with different types as described in Table 3 and 4 (gray color indicates times of low *Cyclotella* concentration).
Table 3: Summary of quantitative morphological characteristics of the different dominant *Cyclotella* “types” spanning the last ~1.2 Ma (CF: central fultoportulae, MF: marginal fultoportulae)

<table>
<thead>
<tr>
<th>Time Interval (ka)</th>
<th>Sampled Time Periods (ka)</th>
<th>Valve Diameter (µm)</th>
<th>Central Area Diameter (µm)</th>
<th>Striae/10 µm</th>
<th>Number CF</th>
<th>Number MF</th>
<th>Number Costae</th>
<th>MF/Costae</th>
<th>Zone</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recent - 182</td>
<td>0.075, 1.3, 24.7, 41</td>
<td>3.9-17.8</td>
<td>1.6-7.33</td>
<td>17-27</td>
<td>1-3</td>
<td>8-27</td>
<td>41-86</td>
<td>1 to 4</td>
<td>I</td>
</tr>
<tr>
<td></td>
<td>57.2, 70.2, 94.8, 123.4, 138.3, 159.7</td>
<td>2.7-22.9</td>
<td>1.6-9.4</td>
<td>13-32</td>
<td>1-8</td>
<td>3-24</td>
<td>21-76</td>
<td>2 to 5</td>
<td>I</td>
</tr>
<tr>
<td>187 – 222.9</td>
<td>190.5, 198.2, 214.2</td>
<td>3.8-31.2</td>
<td>1.9-16.4</td>
<td>14-27</td>
<td>1-23</td>
<td>6-40</td>
<td>22-111</td>
<td>1 to 2(3)</td>
<td>H</td>
</tr>
<tr>
<td>227.9 – 554.8</td>
<td>238.5, 250.9, 278.8, 302.5, 318.7, 333.2, 390.5, 406.7, 417.4, 436.4, 448.3, 484.1, 503.2</td>
<td>3.2-27.5</td>
<td>1.6-13.2</td>
<td>12-28</td>
<td>1-23</td>
<td>3-35</td>
<td>22-96</td>
<td>1 to 3 or 3 to 6</td>
<td>G</td>
</tr>
<tr>
<td>513 – 554.8</td>
<td>554.8</td>
<td>3.2-16.1</td>
<td>1.7-5.7</td>
<td>14-25</td>
<td>1-5</td>
<td>4-10</td>
<td>27-53</td>
<td>3 to 6(7)</td>
<td>F</td>
</tr>
<tr>
<td>612.1 – 676.4</td>
<td>665</td>
<td>5.4-18.3</td>
<td>2.9-10.6</td>
<td>15-24</td>
<td>3-10</td>
<td>13-22</td>
<td>39-74</td>
<td>1 to 2(4)</td>
<td>E</td>
</tr>
<tr>
<td>688.4 – 707.5</td>
<td>696</td>
<td>4.9-16.1</td>
<td>2.0-5.7</td>
<td>14-25</td>
<td>2-8</td>
<td>11-28</td>
<td>31-68</td>
<td>1 to 3</td>
<td>D</td>
</tr>
<tr>
<td>996.2 – 925.7</td>
<td>952.6, 973.5, 987.5</td>
<td>4.4-18.9</td>
<td>2.5-9.6</td>
<td>13-31</td>
<td>1-11</td>
<td>7-24</td>
<td>30-85</td>
<td>2 to 4</td>
<td>C</td>
</tr>
<tr>
<td>1002.6 – 1029</td>
<td>1029</td>
<td>4.8-12.3</td>
<td>3.5-7.6</td>
<td>18-28</td>
<td>1-5</td>
<td>6-14</td>
<td>35-62</td>
<td>(2)3 to 6</td>
<td>B</td>
</tr>
<tr>
<td>1104 - 1126</td>
<td>1108.8, 1113.5, 1126</td>
<td>4.2-10.8</td>
<td>2.4-4.5</td>
<td>14-19</td>
<td>1-5</td>
<td>9-29</td>
<td>23-55</td>
<td>(0)1 to 2</td>
<td>A</td>
</tr>
</tbody>
</table>
Table 4: Summary of qualitative morphological characteristics of the different dominant *Cyclotella* “types” spanning the last ~1.2 Ma

<table>
<thead>
<tr>
<th>Time (ka)</th>
<th>Central Area Pattern</th>
<th>Rimoprotula Position</th>
<th>Rimoprotula Orientation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recent - 182</td>
<td>The central area during this time period is highly variable: all are flat to colliculate, the depressi range from 3-6 large depressi, 1-5 small depressi, or radially positioned small to large depressi</td>
<td>Central margin to the ring of the costae</td>
<td>Radial to oblique</td>
</tr>
<tr>
<td>187 – 222.9</td>
<td>Flat to colliculate with granules and irregular small depressi/puncta; central fultoportulae irregularly positioned on the entire valve face</td>
<td>Two rimoportulae positioned on the central area to central margin</td>
<td>Radial to slightly oblique</td>
</tr>
<tr>
<td>227.9 – 503.2</td>
<td>Flat to colliculate with 3-4 larger depressi or radially oriented smaller depressi; central fultoportulae situated within the depressi</td>
<td>Central margin to the ring of the costae</td>
<td>Radial to slightly oblique</td>
</tr>
<tr>
<td>513 – 554.8</td>
<td>Flat to colliculate with puncta located on the margin</td>
<td>Central area to central margin</td>
<td>Radial to oblique</td>
</tr>
<tr>
<td>612.1 – 676.4</td>
<td>Flat with small radiating depressi, puncta, and granules</td>
<td>Central margin</td>
<td>Radial</td>
</tr>
<tr>
<td>688.4 – 707.5</td>
<td>Flat with puncta located on the margin</td>
<td>Central margin</td>
<td>Radial to oblique</td>
</tr>
<tr>
<td>996.2 – 925.7</td>
<td>Flat to colliculate with radial small to large depressi, puncta may be present; central fultoportulae are radially oriented</td>
<td>Central area</td>
<td>Radial</td>
</tr>
<tr>
<td>1002.6 - 1029</td>
<td>Flat to colliculate with scattered small depressi; puncta may be present; central fultoportulae are oriented radially</td>
<td>Central margin</td>
<td>Radial to oblique</td>
</tr>
<tr>
<td>1104 - 1126</td>
<td>Flat to colliculate with depressi of unequal size irregularly positioned</td>
<td>Central margin</td>
<td>Radial to oblique</td>
</tr>
</tbody>
</table>
1200 ka to 1126 ka

The first observed occurrence within the ~1.2 Ma record occurs within a sample viewed at 1189.4 ka. This interval exhibits low preservation and high levels of dissolution. *Cyclotella* is also viewed in very low concentrations during this time period. The low preservation and low concentration combined make describing the dominant *Cyclotella* morphology difficult. Some valves were viewed in SEM, and exhibit a colliculate central area with small depressi and 1-2 central fultoportulae. Measurements of total valve diameter, central area diameter and the number of striae/10 µm were not calculated for this interval; however, SEM samples generally show evidence of smaller valve sizes of <10 µm.

1126 ka to 1104 ka (Zone A)

The first interval studied with abundant, well-preserved *Cyclotella* occurs at 1126 ka to 1104 ka (Figures 5-10). The type present within this time interval has a total valve diameter ranging from 4.2 µm to 10.8 µm; the central area diameter ranges from 2.4 µm to 4.5 µm and accounts for 31% to 66% of the total valve diameter. The striae/10 µm range from 14-19. The central area pattern is flat to colliculate with depressi of unequal sizes scattered throughout. The central fultoportulae range from 1-5 with 2 satellite pores. The marginal fultoportulae range from 9-29, and the costae range from 23-55 with marginal fultoportulae situated on every (0)1-2 costae. The single rimoportula is positioned along the central margin to just on the marginal area. The rimoportula opening is radially oriented with no sessile labium.

The measurements of total valve diameter, central area diameter, and striae/10 µm support the similarities between the viewed samples with only minor differences in the size of the central area between 1126.0 ka to 1113.5 ka (Appendix B, Figure B1). The continued
similarity in total valve diameter, striae/10 µm, central area pattern, number of central and marginal fultoportulae, number of costae, number of marginal fultoportulae/costa, and the placement of the rimoportula implies that these intervals share the same *Cyclotella* type. Valves within this interval exhibit varying levels of dissolution, particularly within the central area and the striae.
Figures 5-10: Interval 1126 ka to 1104 ka (Zone A) *Cyclotella* type; Fig. 5, 7, 9: SEM external valve view; Fig. 6: LM photograph 1126 ka; Fig. 8: LM photograph 1113.5 ka; Fig. 10: SEM internal valve view (D: depressi, R: rimoportula, CF: central fultoportulae).
1029 ka to 1002.6 ka (Zone B)

At ~1029.0 ka the dominant *Cyclotella* type differs, and the previous type is no longer observed within the record (Figures 11-16). This type has a total valve diameter ranging from 4.8 µm to 12.3 µm with a central area diameter ranging from 3.5 µm to 7.6 µm, accounting for 58% to 79% of the total diameter. Striae/10 µm range from 18-28. The central area pattern is flat to colliculate with some valves transversally undulate and scattered small depressi. Some valve central areas also contain small numbers of punctae. The central fultoportulae range from a minimum of 1 to a maximum of 5 with 2-3 satellite pores, and are radially distributed. The marginal fultoportulae range from 6 to 14 with 2 satellite pores, and the costae range from 35-62 with marginal fultoportulae situated on every (2)3-6 slightly depressed costae. The single rimoportula is located on the valve face margin. The rimoportula is radial to oblique in orientation with an opening with no sessile labium to a partial sessile labium.

The interval from 1029 ka to 1002.6 ka exhibits differences from the previous interval in valve diameter, central area diameter, and striae/10 µm. Valve diameter increases during this time period reaching a high of 18.9 µm, with the previous time interval only reaching 10.8 µm. Central area diameter also increases with the largest 7.6 µm compared to 4.5 µm during the previous time interval. The striae/10 µm shows a great increase in the number of striae/10 µm; it previously ranged from 14-19, while this interval ranges from 18-28. Differences are also observed in marginal fultoportulae number, number of costae, and marginal fultoportulae/costae. The number of marginal fultoportulae exhibits a lower range within this interval with values of 6-14 in comparison to values of 9-29 in the previous interval. The number of costae increases within this interval in comparison to the previous time interval (23-55 and 35-62, respectively). The number of marginal fultoportulae/costae are not as close in their distribution with Zone B.
containing (2)3-6 marginal fultoportulæ/costae, while the interval from Zone A contains 1-2 marginal fultoportulæ/costae.
Figures 11-16: Interval 1029 ka to 1002.6 ka (Zone B) *Cyclotella* types: Fig. 11-13: SEM external valve view; Fig. 14: SEM internal valve view; Fig. 15-16 LM photographs 1029 ka (CD: central diameter, D: depressi, CF: central fultoportulae, R: rimoportulae).
996.2 ka to 925.7 ka (Zone C)

The dominant *Cyclotella* morphology observed from 996.2 ka to 925.7 ka differs after an interval with low *Cyclotella* abundance (Figures 17-22). The total valve diameter ranges from 4.4 µm to 18.9 µm. The central area diameter ranges from 2.5 µm to 9.6 µm, accounting for 32% to 82% of the total valve diameter. The striae/10 µm ranges from 13 to 31. The central area pattern is flat to colliculate with radial small to large depressi and puncta. The central fultoportulae range from 1-11 with 2-3 satellite pores and are radially oriented. The marginal fultoportulae range from 7-24 with 2 satellite pores, and the costae range from 30-85 with marginal fultoportulae situated on every 2-4 slightly depressed costae. A single rimoportula is located in the central area. The rimoportula orientation is radial with no sessile labium to a partial sessile labium.

