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A diatom-inferred water-depth transfer function from a single lake in the northern California Coast Range

Jiwoo Han · Matthew Kirby · Joe Carlin · Benjamin Nauman · Glen MacDonald

Abstract This study examines the relationship between water depth and diatom assemblages from lake-sediment-surface samples at Kelly Lake, California. A total of 40 surface-sediment samples (integrated upper 5 cm) were taken at various depths within the small (~ 3.74 ha) 5.7 m-deep lake. Secchi depths, water temperature, pH, salinity, conductivity, and total dissolved solids were also measured. Some diatom species showed distinct association with depth (e.g., *Fragilaria crotonensis, Nitzschia semirobusta)*. The relationship between the complete diatom assemblages and water depth was analyzed and assessed by depth-cluster analysis, a one-way analysis of similarity, principal components analysis and canonical correspondence analysis. Statistically significant differences were found between the assemblages associated with shallow depth (0–1.25 m), mid-depth (1.25–3.75 m), and deep-water (3.75–5.2 m) locations. The relationship between diatom assemblages and lake depth allowed two transfer models to be developed using the Modern Analogue Technique and Weighted Averaging Partial Least Squares. These models were compared and assessed by residual scatter plots. The results indicate that diatom-inferred transfer models based on surface-sediment samples from a single, relatively small and shallow lake can be a useful tool for studying past hydroclimatic variability (e.g., lake depth) from similar lakes in California and other regions where the large number of lakes required for traditional transfer-function development may not exist.

Introduction

Paleolimnological transfer functions are often developed from multi-lake-training sets and can be a useful paleolimnological tool for reconstructing many variables including lake depth (Gregory-Eaves et al. 1999; Gomes et al. 2014; MacDonald et al. 2016). However, in many hydrologically sensitive regions, including much of California (CA), natural lakes are relatively rare, making the use of multi-lake-training sets unfeasible. CA has experienced prolonged hydroclimatic anomalies over the twenty-first century (e.g., severe droughts) that appear to be, at least in part, related to anthropogenic climate change (MacDonald et al. 2016; Swain et al. 2018; Dong et al. 2019;

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Glover et al. 2020; Zamora-Reyes et al. 2021). Understanding how recent CA hydroclimate variability relates to longer timescale (e.g., Holocene), natural variability has been an important topic of research over the past decade (Briles et al. 2011; MacDonald et al. 2016; Kirby et al. 2019). Unfortunately, instrumental climate records only extend back a little more than a century and do not capture the full range of potential natural hydroclimatic variability. Paleoclimatic approaches can provide proxy hydroclimatic records that extend back millennia. The proxy-climate archives provided by lake sediments are one useful source of such information, and although not as plentiful as in some regions, such lake archives are available in areas of CA.

Diatoms (Class: Bacillariophyceae), single-celled algae and phytoplankton, have been shown to be an important proxy indicator useful to investigate hydroclimatic variability as manifest in lake-level changes or changes in lake salinity (Fritz et al. 1991; Gasse et al. 1995; Battarbee 2000; Smol and Cumming 2000; Zhang et al. 2007; Kingsbury et al. 2012; Ramón Mercau and Laprida 2016; Gushulak et al. 2017; Gushulak and Cumming 2020). There are several reasons why diatoms are good paleoenvironmental indicators—they are common in lake environments, they are sensitive to hydrological and limnological changes (e.g., lake depth, water chemistry), and their distinctive silica frustules are well-preserved and readily identified in lake sediments. Many studies have shown that diatoms can be used to reconstruct past variations in lake depth, including providing quantitative estimates using statistical transfer functions based on modern diatom-water-depth relationships (Yang and Duthie 1995; Gregory-Eaves et al. 1999; Laird et al. 2010, 2011; Wolin and Stone 2010; Gomes et al. 2014; MacDonald et al. 2016).

This research will focus on diatom flora and water depth. Lacustrine hydrologic budgets, which are related to lake-water depth, are closely associated with regional hydrologic budgets and the interplay between precipitation and evaporation. This association is especially robust in regions with strong seasonal precipitation/evaporation contrasts, such as CA and the American West, where winter precipitation and summer evaporation dominate the annual hydrologic budget of lakes (Shuman and Donnelly 2006 as cited in Wigdahl-Perry et al.

2016). Changes in lake level are closely related to paleohydroclimatic changes (Fritz 1990; Smol and Cumming 2000; Kirby et al. 2007; Blazevic et al. 2009; Laird et al. 2010; Kingsbury et al. 2012; MacDonald et al. 2016).

There are very few diatom-inferred paleoecological transfer functions from Californian lakes. Bloom et al. (2003) published a paper that established a diatom-inferred salinity and water-temperature-transfer function from a network of lakes (n=57) in the Sierra Nevada. While the initial study was about salinity and water temperature, not water depth, this was expanded to include a water-depth-transfer function in a subsequent publication (MacDonald et al. 2016). Unfortunately, few areas of CA outside formerly glaciated Sierra Nevada contain an adequate lake density to make a traditional multi-lake-based diatom-transfer-function model.

In recent years, studies have shown that diatom-depth-transfer functions can be successfully developed using multiple sediment-surface samples taken from different depths in a single lake (Laird and Cumming 2009; Laird et al. 2010, 2011; Gushulak et al. 2017). The resulting transfer function can then be applied to sediment cores from the same lake (Laird and Cumming 2009; Laird et al. 2010; Faith and Lyman 2019). This approach is ideal for CA where lake basins in many regions are rare and the development of a multi-lake-transfer function, which requires 30 lakes or more, is not possible. In this study, we address the question of whether or not there is a statistically significant difference in the diatom floral assemblages found in the sediments taken at different depths from a single lake. Moreover, we explore whether or not these relationships are statistically strong enough to develop diatom-depth-transfer functions that could be applied to sediment cores from that same lake. The study site is Kelly Lake, a small lake in the mountains of northwestern CA. The results of this study support the potential wider usefulness of single-lake-transfer-function development in other regions where there are insufficient lakes for traditional training-set development. Kelly Lake is also smaller and deeper than previously published sites from which such transfer functions have been derived, increasing the range of lakes this approach might be applied to.

Study site

Kelly Lake (41.91° N, 123.52° W; 1346 m asl) is located in the Klamath Mountains (northern California Coast Range), approximately 10 km from the Oregon border (Fig. 1). The study site is in the Confederated Tribes of Grand Ronde, Karuk, Cow Creek Umpqua, and Cayuse, Umatilla and Walla Walla Tribes' territory (Native Nation Digital 2021). The lake is landslide-formed, small (~3.74 ha), with a maximum water depth of 5.7 m. The surface drainage basin is small (~47 ha) and sits in sedimentary rocks and metavolcaniclastic sedimentary rocks (Irwin 1994). Although presently a closed basin (as of 2019) with a small inlet, there is a spill point at the east shoreline, approximately 3–4 m above modern lake level, indicating that overflow is possible during wet years. Dead and felled trees are concentrated at the outlet area and suggest a dynamic lake level with flow over the spill. Some active springs characterize the surrounding drainage basin with modern inflow observed occurring at the lake's northwest shoreline. The vegetation surrounding the lake's fringe is mostly reeds and sedges, with submergent macrophytes and mosses near the shoreline. Above the shoreline, there is forested vegetation with an overstory of Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), sugar pine (*Pinus lambertiana* Douglas), incense cedar (*Calocedrus decurrens* (Torr.) Florin) and white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.).

The mean January and July temperatures of the region are approximately 3 °C and 19 °C, and the mean annual precipitation is 176 mm (Western Regional Climate Center 2016; Fig. 2). This data was collected from the Elk Valley Station (42.00° N, 123.43° W), which is the nearest station to the study site (~12 km linear distance) at 521 m asl. The average winter precipitation (December, January, February) is approximately 353 mm, while the average summer precipitation (June, July, August) is roughly 17 mm. Kelly Lake experiences some snow during fall and winter, with ~1148 mm of total snowfall. Therefore, Kelly Lake's annual hydrologic budget is typical of the Mediterranean climate type and driven by variations in winter precipitation and summer evaporation.