The interval from 996.2 ka to 925.7 ka (Zone C) differs from the interval at 1029 ka to 1002.6 ka (Zone B) in striae/10 µm, central area pattern, central fultoportulae, marginal fultoportulae, and marginal fultoportulae/costae. The striae/10 µm increases in this interval, with numbers reaching a maximum of 31, while the previous interval (Zone B) exhibited lower numbers. The central area pattern exhibits a distinct change from the Zone B to Zone C; Zone C exhibits a radial distribution of small to large depressi, while Zone C exhibits scattered small depressi. The central fultoportulae number greatly increases within this interval ranging from 1-11, where it previously ranged from 1-5 in Zones A and B. The marginal fultoportulae number exhibits a higher maximum of 24 within this interval, while the previous maximum in Zone B is 14. The marginal fultoportulae/costae also is different with Zone B ranging from (2)3-6 marginal fultoportulae/costae and Zone C ranging from 2-4 marginal fultoportulae/costae.
Figures 17-22: Interval 996.2 ka to 925.7 ka (Zone C) Cyclotella types: Fig. 17-19: SEM external valve view; Fig. 20: SEM internal valve view; Fig. 21: LM photograph 987.5 ka; Fig. 22: LM photograph 973.5 ka (D_s: small depressi, D_l: large depressi, CF: central fultoportulae).
707.5 ka to 688.4 ka (Zone D)

A sample was viewed during a period of lower *Cyclotella* abundance at 780 ka. This sample exhibits low preservation and high levels of dissolution. The sparse *Cyclotella* concentration also makes it difficult to observe the dominant morphological type. For these reasons an in depth morphological description is not possible within this time period.

After this interval of low abundance, the dominant morphology observed from 707.5 ka to 688.4 ka differs from that observed in 1029 ka to 925.7 ka (Figures 23-28). This type has a total valve diameter ranging from 4.9 µm to 16.1 µm. The central area diameter ranges from 2 µm to 5.7 µm, accounting for 22% to 54% of the total valve diameter. The striae/10 µm ranges from 14 to 25. The central area pattern is flat with either no depressi, or small depressi located on the central area margin. The central fultoportulae range from 2 to 8 with 2-3 satellite pores with no distinct pattern of distribution. The marginal fultoportulae range from 11 to 28 with 2 satellite pores, and the costae range from 31 to 68 with marginal fultoportulae situated on every 1-3 slightly depressed costae. A single rimoportula is located on the central marginal area. The rimoportula orientation is radial to oblique with no sessile labium to a partial sessile labium

This interval is considered to be a different *Cyclotella* type based on its distinctive central area diameter, the slight difference in the number of striae/10 µm, and the extreme change in the central area pattern (Appendix B, Figure B1). The total valve diameter remains relatively similar between these two time intervals; however the central area diameter decreases slightly, with a lower value of 5.7 µm. The striae/ 10 µm exhibits a smaller range from 14-25. Perhaps the most distinct difference is within the central area, which no longer contains a large number of small or large depressi, is flat, much smaller, and contains no radiating patterns of depressi, puncta. The central fultoportulae, marginal fultoportulae, and costae values recorded all exhibit smaller
ranges that lie within the range of the previous time interval. However, the marginal fuloportulae/costae exhibit much lower variability in this interval.
Figures 23-28: Interval 707.5 ka to 688.4 ka (Zone D) Cyclotella types: Fig. 23-25: SEM external valve view; Fig. 26: SEM internal valve view; Fig. 27-28: LM photographs 696 ka (CD: central diameter, CF: central fultoportulae).
676.4 ka to 612.1 ka (Zone E)

The dominant *Cyclotella* type within the sample at 665.0 ka is a type similar to those observed from 1029.0 ka to 956.2 ka (Zone B) (Figures 29-34). The total valve diameter ranges from 5.4 µm to 18.3 µm. The central area diameter ranges from 2.9 µm to 10.6 µm accounting for 41% to 64% of the total valve diameter. The number of striae/10 µm range from 15 to 24. The central area pattern is flat with small radiating depressi, puncta, and small radiating granules. The central fultoportulae number range from 3 to 10 with 2-3 satellite pores. The marginal fultoportulae range from 13 to 22 with 2 satellite pores, and the costae range from 39 to 74 with marginal fultoportulae on every 1-2(4) slightly depressed costae. The single rimoportula is located along the central margin; the rimoportula orientation is radial with no sessile labium to a partial sessile labium.

The main difference from the previous interval is evident in central area diameter, central area pattern, and the orientation of the rimoportula (Appendix B, Figure B1). The central area diameter is larger within this interval, with a maximum of 10.6 µm, compared to 5.7 µm within the previous interval. The striae/10 µm and the number of central fultoportulae are similar between the two time intervals. The marginal fultoportulae/costae remains relatively similar. The central area exhibits a distinctive radiating pattern of small depressi, puncta, and granules. The previous interval contains no evidence of granule ornamentation, depressi, or puncta.
Figures 29-34: Interval 676.4 ka to 612.1 ka (Zone E) *Cyclotella* types: Fig. 29-31: SEM external valve view; Fig. 32: SEM internal valve view; Fig. 33-34: LM photographs 665 ka (Dₚ: small depressi, CF: central fultoportulae).
**554.8 ka to 513ka (Zone F)**

A new morphological type is present from 554.8 ka to 513 ka exhibiting distinct
differences from the previous interval observed (Figures 35-40). This type has a total valve
diameter ranging from 3.1 µm to 16.1 µm. The central area diameter ranges from 1.7 µm to 5.7
µm accounting for 22% to 69% of the total valve diameter. The number of striae/10 µm range
from 17 to 25, similarly to previous interval at 665 ka. The central area pattern is flat to
colliculate with some valves containing puncta or small depressi along the central area rim. The
central fultoportulae range from 1 to 5 with 2-3 satellite pores. The marginal fultoportulae range
from 4 to 10, and the number of costae range from 27 to 53 with marginal fultoportulae situated
on every 3-6(7) costae. The single rimoportula is positioned along the central margin, and is has
radial to oblique orientation. The rimoportula has a single opening with no sessile labium.

The time interval 554.8 ka to 513 ka (Zone E) shows differences in nearly all
morphological features analyzed in comparison to the interval at 667.4 ka to 612.1 ka (Zone E)
(Appendix B, Figure B1). The interval described here has smaller valve diameter (3.2-16.1 µm)
and smaller central area diameter (1.7-5.7 µm). The central area pattern also differs greatly.
Where the previous interval exhibits a radiating pattern of depressi and puncta (Figures 20-21),
this interval contains no distinct radial pattern, a central area that is flat to colliculate, and
irregularly distributed puncta (Figures 22-23). The type exhibited in this interval is similar to
that seen within interval 707.5 ka to 688.4 ka (Zone C), with the exception of the central area of
some valves being colliculate.
Figures 35-40: Interval 554.8 ka to 513 ka (Zone F) *Cyclotella* types: Fig. 35-37: SEM external valve view; Fig. 38: SEM internal valve view; Fig. 39-40: LM photograph 554.8 ka.
503.2 ka to 227.9 ka (Zone G)

The type present within this interval persist for the longest period of time within the ~1.2 Ma record (Figures 41-52). The total valve diameter ranges from 3.2 µm to 27.5 µm, exhibiting the largest valves up to this point in the record. The central area diameter ranges from 1.6 µm to 13.2 µm and accounts for 25% to 72% of the total valve diameter. The number of striae/10 µm range from 12 to 28. The central area pattern is flat to colliculate with 3 to 4 larger depressi or radially oriented smaller depressi. The central fultoportulae range from 1 to 23 with 2 to 3 satellite pores. The central fultoportulae are oriented in radial groupings situated within the larger depressi. The marginal fultoportulae range from 3 to 35 with 2 satellite pores, and the costae range from 22 to 96. The most variable morphological feature within this type interval is found within the situation of the marginal fultoportulae/costae. Some intervals exhibit marginal fultoportulae every 1-3 costae, while other intervals exhibit marginal fultoportulae every 2-5 costae. Specimens from each interval observed contain 2 satellite pores, however, and the marginal fultoportulae were situated on every slightly depressed costae. The single rimoportula is placed mostly along the central margin, with some placed within the ring of costae. The rimoportula orientation is radial to slightly oblique with a partial sessile labium to a developed sessile labium.

From 503.2 ka to 462.1 ka a transitional form of this morphological Cyclotella type occurs (Figures 41-46). The total valve diameter ranges from 3.8 µm to 17.1 µm. The central area ranges from 1.6 µm to 6.4 µm, accounting for 26% to 58% of the total valve diameter. The number of striae/10 µm ranges from 15 to 26. The central area pattern is flat with 3 to 4 large depressi or groups of smaller depressi. The central fultoportulae range from 2 to 11 with 2-3 satellite pores. In some valves the central fultoportulae are found in groupings near or within the
larger depressi. The marginal fultoportulae range from 5 to 16, and the costae range from 26 to 72 with marginal fultoportulae situated on every 3-6 costae. The single rimoportula is located within the central area or the central margin. The rimoportula orientation is radial to slightly oblique with a partial sessile labium to a developed sessile labium.