Methods

Fieldwork

In July 2019, 40 surface sediment samples were obtained at various lake-water depths from the upper 5 cm of the sediment–water interface using a
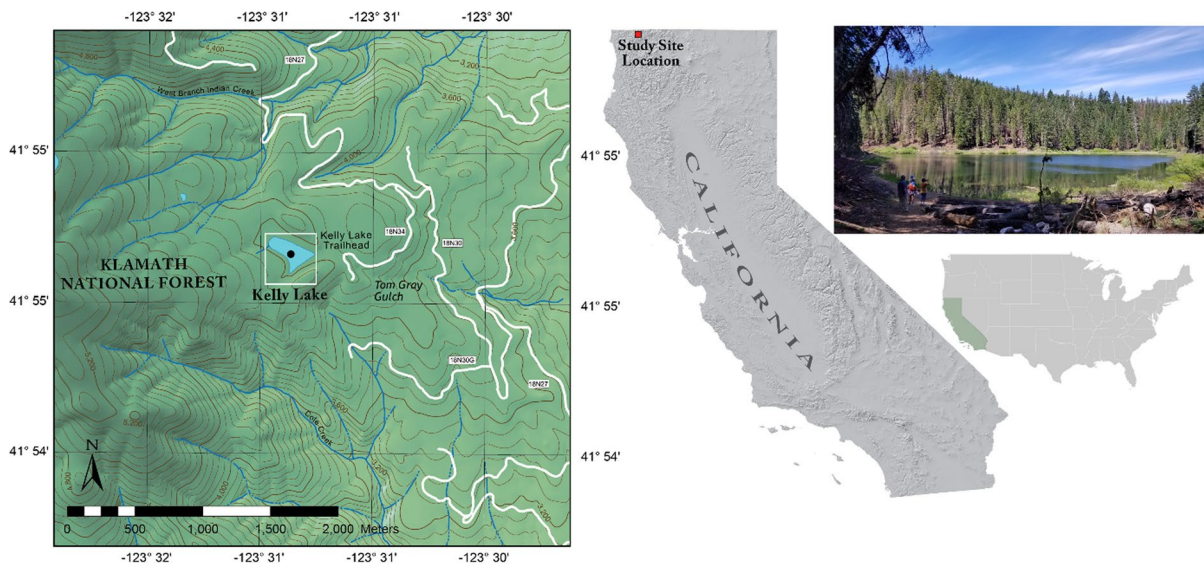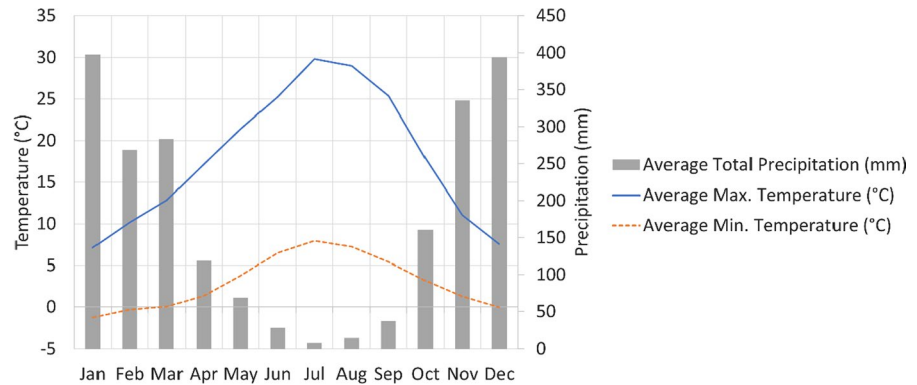

Fig. 1 Map and field picture of Kelly Lake in Klamath Mountains, California, USA. The view is from the outlet location approximately 3–4 m above modern lake level

Fig. 2 Monthly mean precipitation and temperatures from Elk Valley in California, USA (site: 042749), which is the nearest climate station to Kelly Lake (*Source*: Western Regional Climate Center 2016)

mini-Glew gravity corer (Fig. 3). Our sampling technique captured the sediment–water interface, visible in the clear plastic tube, ensuring that we did not over-penetrate into older sediments. The topmost sediments were extremely water-saturated with a diffuse sediment–water interface. We wished to obtain sufficient sediment for diatom analysis and other analyses from each surface site. We also were not aiming

at the annual or near-annual resolution, but rather the integration of diatoms from the past decade or so to have an averaged observation of the diatom flora. We have obtained ^{137}Cs data from the central portion of the lake that indicate that the 1963 peak is deeper than 5 cm (5–10 cm) and ^{210}Pb data suggests sedimentation rates of ~3 yr/cm (Table S2), therefore the upper 5 cm generally represents perhaps 15 years or