Comparing Zone G as a whole to the previous Zone F, differences occur in the number of striae/10 µm, the central area pattern, number of central fultoportulae, number of marginal fultoportulae, and the number of costae (Appendix B, Figure B1). The total valve diameter, central area diameter, and central area diameter/valve diameter ratios are similar in Zones G and F. The number of striae/10 µm within Zone G is higher than Zone F, with Zone F ranging from 14-25 with most values lying in the range of 15-21, and Zone G ranging from 12-28, with most values lying in the range of 18-23. The striae/10 µm remains similar throughout all samples observed in Zone G. The number of central fultoportulae increases, from Zone F to Zone G. Zone F exhibits 1-5 central fultoportulae; Zone G exhibits 1-23 central fultoportulae. Transitional forms from 503.2 to 462.1 ka have intermediate numbers of 1-11. The number of marginal fultoportulae also increases between Zones F and G, with 4-10 in Zone F and 3-35 in Zone G. Transitional forms are also intermediate ranging from 5-16. The costae exhibit a larger range, from 27-53 in Zone F to 22-96 in Zone G; transitional forms exhibit a lower range of 32-72 costae. The number of marginal fultoportulae/costae remains very similar between Zone F and the transitional forms having marginal fultoportulae on every 3-6 costae. However, this feature becomes more variable from 462.1 ka to 227.9 ka with marginal fultoportulae every 1-3 costae, or every 3-6 costae. The central area pattern also differs between Zone G and Zone F with Zone G showing 3 to 4 large depressi (Figures 24-29). Zone F contains either small depressi or puncta along the central area rim or irregularly distributed (Figures 22-23).
Although *Cyclotella* from this interval is the longest lived type, there is some morphological variability present. For example, the samples viewed at 436.4 ka and 417.4 ka have different ranges of total valve diameter and central area diameter. The 436.4 ka type has larger valve diameter and larger central area diameters (5.6-22.2 µm and 2.3-11.1 µm respectively), and the sample at 417.4 ka has smaller measurements (3.2-18 µm and 1.9-6.7 µm respectively). Another example is the number of marginal fultoportulae per costae. From 417.4 ka to the sample at 406.7 ka, the marginal fultoportulae/costae becomes much more variable. At 417.4 ka the marginal fultoportulae range consistently from 1-2, while the sample at 406.7 ka has valves with 2-3 and 4-6 marginal fultoportulae/costae. The marginal fultoportulae and costae values do not exhibit changes within these samples. The sample at 417.4 ka has marginal fultoportulae ranging from 3-30 and costae ranging from 27-81, and the sample at 406.7 ka has marginal fultoportulae ranging from 5-28 and costae ranging from 27-86. Despite these variations the essential character of the morphology remains the same, thus leading to the classification of one variable morphological type.

The interval at 333.2 ka to 302.5 ka may contain more than one type of *Cyclotella* as observed within three samples at 333.2 ka, 318.7 ka, and 302.5 ka. Both SEM and LM observations show a group with features indicating a distinct second type with a different central area. The central area diameter within these is larger, and takes up a greater percentage of the total diameter. The central area pattern is transversal to colliculate with no distinct depressi or puncta. Internally, the costae are thin and unequal in length. The rimoportula is positioned along the margin of the central area, and is oriented oblique to slightly oblique with a developed sessile labium. The type also has lower numbers of central fultoportulae, usually from 1-2.
However, this group is not present in high abundance, and was only observed a few times within each sampled interval.
Figures 41-46: Transitional forms at 503.2 ka and 484.1 ka within interval 503.2 ka to 227.9 ka (Zone G): Figs. 41-43: SEM external valve view; Fig. 44: SEM internal valve view; Fig. 45: LM photograph 503.2 ka; Fig. 46: LM photograph 484.1 ka (D: depressi, CF: central fultoportulae, R: rimoportulae).
Figures 47-52: Interval 503.2 ka to 227.9 ka (Zone G) *Cyclotella* type; Fig. 47-50: SEM external view; Fig. 51: SEM internal view; Fig. 52: LM photograph (D<sub>L</sub>: large depressi; CF: central fultoportulae).
222.9 ka to 187 ka (Zone H)

A prominent transition in the dominant diatom type occurs between this and the previous interval, corresponding to a sparse diatom event in the record (Figures 53-59). The total diameter of valves ranges from 3.8 µm to 31.2 µm. The central area diameter ranges from 1.9 µm to 16.4 µm and accounts for 42% to 72% of the external valve area. Striae/10 µm range from 14-27. The central area pattern is flat to colliculate with granules and scattered puncta or sometimes small depressi. The central fultoportulae range from 1-23 with 2-3 satellite pores and are distributed both centrally and marginally on the internal valve face. The marginal fultoportulae range from 6-40 with 2 satellite pores, and the costae range from 22-111 with marginal fultoportulae situated on every 1-3(4) slightly depressed costae. The presence of 1-2 rimoportulae can be seen on these valves, placed mostly on the central marginal area. The rimoportulae orientation is radial to slightly oblique with a highly developed sessile labium.

The type present at the interval between 222.9 ka to 187 ka is distinguished based on the distinct central area pattern, the orientation of the central fultoportulae, and the number of rimoportulae (Appendix B, Figure B1). The total valve diameter is similar between this time interval and the previous time interval with valves ranging from 2.8 µm to 31.2 µm. The central area is slightly larger within this interval, with values ranging from 1.9 µm to 16.4 µm. The central area pattern in the previous interval contained 3-4 large depressi with the central fultoportulae situated within the depressi. The interval described here contains many small irregularly scattered depressi and puncta. The central fultoportulae are also scattered irregularly across the entire internal valve face, with some located close to the margin. The range of central fultoportulae values within this interval and the previous interval remains the same. The marginal fultoportulae and costae values have slightly higher ranges (6-40 and 22-11).
respectively); however, the number of marginal fultoportulae/costae is similar to the previous interval. Most distinctive of this interval is the presence of two rimoportulae at 190.5 ka, which is not observed at any other time intervals studied. They each contain a highly developed sessile labium, and are radial to oblique in orientation.
Figures 53-59: Interval 222.9 ka to 187 ka (Zone H) *Cyclotella* type; Fig. 53-55, 57: SEM external valve view; Fig. 56: SEM internal valve view; Figs. 58-59: LM photograph 190.5 ka (R: rimoportulae; CF: central fultoportulae).
182 ka to Recent (Zone I)

The interval from 182 ka to recent exhibits increased morphological variability. Valve diameter during this time period ranges from 1.9 µm to 22.9 µm. The central area diameter ranges from 1.3 µm to 9.5 µm, and accounts for 22% to 73% of the total valve diameter. The striae/10 µm range from 13-32. The central area pattern is highly variable ranging from flat to colliculate with 3-6 large depressi, 1-5 small depressi, or radially oriented small to large depressi. The central fultoportulae range from 1-22, either with no distinct orientation or situated within the radial depressi. The marginal fultoportulae range from 3-27, and the costae range from 21-86. The marginal fultoportulae/costae exhibits variability ranging from every 1 to 6 marginal fultoportulae/costae. The rimoportulae is situated variably on the central area to the ring of the costae. The rimoportula is radial to oblique with no sessile labium to a highly developed sessile labium. The following paragraphs explore the various morphologies seen within this time span in depth.

The first dominant Cyclotella type occurs from 182 ka to 43.6 ka after a sparse diatom event (Figures 60-65). The total valve diameter ranges from 2.8 µm to 22.9 µm, reaching the largest valve diameters within Zone I. The central area diameter ranges from 1.6 µm to 9.5 µm, accounting for 25% to 73% of the total valve diameter. The striae/10 µm shows the largest range with a minimum of 13 to a maximum of 32. The central area pattern is flat to colliculate with radially positioned small to large depressi. The central fultoportulae range from 1 to 8 with 2-3 satellite pores. The marginal fultoportulae range from 3 to 24, and the number of costae range from 21 to 76 with marginal fultoportulae situated on every 2-5 slightly depressed costae. The single rimoportula is located along the central margin to the ring of costae and is oriented radial
to oblique. The rimoportula has a highly developed sessile labium that exhibits complete silicification in some observed valves.

The different morphological types observed between the intervals 182 ka to 43.6 ka and 222.9 ka to 187 ka are distinguished by the total valve diameter and central area diameter (Appendix B, Figure B1). The total valve diameter generally smaller in the interval described here, 2.7 µm to 22.9 µm. The central area diameter is also smaller, 1.6 µm to 9.4 µm. The striae/10 µm values between both time intervals remain relatively similar. The range of the number of central fultoportulae significantly diminishes between the two intervals, with interval 222.9 ka to 187 ka ranging from 1-23 and interval 182 ka to 43.6 ka ranging from 1-8. The marginal fultoportulae and costae are fewer within this interval, ranging from 3-24, and 21-76. The marginal fultoportulae/costae became slightly more variable on every 2 to 5 costae. The central area pattern also greatly differs. The previous interval exhibited large central areas with irregularly scattered small depressi, puncta and central fultoportulae. The interval at 182 ka to 43.6 ka once again contains radially positioned small to large depressi, with no distinct orientation of the central fultoportulae.

The time interval described here also displays evidence of multiple types. The dominant type, as described above, is seen within all three intervals. However, at the samples viewed during 138.3 ka and 123.4 ka, two types may be present. Variation is seen within the central area diameter, and the central area pattern. The central area pattern in the second type is colliculate to transversal with no distinct depressi or puncta. The central area diameter is larger than the dominant type. The second type here resembles the second type present within the intervals from 333.2 ka to 302.5 ka (within Group G). The central area patterns are similar, and the central area diameter is larger within both intervals.
A difference within the dominant *Cyclotella* morphological type is observed in samples 41.0 ka and 24.7 ka (Figures 66-67 and 70-71). The type within this interval contains characteristics similar to the type observed from 503.2 ka to 227.9 ka (Zone G). The total valve diameter ranges from 1.9 µm to 19.3 µm. The central area diameter ranges from 1.3 µm to 9.5 µm, accounting for 23% to 65% of the total valve diameter. The number of striae/10 µm range from 13 to 30. The central area pattern is flat to colliculate with valves containing both large and small depressi. The central fultoportulae range from 1 to 22 and are situated near or within the large and small groupings of depressi. The marginal fultoportulae range from 4 to 25, and the number of costae range from 23 to 74 with marginal fultoportulae situated on every 2 to 4 costae. The single rimoportula is located centrally or on the central margin. The rimoportula is radially oriented with a partial sessile labium to a developed sessile labium.

A difference in the dominant *Cyclotella* type is observed in the time interval 8.3 ka to 1.3 ka (Figures 68 and 72-73). The total valve diameter ranges from 3.4 µm to 11.1 µm. The central area diameter ranges from 1.4 µm to 4.8 µm, accounting for 22% to 51% of the total valve diameter. The number of striae/10 µm range from 18-28. The central area pattern is flat to colliculate with 1-5 small depressi. The central fultoportulae range from 1-2 with 2-3 satellite pores, and display no distinct pattern or orientation. The marginal fultoportulae range from 5-14 with 2 satellite pores, and the number of costae range from 29-60 with marginal fultoportulae situated on every 3 to 6 costae. The single rimoportula is positioned on the central margin or on the costae. The rimoportula is oriented radial to oblique with no sessile labium or a partial sessile labium.

The recent *Cyclotella* population is dominated by a different type (Figures 69 and 74). The total valve diameter ranges from 3.9 µm to 17.8 µm. The central area diameter ranges from
1.6 µm to 7.33 µm, accounting for 31% to 63% of the total valve diameter. The number of striae/10 µm range from 17-27. The central area pattern is flat with 3-6 large depressi. There are also valves that exhibit a central area pattern that is colliculate to transversal with no depressi or puncta. The central fultoportulae range from 1-3 with 2-3 satellite pores. The marginal fultoportulae range from 8-27 with 2 satellite pores, and the costae range from 41-86 with marginal fultoportulae situated on every 1-4 costae. The single rimoportula is located on the central valve margin. The rimoportula is radial to oblique with no sessile labium to a partial sessile labium.
Figures 60-65: Interval 182 ka to 43.6 ka (Zone I) *Cyclotella* type; Fig. 60-63: SEM external valve view; Fig. 64 LM photograph 159.7 ka; Fig. 65 LM photograph 138.3 ka.
Figures 66-74: Fig. 66-67 and 70-71: interval 41 ka to 24.7 ka (Zone I) Cyclotella type; Fig. 68 and 72-73: interval 8.3 ka to 1.3 ka (Zone I) Cyclotella type; Fig. 69 and 74: Recent (Zone I) Cyclotella type; Fig. 66-69: SEM external valve view; Fig. 70-74: LM photographs (LM scale bar = 10 µm).
DISCUSSION

This research provides the longest analysis of *Cyclotella* morphological variability within the Lake El’gygytgyn record, documenting multiple transitions in morphology throughout the last ~1.2 Ma. The first dominance of *Cyclotella* occurs at 1126 ka during warm MIS 33. Six different morphologies are present between 1126.0 ka to 503.2 ka (Zones A-F). During this time span, changes in the dominant *Cyclotella* morphology occur in correspondence with low abundance intervals. These low abundance intervals correspond to extreme cold periods and shifts in the dominant planktonic genera between *Cyclotella* and *Pliocaenicus* (Snyder et al., 2013).

From ~500 ka to recent, paleoclimate analyses on the lake show an increased variability in total organic carbon (TOC) and total nitrogen (TN) (Wennrich et al., 2016) and an increase in the occurrence of laminated sediments of alternating gray to black silt and clay horizons (facies A) (Melles et al., 2007). These observations strongly support a trend to intensified glacial periods within the Middle to Late Pleistocene. Pollen records demonstrate landscape openness, with a cold steppe to tundra landscape (Tarasov et al., 2013). During this time period *Cyclotella* becomes the dominant planktonic diatom within the record, and a dynamic record of *Cyclotella* morphology is observed. From 503.2 ka to 227.9 ka (Zone G) the record exhibits a dominance of one single morphological type. Extreme cold events with sparse plankton create habitat availability allowing for shifts in the dominant morphology to occur, as observed within the morphology observed at 222.9 ka to 187 ka (Zone H). From 182 ka to Recent (Zone I), *Cyclotella* morphology becomes highly variably with four different morphologies observed during this time span.
The following sections discuss these morphological changes and associated paleoclimatic events in more detail. The first section discusses warm intervals viewed. The second section focuses on cold intervals, and how these cold events may be driving changes in *Cyclotella* morphology. The final section discusses the morphological variability within the record as compared to previous analyses on *Cyclotella* morphology.

**Peak Warmth Intervals**

The ecological conditions that favor the appearance of *Cyclotella* taxa within lake records are debated. Calibration sets from lakes in northern Fennoscandia supported an increase in *Cyclotella* taxa within lakes with lower temperatures (~10°C) and high alkalinity (Weckstrom et al., 1997). This was contradicted by an earlier calibration set from Pienitz et al. (1995) indicating an association between *Cyclotella* taxa and warmer temperatures from lakes in Canada. The data set analyzed here exhibits *Cyclotella* taxa dominance across both warm and cold intervals throughout the last ~1.2 Ma. *Cyclotella* particularly experiences morphological changes during extreme warm super-interglacials MIS 5e and MIS 11 and during warm MIS 1 and MIS 7.5.

The recent interglacial (MIS 1) is characterized by the presence of *Cyclotella* and *Pliocaenicus*. *Cyclotella* species within the modern community include *C. ocellata*, *C. tripartita*, *C. schumannii* (Cremer et al., 2005) with *C. ocellata* numerically dominant (Cherepanova et al., 2010). Previous core analysis exhibits dominance of the *C. ocellata* “morphotype” with occasional occurrences of *C. tripartita* and *C. arctica* “morphotypes” from 0-2 cm (recent to ~3 ka) (Cherepanova et al., 2010). Within this analysis, warm MIS 1 exhibited two *Cyclotella* morphologies from samples viewed at 1.3 ka and 0.075 ka (Zone I). The absence of significant temperature changes and consistent seasonal ice melt suggests that changes within these
morphologies are being driven by other factors. The main differences between these morphologies are the central area diameter, the marginal fultoportulae, and the costae. More samples are needed to better constrain this time of warmth. The return of *Pliocaenicus* as a significant member of the planktonic assemblage occurs at ~15 ka (Snyder et al., 2013). The reintroduction of this genus into the planktonic assemblage corresponds to a decrease in the total valve diameter within the *Cyclotella* morphologies as exhibited in samples viewed at 1.3 ka (3.4 µm to 11.1 µm) and at 0.075 (3.9 µm to 17.8 µm). Small valve diameters were also recorded (2.6 µm to 12.6 µm) within previous down core analysis (Cherepanova et al., 2010).

The dominant *Cyclotella* morphology remains constant from 43.6 ka to 182 ka (Zone I), however during MIS 5e (111-135 ka) the LM and SEM intervals exhibited evidence of a second morphological type that is not present throughout the rest of this morphologically stable time interval. Two central area patterns are visible; the most dominant pattern is flat to colliculate with radially positioned depressi, and the second type is colliculate to transversal and depressi are absent. Valve diameter is bimodal, indicating a smaller type and a larger type. Genus level diversity does not significantly increase during this super-interglacial in comparison to the super-interglacials at MIS 11 and MIS 31 (Snyder et al., 2013). The concentration of *Cyclotella* is driving the increase in total planktonic diatom concentration. Genus level diversity may have been inhibited by the presence of two morphological types of *Cyclotella*. Although, the presence of two morphological types is also demonstrated within one sample observed during MIS 11, which exhibits considerable genus level diversity suggesting this may not be a limiting factor. The presence of large, thick, robust valves suggests suspension in deep, open, or turbulent waters after summer ice break-up (Jewson et al., 2015); large valves may also reflect enhanced nutrient conditions with increased silica availability.
The warm interglacial at MIS 7.5 coincides with the appearance of a *Cyclotella* morphological type limited to the time span from 187 ka to 222.9 ka (Zone H). Prior to this warm period, a cold event eliminates planktonic diatoms from the record. In previous morphological analysis, this time interval was characterized as the *C. kuetzingiana* morphotype (Cherepanova et al., 2010). Valves reach large sizes and are robust/highly silicified exhibiting large granular ornamentation on some valves. One sample within this interval also exhibited the distinct presence of two rimoportulae located on the central area to central margin. Large, highly silicified valves, once again suggest open water conditions and seasonal ice melt. Valves of *C. kuetzingiana* have mainly been found in littoral and pelagic zones of alkaline lakes (Houk et al., 2010) suggesting a deviation from present day conditions of circum-neutral to weakly acidic lake water (Cremer et al., 2003; Cremer & Wagner, 2005). However, there is no evidence to suggest that pH experienced significant variability during this time span. Alternatively, the extreme cold interval with sparse plankton created habitat availability. The *C. kuetzingiana* morphology may provide an example of an opportunistic ecological strategy within the planktonic diatom assemblage.

From 227.9 ka to 503.2 ka (Zone G) the dominant morphological type remains constant, making this the longest stable *Cyclotella* morphology observed in the record. Biogenic silica (BSi) accumulation rates during the latter half of the Pleistocene are slower than previously observed in the core record, indicating progressive deterioration of environmental and climatic conditions within the Siberian Arctic (Meyer-Jacob et al., 2014). However, BSi measurements do not capture extreme lows in diatom abundance. Previous diatom analysis has also exhibited the presence of an observed stable period from 550 to 225 ka (Snyder et al., 2013). This time of relative stability also occurs during lower-amplitude summer insolation (Laskar et al., 2004); it
has been suggested this may be unique to conditions during summer insolation lows (Snyder et al., 2013). During this time span, valves reach exceptional sizes, particularly during MIS 11 (maximum of 27.5 µm). Generic diversity increases with the presence of *Stephanodiscus, Fragilaria, and Asterionella* in significant concentrations (Snyder et al., 2013). The large valve diameter of *Cyclotella* during this time span is also marked by the absence of other large-valved plankton, namely *Pliocaenicus*, within the core, possibly reflecting a competitive exclusion of other large-valved plankton. The maximum valve diameter attained within the ~1.2 Ma time span (31.2 µm) during MIS 7.5 also occurs with a marked absence of *Pliocaenicus*, further supporting this conclusion.

**Cold Productive Intervals**

The Lake El’gygytgyn record is punctuated with cold stages that maintain high planktonic diatom abundance. These intervals are characterized by abundant total diatom concentrations, periodic expansion in plankton generic diversity, and a general dominance of *Cyclotella* (Snyder et al., 2013). However, other proxy records such as pollen, sediment facies, geochemical, and diatom isotopes suggest colder summer temperatures during these time periods (Melles et al., 2007). For example, lithological characteristics indicate cold temperatures as inferred from high TOC, TN and total sulfur (TS) concentrations, with low precipitation as inferred from intermediate to high BSi or opal content (Melles et al., 2007). Significant primary production during these cold intervals suggests that the lake ice cover was widely free of snow, and therefore exhibits lower precipitation levels than intervals exhibiting low values of primary production (Melles et al., 2007)

The cold interval at MIS 2 coincides with the *Cyclotella* morphology observed in samples at 24.7 ka. The *Cyclotella* morphology present exhibits similar characteristics to that observed
during a period of prolonged Cyclotella stability (227.9 ka to 455.6 ka, Zone G). Valve diameter reaches a maximum of 19.3 µm and a mean of 8.7 µm, exhibiting a relatively large size range. However, these valves at this time do not reach the large sizes observed within the morphological type from 227.9 ka to 455.6 ka (Zone G) during warmer conditions. The presence of diatoms within the lake indicates that temperatures were high enough for periodic melting along the ice margins, and precipitation levels were low enough for sustained light availability. The presence of one dominant Cyclotella morphology and the lower size range suggests an adaptation for living under ice-covered conditions. Low precipitation would be necessary to allow for sufficient light availability, and periodic melting along the margins would allow for circulation of seasonal nutrient input. The Cyclotella valves within this interval may have formed as blooms during this periodic lake circulation. Smaller valve size during cold periods has been recorded previously within the Lake El’gygytgyn record (Phillips, 2013). Small valve diameters may be an adaptation to less extensive open-water conditions, which is also supported by the absence of Pliocaenicus (Snyder et al., 2013).

Not every cold productive interval exhibited evidence of a morphological response from the Cyclotella taxa. Two productive intervals were recorded during cold MIS 6, neither of which produced an observed morphological change, with the exception of slightly lower valve diameter. During the early portion of the record, cold productive intervals occur at ~1126 ka and ~987 ka. These coincide with two Cyclotella intervals (1126-1104 ka, Zone A; 1029-925 ka, Zone B), and an absence of the large diatom Pliocaenicus. The presence of planktonic diatoms suggests that the lake was cold, but achieved temperatures warm enough for partial lake melt, as well as low precipitation conditions. The extremely small valve sizes during this time interval also suggests that they were adapted for less extensive open-water conditions.
Response to Sparse Plankton Events

Many of the morphological changes within *Cyclotella* were observed after extreme cold events characterized by the absence of planktonic diatoms. The disappearance of planktonic diatoms during these intervals suggests perennial ice-cover with substantial amounts of precipitation, therefore limiting the amount of light availability. Upon the return to more favorable conditions, a new morphological group becomes dominant as seen at 676.4 ka (Zone D), 554.8 ka (Zone E), 222.9 ka (Zone H), and 182 ka (Zone I). This suggests these events drive changes within the dominant phenotype. The absence of planktonic diatoms creates open habitat availability within the water column. The opening of an ecological niche within the diatom assemblage creates opportunity for a new morphological type to become dominant, competitively excluding other morphological types. However, not all morphological changes coincide with sparse plankton events, suggesting that this is not the only driving factor of phenotypic change within the lake history.