Fig. 3 Surface sediment samples from Kelly Lake (KLSS2019) were obtained along three transect lines (three blue lines with numbers 1, 2, 3) mostly (two yellow lines are ropes tied for the transects). Most samples were taken within the lake except for a few points near the margin and exposed shoreline outside of the lake (x marks). The samples along the transects were taken ~2 m apart at a constant interval
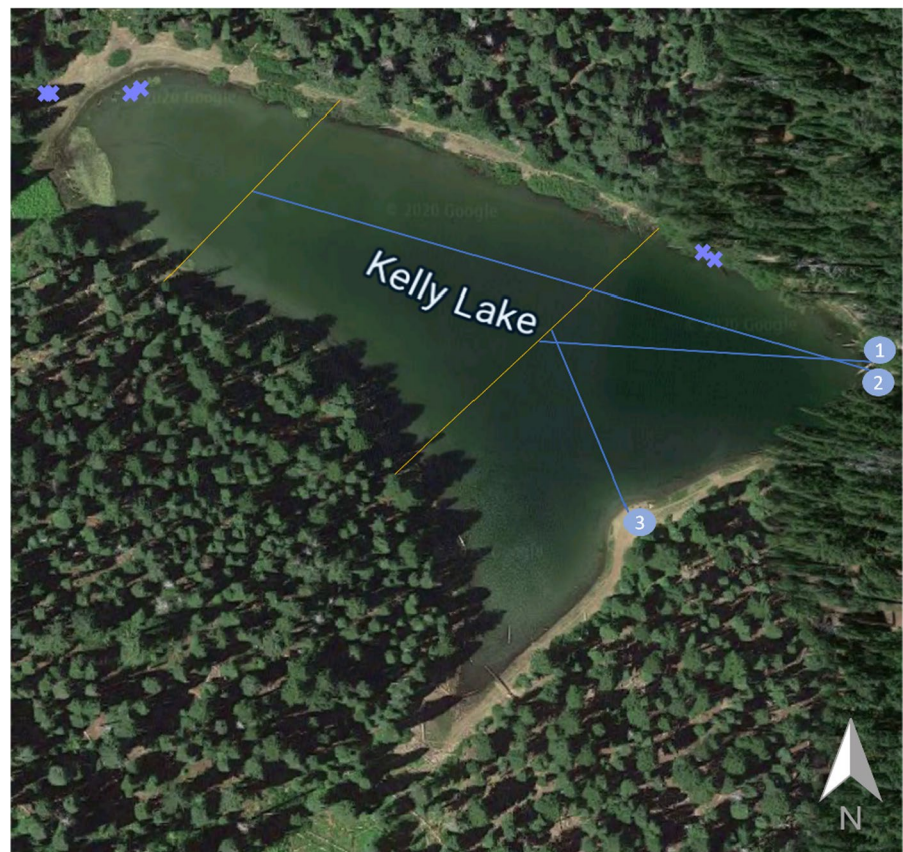
so of time. Although there may have been some slight variations in lake conditions over this time period, we believe that our sampling regime captures a reasonable representation of the overall recent conditions of Kelly Lake. The samples were designated as KLSS2019 #. KLSS2019 1 to 26 and KLSS2019 33 to 40 were taken along three transects: nine samples from Transect 1, seventeen samples from Transect 2, and eight samples from Transect 3 (Fig. 3, Fig. S1). Each sediment sample was collected at approximately 2 m distance from adjacent samples. KLSS2019 27 to 32 were collected at the very margin of the lake and from the lake's inlet emergent vegetation (Fig. 3). Lake-water depths were measured at each sampling point. Secchi-disc depths were also measured at each sampling point to delineate the average depth of the modern photic and aphotic zones and the light conditions at the sediment surface for each sampling point.

The lake's water chemistry was also measured near the surface at the center of the lake three times and averaged. Table 1 shows the average values of all the measurements. Five variables, such as pH, conductivity, water temperature, total dissolved solids, and salinity, were measured with a digital water testing meter (Apera Instruments PC60 Premium Multiparameter Tester Meter).

Diatom-sample preparation and identification

Approximately 0.2 g of wet surface sample was treated with 5 ml of 30% H_2O_2 in a 100 ml beaker with 10 ml of distilled water to remove organic materials in the sediments. After the sample was heated on a hot plate at 120 °C for an hour, the top solution was decanted. A micro spatula of sodium hexametaphosphate was put in the beaker for deflocculation. After 15–30 min of reaction, the beaker was filled with distilled water, and let the diatoms be deposited. The prepared diatoms were mounted using Pleurax (mountmedia) on microscope slides. At least 400 diatom valves were counted per sample at

1000 × magnification under a light microscope (Nikon Labophot-2) with oil immersion. For diatom-species identifications we followed the taxonomy of Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b) with supplementary printed and online sources (Kulikovskiy et al. 2016; Spaulding et al. 2019; Potapova et al. 2020; Jüttner et al. 2022).

Data selection and analysis

The taxa used for statistical analysis and calibration-set development were selected after screening the diatom data. Taxa that appear at more than 5% abundance were selected for constructing the stratigraphic diatom diagram and constrained clustering, and taxa occurring at more than 1% abundance in at least one sample were chosen for statistical analyses and transfer-function development. A diatom-stratigraphy diagram was drawn in R version 4.1.3 (RStudio Team 2020) using the rioja package (Juggins 2020). A depth-constrained cluster analysis (CONISS) was also performed in R with the vegan package (Oksanen et al. 2020) to determine if lake-depth zones could be discerned in the diatom assemblages from Kelly Lake. The cluster analysis-based zones were calculated with the Bray–Curtis distance method to measure the dissimilarity between communities (Grimm 1987). A one-way analysis of similarity (ANOSIM) was also conducted using PAST (PAleontological STatistics, version 4.01) software package to test statistically the differences in the distribution of diatom assemblages among the identified depth zones (Hammer et al. 2001). Principal component analysis (PCA) was conducted in R on the covariance matrix to further explore differences in the diatom assemblages from different lake depths and the important diatom taxa contributing to those differences. Canonical correspondence analysis (CCA) with Monte Carlo permutation tests (999 permutations) was also performed in R with the vegan and CCP packages to examine if water depth is a significant variable on the diatom distribution for developing a transfer function (Oksanen et al. 2020; Menzel 2022). The CCA incorporated 22 diatom taxa from 40 surface samples and two environmental variables—water depth of the surface-sample location and its depth below the photic zone as measured using the Secchi disc. Lastly, two diatom-inferred water-depth-transfer functions were developed with the modern analogue technique (MAT),

Table 1 Average (n = 3) water chemistry and depth of photic zone in deep waters for Kelly Lake in July 2019

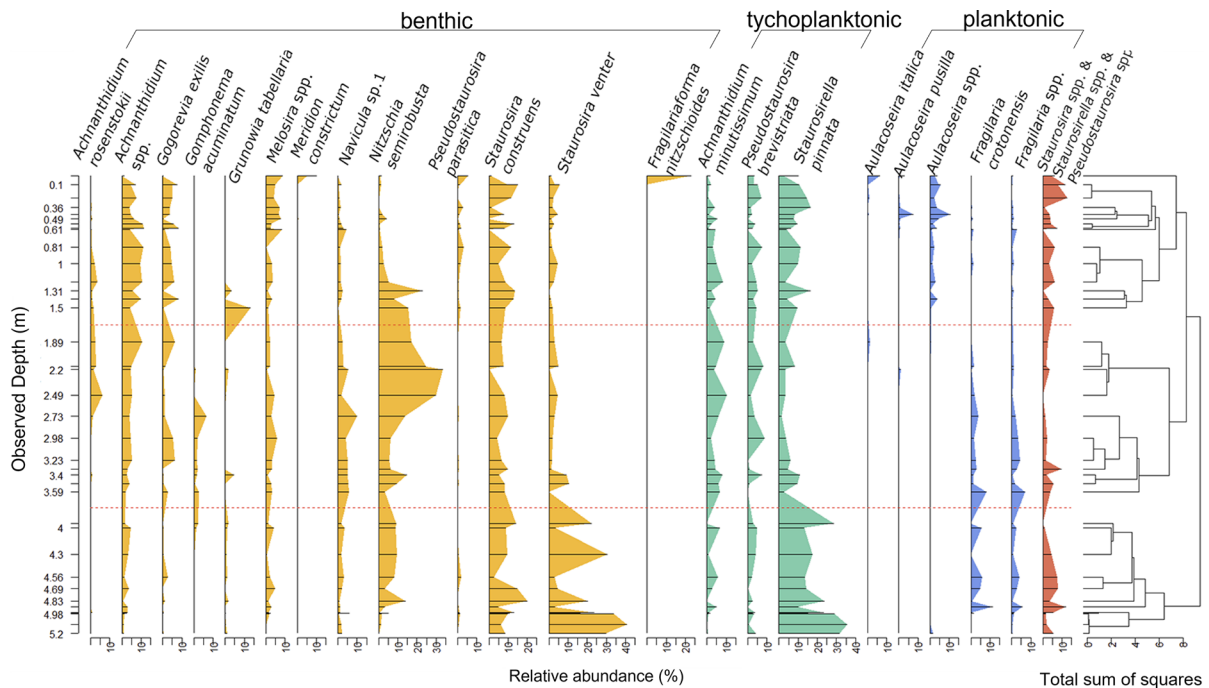| pH	Conductivity	Water temperature	Total dissolved solids	Salinity	Avg. photic zone depth
8.21	66.27 μS/cm	23.4 °C	42.57 ppm	0.03 ppt	4.12 m

Fig. 4 Diagram of diatom taxa which appear in more than 5% in at least one sample in surface sediment samples from Kelly Lake (KLSS2019). The y-axis indicates lake-water depth. The x-axes indicate the relative abundances in % for the diagram part and the total sum of squares for the CONISS part. Yellow color-coded indicates benthic, green color-coded means tychoplanktonic, blue color-coded indicates planktonic, and red-color coded means sum of broken or unidentifiable girdle-view species from *Staurosira* spp., *Staurosirella* spp., and *Pseudostaurosira* spp.

and with weighted average partial-least squares (WA-PLS) using the PAST software. The dissimilarity for MAT was measured using squared chord distance. The root mean square error of prediction (RMSEP) was estimated for both models, and the RMSEP values are based on the degree of error between the observed and the expected value. Thus, the lower the value, the more significant it is.

Results

Diatom diagram

We identified over 150 diatom taxa in Kelly Lake. Among them, 21 taxa (14 genera and 17 species) were selected for statistical analysis. These all appeared at > 5% abundances in at least one sample (Fig. 4). There were thirteen benthic taxa (*Navicula* spp., *Achnanthidium* spp., *Achnanthicium rosenstockii* (Lange-Bertalot) Lange-Bertalot, *Gogorevia*