Comments on *Cyclotella* Morphology

The morphological analysis provides the longest spanning analysis of the *Cyclotella* record within Lake El’gygytgyn. The modern community spanning to the cold sparse event at 185 ka (Zone I) exhibits multiple morphologies, but has previously been shown to be dominated by *C. ocellata*, with *C. arctica* and *C. tripartita* “morphotypes” in the recent community (Cherepanova et al., 2010). Solitary valves of *C. kuetzingiana* “morphotype” were also viewed during cold MIS 2 and cold MIS 3. The dominant morphologies observed within this study did not exhibit typical *C. ocellata* characteristics. *C. ocellata* as described within Houk et al., 2011 ranges from 5-22 µm in diameter, has 14-20 striae/10 µm, marginal fultoportulae every 2-5 costae, 1-4(5) central fultoportulae, and a central area pattern ranging from flat to colliculate with
3-6 large depressi. *Cyclotella* within the recent sample (0.075 ka) have similar characteristics, except for higher striae/10 µm ranging from 17-27. *Cyclotella* within the sample viewed at 1.3 ka also exhibits similar characteristics, with a smaller valve diameter, and a similar striae/10 µm range of 18-28. However, previous to these time periods, the dominant *Cyclotella* morphology does not exhibit *C. ocellata* characteristics with higher central fultoportulae numbers, and much higher striae/10 µm, ranging from 13-32.

A unique morphology within the record occurs from 187 ka to 222.9 ka (Zone H). During this time period valves attain their maximum size in the record reaching 31.2 µm, and the central area diameter accounts for a large percentage of the total valve diameter, in most cases >50%. The central area pattern is flat to colliculate with irregularly to radially scattered puncta. The central fultoportulae range from 1-23 and are irregularly scattered across the entire valve face. This morphology also contains several examples of valves with two rimoportulae. This is a distinct feature within the record. Size ranges and central area pattern are comparable to descriptions of *C. kuetzingiana* (Houk et al., 2010). The presence of the “*kuetzingiana*-morphotype” was also recorded in the analysis performed by Cherepanova et al. (2010). This is the only time interval within the Lake El’gygytgyn record that exhibits this *Cyclotella* morphology.

Prior to this point within the record, the morphology of *Cyclotella* valves differs greatly from other recorded *Cyclotella* species that have been documented as part of the *C. ocellata* complex. The longest lived morphological type (227.9 ka to 455.6 ka, Zone G; 41-24.8 ka, Zone I) in the record exhibits distinct characteristics. The central area pattern is similar to *C. ocellata* in being flat to colliculate with three to four large orbiculi depressi. The central fultoportulae are situated in groups within or along the edges of the depressi. The placement of the central
fultoportulae differs from *C. ocellata*, bearing a closer resemblance to *C. tripartita*. The number of central fultoportulae range from 1-23. Taxa regarded as possible members of the *C. ocellata*-complex exhibit much lower central fultoportulae values ranging from 1 to 7 (Houk et al., 2010). The valve diameter reaches a maximum of 27.5 µm. This exceeds typical values of *C. ocellata*, *C. tripartita*, *C. rossii*, *C. arctica*, *C. comensis*, *C. pseudocomensis*, and *C. costei* (Houk et al., 2010). Valve diameters lie within the range of *C. kuetzingiana* and *C. polymorpha*, but other valve characteristics do not indicate similarities with these species. Valves of *C. ocellata* were recorded with diameters of 21-30 µm by Genkal & Popovskaya (2011), but has not been recorded at this size within other morphological analyses. These observations suggest this morphological type may be considered as a new, separate *Cyclotella* species.

The first abundant *Cyclotella* observed within the ~1.2 Ma interval occurs from 1104 ka to 1126 ka (Zone A). The documented morphological characteristics lie within very specific ranges, indicating that only one morphological type is present. The size range observed here is the smallest, ranging from 4.2-10.8 µm. The striae/10 µm also exhibits the smallest range from 14-19. The central area is flat to colliculate with irregularly positioned depressi of unequal size. It is difficult to determine the exact central area pattern due to varying levels of dissolution on the external valve face. The size range and striae/10 µm are comparable to *C. ocellata*, *C. polymorpha*, and *C. rossii* (Houk et al., 2010). The number of central fultoportulae (1-5) and the marginal fultoportulae/costae (1 to 2) fall within similar ranges to *C. rossii* which has 2-3 central fultoportulae and 2-3 marginal fultoportulae/costae. However, dissolution causes possible complications when comparing the central area pattern with *C. rossii*. Further morphological analysis on this time interval may yield more evidence to distinguish this at the species level.
CONCLUSIONS AND FUTURE WORK

The morphological analysis of *Cyclotella* valves spanning the last ~1.2 Ma has revealed that the changes in dominant morphological type present are primarily driven by cold sparse events in which the diatom population is almost or completely eliminated. Cold productive intervals exhibit less morphological variability and generally smaller valve diameters than exceptionally warm intervals. Assemblages following cold sparse events frequently show different morphologies than seen in the previous, high-abundance interval. *Cyclotella* responded differently during super-interglacials MIS 5e and MIS 11. Two morphologies were observed during warm MIS 5e, while MIS 11 exhibited larger valves. Higher generic diversity during MIS 11 may have contributed to the lack of diversity within the *Cyclotella* taxa during this time. Generally, types from the most recent intervals can be referred to *C. ocellata*; the interval 222.9-187 ka (Zone H) contains the distinctive *C. kuetzingiana*. Morphologies observed during 227.9 ka to 455.6 ka (Zone G) and 1104 ka to 1126 ka (Zone A) are unique and are under consideration as new *Cyclotella* species.

Future analysis should focus on better constraining the morphological types present within the intervals of high morphological variability. Previous analyses on morphological variability have yielded results that suggest some individually named species may form a morphological continuum of diverse but related species (Duleba et al., 2015). Morphological analysis using conventional and geometric morphometric statistical analyses may help to narrow down and differentiate between morphological types observed within this record. The interval between 21.5 ka to 11.4 ka was not observed in SEM samples. This places a small gap within the record, and should be revisited.
CHAPTER III: SURIRELLA

INTRODUCTION

Diatom records found in ancient lake sediments serve as a powerful proxy for environmental change on glacial-interglacial scales. Ancient lakes also serve as an outstanding example of biodiversity and endemism “hot spots,” including diatoms (Douglas & Smol, 2010). The benthic diatom genus *Surirella* Turpin has been shown to exhibit particularly high levels of biodiversity, endemism, and adaptation, as shown from multiple analyses on ancient lake systems such as Lakes Malawi, Victoria, and Tanganyika (Cocquyt & Vyverman, 1993; Cocquyt & Jahn, 2007), the Malili Lakes in Indonesia (Bramburger et al., 2008), Lake Prespa (Cvetkovska et al., 2014a; Cvetkovska et al., 2014b), and Canadian Lake Opeongo (McCabe & Cyr, 2006).

*Surirella* is characterized by its isopolar or heteropolar frustules and by the raphe positioned along the entire valve margin located in the canal area (possibly raised above the valve surface) (Round et al., 1990). Cells vary in size from small (~10 µm length, ~5 µm width) to very large (~235 µm length, ~120 µm width) and have strongly silicified valves (Round et al., 1990). Valves are linear, elliptical, or obovate and may exhibit ornamentations including warts, ridges, or spines (Round et al., 1990).

*Surirella* benthic freshwater forms are divided into two groups: the Pinnatae and the Robustae (Krammer, 1989). The Pinnatae group (*Surirella gracilis* (W. Smith) Grunow, *Surirella minuta* Brébisson ex Kützing, *Surirella ovalis* Brébisson) has frustules with no costae, transapical or radial corrugations, raphe canal in the form of a keel with fibulae and portulae, and areolae situated in troughs or irregular rows (Krammer, 1989). The Robustae group (*Surirella*...
*Surirella* capronii Brébisson & Kitton, *Surirella robusta* Ehrenberg, *Surirella elegans* Ehrenberg) has a valve morphology with marked alae and alar canals, undulated valve plane, and areolae distributed over the entire valve surface in irregular or transapical rows (Krammer, 1989).

Multiple *Surirella* species have been recorded from the modern Lake El’gygytgyn periphyton community. These include *Surirella biseriata* var. *biseriata* Brébisson, *S. capronii* var. *capronii* Brébisson, *Surirella capronii* var. *anadyrensis* Sechkina, *Surirella gravei* Sechkina, *Surirella lacus baicali* Skvortzov var. *lacus baicali*, *Surirella ovalis* Brébisson, *S. robusta* var. *robusta*, *Surirella splendidia* Kützing, *Surirella spiralis* Kützing, and *Surirella tenera* Gregory var. *tenera* (Table 5) (Sechkina, 1956; Kharitonov, 1980). Of these recorded species, *S. gravei*, *S. robusta* var. *ovalis*, and *S. capronii* var. *anadyrensis* were all first described in the Lake El’gygytgyn by Sechkina (1956).

The present study analyzed core sediment samples using a combination of light microscopy and scanning electron microscopy for the genus *Surirella* spanning the last ~1.2 Ma. Three objectives of the study were to (1) obtain a better understanding of the *Surirella* population within Lake El’gygytgyn, (2) assess the evolutionary history and endemism of *Surirella* at this location, and (3) compare species turnover and morphological changes in *Surirella* to changes observed in the planktonic diatom taxa.

**SURIRELLA BIODIVERSITY AND ENDEMISM**

The traditional view of diatom biogeography maintains that most diatom species are widespread (cosmopolitan) in their distribution. Analysis of diatom dispersal by Finlay et al. (2002) predicted that rare diatom species, some of which are considered endemic, may prove to have a wider geographic distribution as a result of additional sampling. However, recent analysis
of biogeographical patterns in diatoms supports the conclusion that regional patterns of diversity are consistent with macro-organisms (Kilroy et al., 2007). The dynamic equilibrium model (DEM) suggests that maintenance of endemic taxa occurs as a result of stable, unproductive environments (Kilroy et al., 2007). Diatom communities were examined from multiple sites and were assigned to endemic or potential endemic categories (Kilroy et al., 2007). Patterns generally conformed to the DEM supporting dispersal limitations on diatoms (Kilroy et al., 2007). Furthermore, an analysis using latitudinal gradients in local and regional genus richness on a global data set revealed that historical processes (dispersal limitation, migration) have a larger effect on regional to global scale geographic patterns in genus richness than contemporary environmental processes. These results further support the prevalence of endemism within microbial communities, specifically for diatoms.