exilis (Kützing) Kulikovskiy & Kociolek, *Gomphonema acuminatum* Ehrenberg, *Grunowia tabellaria* Rabenhorst, *Meridion constrictum* Ralfs, *Nitzschia semirobusta* Lange-Bertalot, *Pseudostaurosira parasitica* (W.Smith) E. Morales, *Staurosira construens* Ehrenberg, *S. venter* (Ehrenberg) Cleve & J.D.Möller, *Melosira* spp., *Fragilariforma nitzschioides* (Grunow) Lange-Bertalot), five planktonic taxa (*Aulacoseira* spp., *A. italica* (Ehrenberg) Simonsen, *A. pusilla* (F.Meister) A.Tuji & A.Houki, *Fragilaria crotonensis* Kitton, *Fragilaria* spp.), and three tychoplanktonic taxa (*Achnanthidium minutissimum* (Kützing) Czarnecki, *Staurosirella pinnata* (Ehrenberg) D.M.Williams & Round, *Pseudostaurosira brevistriata* (Grunow) D.M.Williams & Round). Due to the difficulties in identification under 100× light microscopy, some *Staurosira* spp., *Staurosirella* spp., and *Pseudostaurosira* spp. are counted together as *S & S & P* spp. Figure 4 shows the diatom diagram and the CONISS dendrogram where the Kelly Lake surface-sediment samples are divided into

three diatom-water-depth zones: shallow (0–1.25 m), mid-depth (1.25–3.75 m), and deep-water zones (3.75–5.2 m).

A one-way analysis of similarity (ANOSIM)

According to the CONISS analysis, Kelly Lake was divided descriptively into three depth zones, which are shallow (0–1.25 m), mid-depth (1.25–3.75 m), and deep (3.75–5.2 m). The deep-water zone generally represents samples where the sediment–water interface is in the aphotic zone of the lake. A cluster analysis that was unconstrained by depth and thus allowed samples to be freely grouped was also performed (Fig. S2). It displays prominent clusters of samples from the constrained cluster zones, particularly samples from the shallow and deep-water zones. However, there are also some clustering of mixed samples and some samples which do not cluster closely with any others. ANOSIM was subsequently conducted to determine whether there was a statistically significant difference between the three depth zones by examining the similarity of the diatom communities (Elmslie et al. 2020).

There are statistically significant differences between the three depth zones based on the result of ANOSIM. The P values in Table 2a indicate significant differences between the groups. The values are close to 0, which allowed us to reject the null hypothesis ("there is no difference") and indicated that there were statistically significant differences between the diatom assemblages from the three different water-depth zones (i.e., shallow, mid-depth, and deep zones).

R values were also calculated in ANOSIM, which showed the strength of the depth factors on the samples. Generally, if an R value is lower than 0.2, it means that the factors had a small effect on the variables. However, the R values in Table 2b were larger than 0.2. Accordingly, it further indicates that the lake depth was influential on the composition of diatom communities observed in the lake sediments and the differences between the depth zones.

Therefore, the ANOSIM results indicate that there were differences in the diatom communities by specific depth zones, and lake depth was an influential factor in the diatom-assemblage composition in the sediments of Kelly Lake.

Principal component analysis (PCA)

The cumulative variation of PCA axis 1 and axis 2 was 70.5%, the first two axes were considered in this study (Fig. 5). The diatom assemblages were clustered on the PCA biplot by depth, reinforcing the conclusion that lake depth has a strong control on the diatom assemblages preserved in the sediments. PCA axis 1 appears to represent water depths between middle to deep, while PCA axis 2 reflects shallow to middle water depths. The three most important diatom taxa in determining these PCA axes were *Staurosirella pinnata*, *Staurosira venter* and *Nizschia semirobusta*.

Canonical correspondence analysis (CCA) with Monte Carlo permutation tests

Analysis of diatom-lake-environment variables using CCA analysis, including data sets used for transfer-function development, typically yield a percentage of diatom variance explained of between 4 and 23% (Finkelstein et al. 2014; Weckström and Korhola 2001). The CCA analysis indicates that the depth of the sampling site is important in determining the taxonomic composition of the diatom flora recovered. CCA axis 1, which is strongly associated with lake depth at the surface-sample location, accounted for 15.5% of the variance (Fig. 6). CCA axis 2 is more

Table 2 Results of ANOSIM significance parameters between depth zones of surface-sediment samples from Kelly Lake. (a) indicates P values showing significance levels, (b) indicates R values showing the strength of the factors on the samples

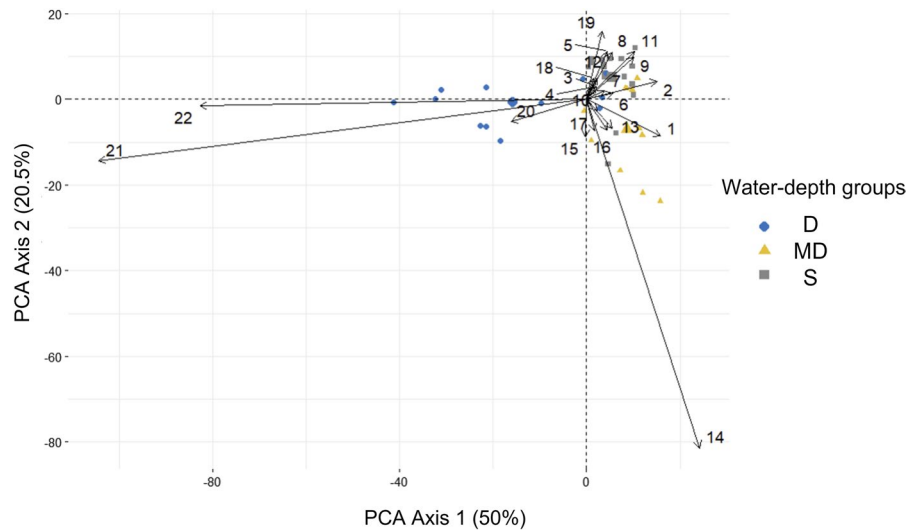|	Shallow	Mid-depth	Deep		Shallow	Mid-depth	Deep
(a) P values				*(b) R values*			
Shallow		0.0027	0.0001	Shallow		0.2983	0.5265
Mid-depth	0.0027		0.0001	Mid-depth	0.2983		0.4732
Deep	0.0001	0.0001		Deep	0.5265	0.4732	

Fig. 5 Principal component analysis biplot showing main diatom taxa and the surface-sediment samples by water-depth groups from Kelly Lake. Water-depth groups are: D: deep (3.75–5.2 m), MD: mid-depth (1.25–3.75 m), S: shallow (<1.25 m). The diatom-taxa codes are as follows: 1=*Achnanthidium minutissimum*, 2=*Achnanthidium* spp., 3=*Aulacoseira italica*, 4=*Aulacoseira pusilla*, 5=*Aulacoseira* spp., 6=*Fragilaria crotonensis*, 7=*Fragilaria* spp., 8=*Fragilariforma nitzschioides*, 9=*Gogorevia exilis*, 10=*Gomphonema acuminatum*, 11=*Melosira* spp., 12=*Meridion constrictum*, 13=*Navicula* sp. 1, 14=*Nitzschia semirobusta*, 15=*Grunowia tabellaria*, 16=*Achnanthidium rosenstockii*, 17=*Pseudostaurosira brevistriata*, 18=*Pseudostaurosira parasitica*, 19=*Staurosira & Staurosirella & Pseudostaurosira* spp., 20=*Staurosira construens*, 21=*Staurosira venter*, 22=*Staurosirella pinnata*

Fig. 6 CCA axis 1 versus axis 2 biplot showing ordination of the main diatom taxa indicated by taxon-species code (see Fig. 5 for diatom taxa and codes) and with the axes loadings for the variables Lake Depth and Depth Below the Photic Zone
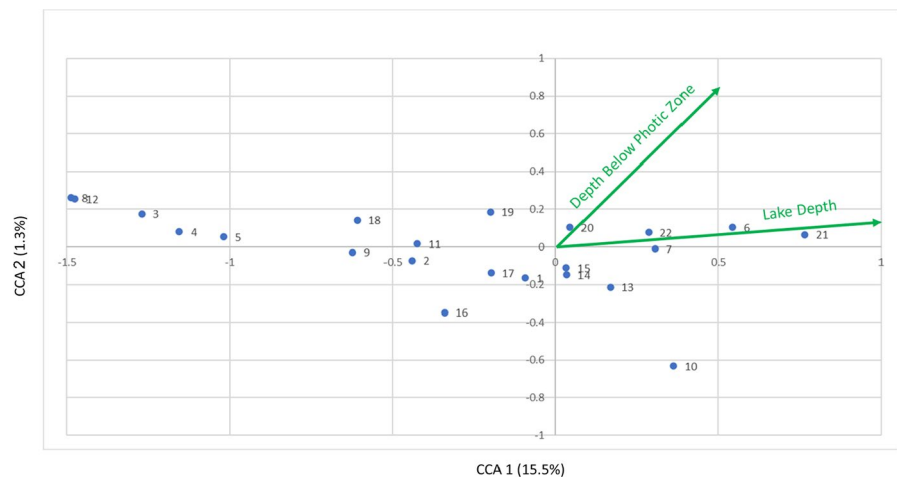
associated with the depth below the photic zone and accounted for 1.3%. CCA axis 1 was indicated as significant by Monte Carlo permutation texts ($p \leq 0.01$; Fig. S3). Species 8=*Fragilariforma nitzschioides* and 12=*Meridion constrictum* are associated with shallow and ephemeral sites and were found at the

shallowest sampling sites at the edge of the lake and ordinate at the extreme negative end of CCA axis 1, while 6=*Fragilaria crotonensis*, 20=*Staurosira construens*, 21=*Staurosira venter*, 22=*Staurosirella pinnata* are considered as planktonic and tychoplanktonic species, more likely to be relatively abundant

in deeper waters, and ordinate at the positive end of CCA axis 1.

Diatom-lake-depth-transfer-function models

Two diatom-lake-depth-transfer functions were developed using MAT and WA-PLS. Model construction incorporated diatom taxa that occur > 1% in at least one sample.