Endemic patterns have particularly been exhibited in the genus *Surirella* within multiple freshwater lakes. For example, *Surirella* has been extensively studied in Lakes Ohrid and Prespa located on the Balkan Peninsula. Two previously undescribed species of *Surirella* were found within the sediment of Lake Prespa, including *Surirella subrotunda* Cvetkovska, Levkov, & Hamilton and *Surirella parahelvetica* Cvetkovska, Levkov, & Hamilton (Cvetkovska et al., 2014). Studies on the Malili Lakes in Indonesia also exhibit endemism of *Surirella*. The genus exhibits ~7% of its global diversity within this lake system, and species such as *Surirella sublinearis* var. *suggesta* Bramburger & Hamilton and *Surirella tenacis* Bramburger & Hamilton are endemic (Bramburger et al., 2008). Analysis of the diatoms within the Malili Lakes supports the role of deterministic processes (competition, extirpation) contributing to the maintenance of highly endemic communities (Bramburger et al., 2008).
Environmental variability can promote biodiversity in terms of species richness and evenness (McCabe & Cyr, 2006). Two main factors that promote the coexistence of species within a single system are stabilizing factors (that prevent competitive exclusion) and equalizing factors (that slow the rate of competitive exclusion) (McCabe & Cyr, 2006). Benthic algal communities in the littoral zones of lakes are particularly sensitive to these factors (McCabe & Cyr, 2006). For example, benthic diatom taxonomic richness increases as temperature variability increase (McCabe & Cyr, 2006). Other factors that affect biodiversity include turbidity (Shteinman et al., 1997), light availability (Schallenberg & Burns, 2004), and nutrient availability (Riber & Wetzel, 1987).

METHODS

A systematic analysis of the presence of Surirella spanning the last ~1.2 Ma (composite core depths 0.005 m to 51.017 m) was performed using light microscopy (LM) and scanning electron microscopy (SEM). The genus Surirella was chosen because of the large unique species described within the modern lake. Only valves >100 µm were used for LM analysis, as these were the most visible at low magnification and most likely to be found in samples. Sample pretreatments for microscope analyses followed standard procedures developed for the Lake El’gygytgyn sediments (Battarbee, 1974; Scherer, 1994) (see Appendix A). SEM cover slips were sputter coated with gold palladium. LM analyses were performed using a Leica DMLB, with differential interference contrast, and a DFC 425 digital camera was used to take images and measurements. SEM analyses were performed at the University of Toledo using the Hitachi S-4800; SEM measurements were taken using the tpsDig program.

Samples were analyzed at a time resolution of every ~5 ka for the presence of Surirella. A total of 234 intervals were analyzed under LM, and SEM investigation was done on Surirella
in selected intervals, regardless of size. The total number of *Surirella* valves on a slide were counted for each LM interval. *Surirella* individuals were placed into morphological groups defined by the following characteristics: valve shape (isopolar, heteropolar), valve silicification (linear, elliptical, ovulate), ornamentation (spines, ridges), areolae pattern, shape of fenestrae, undulation or porcae pattern on the valve face, and valve size (Figure 75). Measurements were taken of the valve length and width.

Microsoft Excel and PAST (Paleontological Statistics) were used for statistical analysis. The mean, median, mode, minimum, maximum, and standard deviation were calculated for the length and width measurements of the whole *Surirella* population, as well as within each individual morphological group.
Figure 75: *Surirella* characteristics used for morphological classification (L: length, W: width, O: ornamentation, F: fenestrae).
RESULTS

A total of nine *Surirella* morphological groups were documented in the Lake El’gygytgyn core record spanning the last ~1.2 Ma. A total of 763 valves were observed in LM. The observed valve lengths attained a maximum of 235.5 µm, and the observed widths ranged from 23.5 µm to 120.9 µm (Table 5). Each morphological group occurred in multiple samples within the core record (Figure 76a and 76b). Groups A, C, D, and to an extent Group H display higher valve occurrences from ~500 ka to the present day. Group F has the highest valve occurrences prior to this from ~1110 ka to ~500 ka. Group B, E and G show no specific time constraints, and were observed throughout the entire record in low numbers, although their occurrences generally also increase from ~1.2 Ma to recent time. Finally, Group I was found in the lowest numbers in the record, and occurs the most from ~422 ka to ~40 ka. The following sections describe the morphological groups, including a comparison to published species descriptions.
Table 5: Length and width ranges for *Surirella* groups

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<th><em>Surirella</em> Group</th>
<th>Maximum Length (µm)</th>
<th>Width (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group A</td>
<td>211</td>
<td>35-106</td>
</tr>
<tr>
<td>Group B</td>
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<td>46-107</td>
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<td>41-121</td>
</tr>
<tr>
<td>Group D</td>
<td>187</td>
<td>41-83</td>
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<td>191</td>
<td>56-118</td>
</tr>
<tr>
<td>Group F</td>
<td>167</td>
<td>42-81</td>
</tr>
<tr>
<td>Group G</td>
<td>162</td>
<td>29-72</td>
</tr>
<tr>
<td>Group H</td>
<td>154</td>
<td>34-68</td>
</tr>
<tr>
<td>Group I</td>
<td>236</td>
<td>24-69</td>
</tr>
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</table>
Figure 76a: Concentrations (valves/gram) of *Surirella* groups A-E plotted against time (ka); total valve concentration (valves/gram), 65°N June insolation (Laskar et al., 2004) and marine isotope stack (Lisiecki & Raymo, 2005) are plotted for comparison.
Figure 76b: Concentrations (valves/gram) of *Surirella* Groups F-I plotted against time (ka); total valve concentration (valves/gram), 65°N June Insolation (Laskar et al., 2004), and the marine isotope stack (Lisiecki & Raymo, 2005) are plotted for comparison.
Group A

The valve of the frustules are elongate-ovate and heteropolar with observed lengths up to 211 µm. Widths range from 35-106 µm, with the width 32-63% of the length. Areolae cover the entire valve face, and striae are indistinct. Porcae are planar, narrow, and converge at the valve poles. The fenestrae are small and round with 4-6 fenestral bars. The central valve face contains a round depression. Valves contain various levels of silicification; however, most examples viewed had poles ornamented with small granules or conical spines (Figures 77-79). Group A valves were the most common Surirella group recorded throughout the observed intervals, gradually diminishing in numbers further down the core record. Group A is consistent with the description of S. gravei.
Figures 77-79: Surirella Group A SEM (Fig. 77) and LM (Fig. 78-79) views (A: apical axis acute heteropolar, O: ornamentation, CD: central depression, R: radial ribs converging at the poles) (LM scale bar = 10 µm).
**Group B**

The valves are elliptical and slightly heteropolar to isopolar with broadly rounded ends. Lengths attain a maximum of 178 µm. The width of the valves range from 46-107 µm, and the width is 42-77% of the length. Areolae cover the entire valve face, and striae are indistinct. Porcae are thick, well developed, and converge at the poles. Alar wings are well developed. Fenestrae are rounded and fenestral bars are absent. No ornamentation is present within this group. The central area forms a small linear depression (Figures 80-82). Group B was found throughout the entire 1.2 Ma time span, although it was found in low numbers. Group B is consistent with the description of *S. robusta* var. *ovalis.*
Figures 80-82: *Surirella* Group B SEM (Fig. 80) and LM (Fig. 81-82) views (A: apical axis broadly rounded, CD: central depression thin, linear, F: fibulae distinct, R: thick ribs) (LM scale bar = 10 µm).
Group C

The valves are elongate-ovate or elliptical and isopolar. The maximum observed length is 210 µm. The widths range from 41-121 µm, and the width is 30-75% of the valve length. Areolae are present on the entire valve face, and striae are indistinct. Prominent radial porcae are present. The fenestrae are rounded to slightly rectangular. The valves are ornamented with two large spines located within the central area at opposite ends (Figures 83-85). Group C is present in high concentration throughout the first ~200 ka, and gradually decreases in abundance further down the record. This group is consistent with the description of *S. capronii* var. *anadyrensis*. 
Figures 83-85: *Surirella* Group C SEM (Fig. 83) and LM (Fig. 84-85) views (F: fibulae variation, O: ornamentation large spines) (LM scale bar = 10 µm).
Group D

The valves are elongate-ovate or elliptical and isopolar with a maximum observed length of 187 µm. The widths range from 41-83 µm and was 35-67% of the valve length. Areolae are present on the entire valve face, and striae are indistinct. Prominent radial porcae are present. The fenestrae are rounded to slightly rectangular. The valves are ornamented with two large spines, smaller conical spines or granules limited to the polar valve regions, and papillae within the porcae depressions (Figures 86-88). Group D resembles Group C in many aspects; however, the ornamentation varies between the two groups. This group is consistent with the description for *S. capronii*, distinguished by the ornamentation.
Figures 86-88: *Surirella* Group D SEM (Fig. 86) and LM (Fig. 87-88) views (F: fibulae, O: ornamentation large and small spines) (LM scale bar = 10 µm).
Group E

The valve is elliptical with broadly rounded to ovate ends and valves are heteropolar. The maximum observed length is 191 µm. The width ranges from 56-118 µm, and the width is 51-99% of the valve length. This group exhibited the largest width values recorded. Areolae cover the entire valve face, and striae are indistinct. Porcae are present, but not prominent. Fenestrae are small and oval, and fenestral bars were not observed in SEM samples. The central area contains a large round depression. The valve exhibits no ornamentation (Figures 89-91). This group also exhibits some valve torsion, with rare occurrences of twisted valves. Group E is not numerically dominant at any point within the record, but appears sporadically throughout.

This group is consistent with the description for *Surirella subcontorta* Hustedt.
Figures 89-91: *Surirella* Group E SEM (Fig. 89) and LM (Fig. 90-91) views; Fig. 81 Group E exhibiting torsion (LM scale bar = 10 µm).
**Group F**

The valve is elongate-ovate and slightly heteropolar. The maximum length is 166.8 µm. The valve width ranges from 42.4-80.8 µm, and the width is 35-63% of the valve length. Areolae cover the entire valve face, but striae are indistinct. Fibulae are distinct terminating near the central area. Fenestrae are large and rectangular, with 16-20 fenestral bars. The central area contains a linear ridge on the external valve or linear depression on the internal valve. Ornamentation is restricted to the poles as small conical spines (Figures 92-94). Group F is found rarely in the more recent portion of the record, increasing down core. It becomes most prominent from ~750 ka to ~1200 ka. Group F is consistent with the description of *Surirella distinguenda* Hustedt, which has not been recorded from the modern population.
Figures 92-94: *Surirella* Group F SEM (Fig. 92a-92b) and LM (Fig. 93-94) views (C: thin costae, CD: central linear depression, F: fibulae); Fig. 92b close up view of the valve ornamentation (LM scale bar = 10 µm).
Group G

The valve is heteropolar with one end broadly rounded and one end cuneate. The maximum length is 162.3 µm. The width ranges from 28.7-71.7 µm, and the width is 23-40% of the valve length. Areolae are present on the entire valve face, and striae are indistinct. Porcae are thick and well defined. Alar wings are well developed similar to Group B. Fenestrae are round, with no evidence of fenestral bars in the SEM valves viewed. No valve ornamentation is present on any of the valves viewed (Figures 95-97). Group G is found in low numbers throughout the entire record studied, with a total of 34 recorded occurrences. The group greatly resembles that of Group B. This group is consistent with the description of *Surirella robusta* var. *splendida* Ehrenberg.
Figures 95-97: *Surirella* Group G SEM (Fig. 95) and LM (Fig. 96-97) views (LM scale bar = 10 µm).
Group H

The valve is elongate-ovate or elliptical and heteropolar. The maximum length is 153.6 μm. The valve width ranges from 33.8-67.5 μm, and is 29-62% of the valve length. Areolae are present on the entire valve face, and striae are indistinct. Prominent radial porcae are present. The fenestrae rounded to slightly flattened. The central area is depressed in the internal valve, with a large spine present on the external valve (Figures 98-99). Group H is found in low numbers throughout the record. Group H shows similarities to groups C and D; however, the ornamentation differs, as well as the central area and the less prominent radial ribs in Group H. This group is consistent with the description of *S. capronii* and may be another variation within the record.
Figures 98-99: *Surirella* Group H SEM (Fig. 98) and LM (Fig. 99a-99b) views of one valve in different focus (CD: central depression, O: ornamentation external large spine) (LM scale bar = 10 µm).
Group I

The valves are elongate or panduriform and isopolar with a maximum length of 235.5 μm. The width ranges from 23.5-68.9 μm, and is 14-45% of the valve length. Striae are indistinct. Alar wings are prominent. Porcae are narrow, symmetrical and radiate converging at the poles. Some valves exhibit ornamentation, such as granules along the entire valve face (Figures 100-102). Group I was only observed 13 times in the core record, and most observed occurrences happen between the span of ~422 ka to ~40 ka. This group is consistent with *S. tenera*, and may have two variations present: *S. tenera* var. *tenera* and *S. tenera* var. *constricta*. 
Figures 100-102: *Surirella* Group I LM view (F: fibulae, P: panduriform valve shape) (LM scale bar = 10 µm).
DISCUSSION

This study is unique in providing the first observations of *Surirella* within the Lake El’gygytgyn composite core record. Most analyses on *Surirella* are limited to the modern assemblages (Krammer, 1989; Cocquyt & Vyverman, 1993; Cocquyt & Jahn, 2007; Bramburger et al., 2008; English & Potapova, 2012; Cvetkovska et al., 2014), making this study an exceptional example of *Surirella* observations within an ancient lake record. The results demonstrate a long and distinct history of these diatoms that provides information on the evolutionary history of *Surirella*, as well as possible species responses to paleoclimatic changes.

The discussion section is organized into two sections. The first discusses the response of *Surirella* species to paleoclimatic events recorded from other El’gygytgyn proxy records, and the second discusses morphological variations observed within the record.

**Paleoclimatic and Paleoecological Responses**

*Surirella* is present throughout the entire ~1.2 Ma time span analyzed. Valve concentrations remain <20,000 valves/gram until 519.2 ka, where the occurrence of valve concentrations >20,000 valves/gram occurs more frequently. Particularly, the presence of groups A, C, D, and H increase from 519.2 ka to present day. This increase occurs during a transition to *Cyclotella* as the dominant planktonic genus within the lake. This time period is characterized by a series of warm productive intervals, cold productive intervals, and sparse plankton events. The productivity of diatoms within the lake is primarily driven by light and nutrient availability, which in turn is driven by duration of ice cover as inferred from BSi and total diatom abundance (Snyder et al., 2013; Meyer-Jacob et al., 2014). *Surirella* taxa are epipelic and exhibit varying degrees of motility, living within the littoral zone of the lake. Unattached diatom forms have been shown to be sensitive to physical disturbance and temperature changes (McCabe & Cyr,
Motile taxa are also suggested to be strong competitors for dissolved nutrients, with the ability to move to a suitable habitat (Passy, 2007). However, *Surirella* species within the lake El’gygytgyn assemblage exhibit high levels of ornamentation and silicification. The presence of large spines within three groups observed suggests lower levels of motility. There are forms that exhibit less ornamentation and may be more suited for a motile lifestyle, suggesting that the *Surirella* taxa within the lake are present in multiple ecological niches.

Peak warmth intervals occur in the record at 111-135 ka (MIS 5e), 360-430 ka (MIS 11), and 1057-1113 ka (MIS 31). High concentrations (<20,000 valves/gram) are exhibited from ~1-25 ka, ~70-100 ka, ~240-260 ka, ~280-295 ka, and ~475-520 ka. None of these exceptionally high concentration intervals correspond to the peak warmth “super-interglacials”. Warm intervals may be associated with lake-levels higher than the modern level as interpreted from lacustrine terraces that are situated 80 m and 60 m above the modern lake level that contain prominent rounded pebbles (Gurov et al., 2007). Higher lake level would create more extensive shallow water habitat for the periphyton assemblage. Furthermore, persistent open water conditions during warm intervals could increase the transport of the periphyton assemblage into the pelagic zone of the lake. These would all suggest that higher abundances should be observed within the *Surirella* species assemblage; however, this pattern was not observed within this study. Lower lake-level has also been observed reaching levels of ~10 m below present day (Juschus et al., 2011). This would create less shallow water habitat, and persistent ice-covered conditions, which could limit the transport of the periphyton community to the pelagic zone of the lake. Diatom concentrations should be corrected for sedimentation rate to better constrain accumulation rates within the core record.
The high abundance zones observed do not correspond to particularly warm or cold climate intervals. Furthermore, the high concentration intervals at ~1-25 ka, ~70-100 ka, ~240-260 ka, ~280-295 ka, and ~475-520 ka are present throughout both warm and cold intervals. For example, the interval from ~1-25 ka exhibits high concentrations during both warm MIS 1 and cold MIS 2. This suggests that factors outside of climate and climate-driven lake-level changes are driving the *Surirella* species assemblage within Lake El’gygytgyn. A possible driving mechanism of species assemblage changes and concentrations may lie within interactions with other members of the periphyton assemblage such as interspecific competition (within *Surirella* species) or generic level competition.

Intraspecific competition is observed within Groups C and D, which exhibit a unique pattern within the record. The two groups share many morphological characteristics, and are only distinguished based on the difference in ornamentation and their presence during specific times in the record. These two groups are consistent with the description for *S. capronii*, and may be multiple variations. The two groups persist together for a period of time, then group D is seen in higher concentrations with sparse amounts of group C valves. This pattern suggests a time period where conditions were more favorable for group D, allowing it to out compete Group C. Group D valves exhibit higher silicification and are not only ornamented by the two large spines, but have small spines or bumps along the poles. This event occurs during a time of change in *Cyclotella* morphology (Chapter II) between 238.5 ka and 142.3 ka.

Groups B, E, F, G, and I are viewed in small numbers throughout the studied time span. Group B and F exhibit the most dominance within the early portion of the record. Group F gradually decreases in concentration towards present day, while group B persists and generally increases in numbers. Groups, E, G, and I exhibited the smallest numbers throughout the record,
and show no general pattern. However, there are certain time periods within which they show more abundance. Group E was observed more often from 891.3 ka to 818.7 ka, 314.2 ka to 255.6 ka, and 98.3 to 70.2 ka. Group G occurrences are mostly between the times 596.2 ka to 487.1 ka and 52.6 ka to Recent. These time periods, however, do not correspond to any significant climatic events recorded from proxy records. Once again, this observation suggests that other parameters are affecting the species population dynamics within *Surirella*.

The increases in *Surirella* abundance do not have a relationship with changes in the planktonic diatom community. However, the valve abundance does increase at the onset of *Cyclotella* dominance within the record. The increase in *Surirella* abundance also exhibits an increase in species diversity with many samples exhibiting >3 *Surirella* groups. *Surirella* has been shown to become one of the dominant genera during times of increasing temperature and current variability (McCabe & Cyr, 2006). Changes in the epipellic community may be driven by different factors than those within the planktonic community.

**Remarks on Morphological Variations**

The three most common groups seen within the record are groups A, C, and D. Two of these groups correspond to the species and variations that are unique to the Lake El’gygytgyn record as described by Sechkina (1956): *S. gravei* (Group A), *S. capronii* var. *anadyrensis* (Group C). Group D is separated from group C based on its ornamentation and the switches in dominance between the two exhibited in the core record. However, this group may be another variation of *S. capronii*. Group H is consistent with the description for *S. capronii*, indicating the presence of three variations of *S. capronii* throughout the entire ~1.2 Ma time span. Groups C, D, and H may be combined as variations of a single dominant species. These groups may be a species complex that exhibits phenotypic plasticity similar to complexes like the *S. ovalis*-S.
brebissonii complex (English & Potapova, 2012). An alternative explanation is that S. capronii may be exhibiting heterovalvity. However, this explanation is not as likely considering full frustules with identical valves were observed within LM scans.

CONCLUSIONS AND FUTURE WORK

The Lake El’gygytgyn record revealed nine distinct morphological groups of Surirella spanning the last ~1.2 Ma. The groups include S. gravei, S. robusta var. ovalis, S. capronii var. anadyrensis, S. capronii var. nov., S. subconstricata var., S. distinguenda, S. splendida, and S. tenera. Groups A, C, D, and H exhibit the highest valve concentration from 519.2 ka to Recent corresponding to the transition to more intense glacial-interglacial cycles, while groups B, E, G, and I exhibit no distinct pattern and persist in low valve numbers throughout the record. Group F exhibits the most valves within the early portion of the record, and generally decreases in numbers after ~596.2 ka. There appears to be no direct relationship of Surirella occurrences to climate, suggesting that Surirella habitats are less influenced by events affecting the lake’s plankton.

Future work should analyze the record prior to 1.2 Ma. The initial occurrence of Surirella remains to be described. Further morphological analysis may also be performed on the groups C, D, and H to potentially document evolutionary divergence and the creation of a different species variations. LM analysis was limited to valves that were >100 µm, but valves exhibiting sized of <100 µm were observed multiple times throughout the record. Future work should extend these observations on smaller Surirella taxa to obtain a more comprehensive record of these taxa.
CHAPTER IV: DISCUSSION

INTRODUCTION

This research provides the longest analysis of both the planktonic genus *Cyclotella* and the benthic genus *Surirella* within the Lake El’gygytgyn sediment record. The observed intervals spanning the last ~1.2 Ma demonstrate a unique history of morphologies within both genera. The morphologies present within *Cyclotella* appear to reflect responses to both cold and warm events within the lake. Different morphologies were observed after intervals exhibiting low plankton abundance, and within cold productive intervals. Some warm productive intervals exhibited higher morphological variability, while some warm intervals exhibited an increased size range. These observations suggest that *Cyclotella* changes are driven mostly by changes in climate.

*Surirella* does not appear to exhibit distinct changes associated with particularly warm or cold events. The benthic genus was observed throughout the entire ~1.2 Ma record alongside *Cyclotella*. Generally, the presence of *Surirella* valves observed in high numbers occurs during the time span where *Cyclotella* is the dominant planktonic genus. This occurs during heightened glacial-interglacial activity within the last ~500 ka. Although the genus appears in higher abundance during this interval, species and variation changes in *Surirella* do not reflect the same changes that were observed in *Cyclotella*. The patterns within *Surirella* suggest that *Surirella* habitats are less influenced by events that affect the lake’s plankton.

PEAK WARMTH INTERVALS

The Lake El’gygytgyn record provides evidence for peak warmth intervals throughout the core record. These intervals reflect present day conditions with semi-permanent ice cover,
high primary production, low terrestrial input, and high chemical weathering (Melles et al., 2007). Periods also achieve conditions warmer than today, exhibiting semi-permanent ice cover, high primary production, oxic bottom waters, high terrestrial input, and an increase in autochthonous production (Melles et al., 2007). The diatom record reflects these time periods, exhibiting increases in productivity as well as increases in planktonic diversity (Snyder et al., 2013). *Cyclotella* appears to exhibit climate driven changes associated with these warm intervals, while *Surirella* changes do not appear to reflect a climate driven response.

The most recent interglacial period (MIS 1) contains two *Cyclotella* morphologies observed within samples at 1.3 ka and 0.075 ka, and within previous analysis the *C. ocellata* and *C. arctica* phenotypes dominate this time period (Cherepanova et al., 2010). The presence of smaller *Cyclotella* valves, and the increased ice-free period creates conditions suitable for the return of *Pliocaenicus* within the planktonic community. During this time period the most abundant *Surirella* taxa belong to groups A, B and C, with single occurrences of groups F, G, and H. Valve abundances of >20,000 valves/gram occur at 1.3 ka and 3.05 ka. These taxa are not unique to this time interval, however, and are also observed within cold intervals.

During MIS 5e (111-135 ka) *Cyclotella* exhibits evidence of two morphological types. These include a larger and a smaller type with variations in the central area pattern and diameter. The large size of the valves within this interval may represent a competitive exclusion of other large planktonic genera, as supported by the absence of *Pliocaenicus*. The *Surirella* taxa exhibit a period of low abundance within this extreme warm interval with values <20,000, and no valves observed at 119.3 ka. The highest abundance observed at 125.6 ka exhibits a complete dominance of group A.
Warm interglacial MIS 7.5 exhibits the most distinct morphological changes within both *Cyclotella* and *Surirella* throughout the ~1.2 Ma time span. *Cyclotella* valves reach their maximum size range observed, and the morphology present is best described as *C. kuetzingiana*. Simultaneously, *Surirella* is present in low abundances of <20,000 valves/gram, however the interval exhibits high abundances of group D (*S. capronii* var.). All other groups are present in single occurrences. The unique morphologies present within both *Cyclotella* and *Surirella* indicate that the lake may have experienced different conditions than seen within other warm intervals. This event is preceded by a collapse within the planktonic diatom assemblage. The presence of *C. kuetzingiana* may alternatively reflect the increase in habitat availability. The morphological changes observed subsequent to plankton collapse may reflect an opportunistic strategy within the planktonic assemblage.

Super-interglacial MIS 11 (360-430 ka) contained *Cyclotella* valves with maximum diameters second to that observed within MIS 7.5. The large valve sizes, and the absence of *Pliocaenicus* once again supports the hypothesis that *Cyclotella* may be competitively excluding other large planktonic genera. This time period exhibits low abundances of *Surirella* valves, with the exception of an extremely abundant sample observed at 370.1 ka (18 valves). This is the most abundant *Surirella* sample viewed within these intervals characterized by extreme warmth. Valves belong mostly to group A and B, with occurrences of valves from groups C, D, F, G, and H. Low *Surirella* abundances are observed across multiple warm intervals including MIS 31, where *Surirella* is found in abundances of <10,000 valve/gram, and *Cyclotella* is absent from the record. This pattern may indicate that *Surirella* may be out-competed by other members of the periphyton community during these warm interglacials.
COLD EVENTS

The Lake El’gygytgyn core record exhibits evidence of multiple cold events, some of which are characterized by an abundance of planktonic diatoms, and some of which are characterized by sparse planktonic diatoms. Cold intervals exhibit evidence of permanent ice coverage, anoxic bottom waters, and nitrogen limitation (Melles et al., 2007). Cold intervals with abundant plankton and high biogenic silica have been interpreted to reflect low levels of precipitation (Melles et al., 2007). In contrast, cold intervals with sparse plankton and low biogenic silica have been interpreted to reflect high levels of precipitation (Melles et al., 2007), limiting light availability. Furthermore, diatom abundance in cold intervals may indicate sufficient melting along the lake margins to allow for seasonal impulses of nutrients, while sparse plankton abundance may signify ice coverage over multiple consecutive summers.

A cold productive interval occurs during MIS 2, and exhibits low valve diameters and a switch in morphology within Cyclotella. During this time period, Surirella is present in abundances of >20,000 in samples observed at 21.4 ka and 24.8 ka, but in low concentrations throughout the remainder of this time span. Groups A and C are present in the largest abundances; however, this interval exhibits small abundances of valves from groups B, D, E, and G. In comparison to warm MIS 1, the Surirella taxa observed experience no major changes. The dominant groups remain the same, and species diversity remains similar. This observations suggests that despite evidence of temperature changes and lake level changes (Juschus et al., 2011) habitat and nutrient levels remained suitable for Surirella. Furthermore, the Surirella species assemblage does not show evidence of climate driven change.

A period of high Surirella concentration occurs from 70.2 ka to 81 ka, corresponding to a cold productive plankton event. The Cyclotella valves exhibit smaller valve diameters, and a
single morphological type. The presence of small valves supports limited open water conditions. *Surirella* valves were observed in the largest concentrations in the record during this time (maximum of 39 valves or ~113,000 valves/gram). Valves from group C exhibit the highest numbers, followed by groups A and B, although, valves from every distinguished group were observed. Seasonal nutrient impulses during periodic lake melting would allow for both *Cyclotella* and *Surirella* to be present in these high numbers.

The high *Surirella* abundances exhibited in the cold interval from ~70-80 ka are limited to that interval. Cold productive plankton events at ~150 ka and ~165 ka exhibit very low abundances of *Surirella* valves. The low abundances observed within this interval, and the high abundances observed within the previous cold interval discussed contradict one another. This disconnect suggests that factors driving the *Surirella* abundances and species diversity lie outside of climate. *Cyclotella* remains the same morphology throughout these cold abundant intervals, and remains at small sizes. These observations support the idea that the factors driving these genera differ.

**CYCLOTELLA AND SURIRELLA RELATIONSHIP**

Although the factors driving morphological changes and species changes may differ between *Cyclotella* and *Surirella*, there appears to be a relationship between the two genera. From ~1200 ka to ~500 ka, the planktonic diatom population alternates in dominance between *Cyclotella* and *Pliocaenicus*. At 554.8 ka *Cyclotella* becomes the most dominant planktonic genera, which persists until ~15 ka, where *Pliocaenicus* re-enters the planktonic assemblage. A similar pattern is observed within the total abundance of *Surirella* valves. Abundances of <20,000 valves/gram occur until 519.2 ka, above which higher valve abundances occur more frequently. Furthermore, both of these genera exhibit different dominant species during the
earlier portion of the core record (~1200-500 ka). The *Surirella* valves observed in this older interval are limited to groups B, E, F, and H, while from ~500 ka to Recent, *Surirella* valves are mostly observed in groups A, C, and D. These similarities suggest a relationship between the two genera, and further analysis may help to clarify this dynamic.
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APPENDIX A: SYNONYMS AND METHODS

LINDAVIA SYNONYMS

*Lindavia arctica* (Genkal & Kharitonov), Nakov et al. (2015); *Cyclotella arctica* Genkal & Kharitonov

*Lindavia comensis* (Grunow), Nakov et al. (2015); *Cyclotella comensis* Grunow

*Lindavia costata var. leprindica* (Flower, Ozornina & Kuzmina), Nakov et al. (2015);
*Pliocaenicus costatus* (Flower, Ozornina & Kuzmina)

*Lindavia costei* (Druart & Straub), Nakov et al. (2015); *Cyclotella costei* Druart & Straub

*Lindavia fottii* (Hustedt), Nakov et al. (2015); *Cyclotella fottii* (Hustedt)

*Lindavia kuetzingiana* (Thwaites), Nakov et al. (2015); *Cyclotella kuetzingiana* Thwaites

*Lindavia kuetzingiana var. radiosa* (Fricke), Nakov et al. (2015); *Cyclotella kuetzingiana var. radiosa*

*Lindavia ocellata* (Pantocsek), Nakov et al. (2015); *Cyclotella ocellata* Pantocsek

*Lindavia polymorpha* (Meyer & Håkansson), Nakov et al. (2015); *Cyclotella polymorpha* Meyer & Håkansson

*Lindavia pseudocomensis* (Scheffler), Nakov et al. (2015); *Cyclotella pseudocomensis*

*Lindavia rossii* (Håkansson), Nakov et al. (2015); *Cyclotella rossii* Håkansson

*Lindavia Sechkinae* (Stachura-Suchoples, Genkal & Khursevich), Nakov et al. (2015);
*Pliocaenicus Sechkinae* Stachura-Suchoples, Genkal & Khursevich
*Lindavia tripartita* (Håkansson), Nakov et al. (2015); *Cyclotella tripartita* Håkansson

**METHODS**

**Slide preparation:** The sediment sample is weighed to ~0.0075g. 30% hydrogen peroxide is added and heated at 100°C for approximately two and a half hours. After the sediment is washed it is deposited into chambers where it mixes and settles onto the cover slips for approximately twelve hours. The water is drained from the chambers, and the cover slips are left to air dry. The dried cover slips are mounted onto slides using Naphrax.
APPENDIX B: CYCLOTELLA FIGURES AND TABLES

Table B-1: *Cyclotella* summary statistics (minimum, maximum, mean, and standard deviation) of diameter measurements from the sampled time periods.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Age (ka)</th>
<th>Total Valve Diameter (TVD) (µm)</th>
<th>Central Area Diameter (CAD) (µm)</th>
<th>CAD/TVD Ratio (%)</th>
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Figure B-1: Log transformed histogram comparisons of total valve diameter (µm), central area diameter (µm), and striae/10µm between samples.
Figure B-1 Continued: Log transformed histogram comparisons of total valve diameter (µm), central area diameter (µm), and striae/10µm between samples.
Figure B-1 Continued: Log transformed histogram comparisons of total valve diameter (µm), central area diameter (µm), and striae/10µm at between samples.
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Figure B-1 Continued: Log transformed histogram comparisons of total valve diameter (µm), central area diameter (µm), and striae/10µm between samples.
APPENDIX C: *SURIRELLA* FIGURES AND TABLES

Figure C-1: Bivariate plot of the length and width (µm) of the *Surirella* groups (A: red, B: blue, C: green, D: orange, E: purple, F: light blue, G: dark pink, H: light brown, I: light pink).
Figure C-2: Log transformed histograms of length and width within the *Surirella* groups (µm).
Figure C-2 Continued: Log transformed histograms of length and width within the *Surirella* groups (µm).
Figure C-2 Continued: Log transformed histograms of length and width within the *Surirella* group (μm).