The first diatom-inferred water-depth-inference model was developed using WA-PLS (Fig. 7a). The R^2 value is 0.96 and indicates a high degree of correlation between the observed depths and diatom-inferred depths. In this study, the third component for WA-PLS has the lowest RMSEP value (0.66). Therefore, the third component was selected for the WA-PLS transfer function. As seen in the graphs (Fig. 7a),

the WA-PLS model performed better in mid-depths between 2 and 3 m than in shallow and deep depths.

The second transfer function was developed using the MAT method (Fig. 7b). The R^2 value of the MAT transfer function is 0.98, and the RMSEP value is 0.39. In general, the MAT model displays good performance; it performs well in shallow and deep zones and shows a slight over-representation in the mid-depths.

Residual scatter plots

Residual scatter plots (Fig. 8) determined whether there is a trend, and thus a bias, in the models. This was done to determine whether there is a trend in residuals, and thus a bias, in the models. The residuals in the MAT model show a lower trend than the
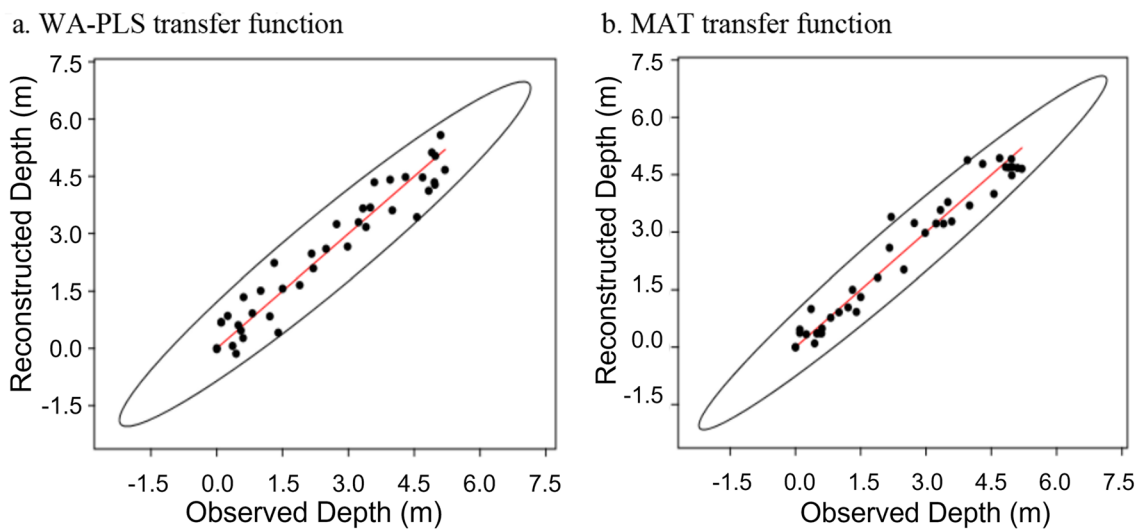

a. WA-PLS transfer function

b. MAT transfer function

Fig. 7 **a** Diatom-inferred water-depth-transfer function using WA-PLS, **b** Diatom-inferred water-depth-transfer function using MAT. The 95% confidence ellipses are indicated

Fig. 8 Residual scatter plots for the two diatom-inferred water-depth-transfer functions developed for Kelly Lake. **a** Residuals of the MAT transfer function, **b** residuals of the WA-PLS transfer function

a. MAT residuals
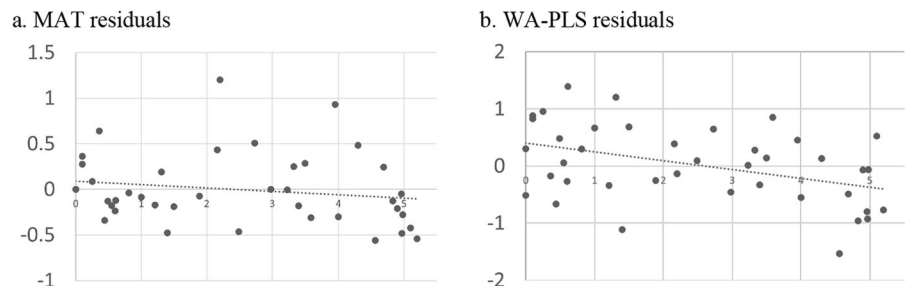
b. WA-PLS residuals

residuals in the WA-PLS model according to the R^2 values. The residuals in MAT are more scattered in the mid-depths, while the ones in WA-PLS are more scattered at the edges of the depths. Even though MAT shows a lower trend than WA-PLS, both have small R^2 values and small slopes. Thus, the residuals in both MAT and WA-PLS do not suggest a strong bias.

Discussion

The statistical analysis indicates that the diatom assemblages found in the surface sediments at Kelly Lake can be statistically grouped into three different depth zones. There are at present a few studies that have examined the relationship between the composition of the diatom community and water depth from a single small lake (Laird and Cumming 2009; Laird et al. 2010, 2011; Gushulak et al. 2017). It is notable that the studies cited above are from boreal Canada and represent lakes that are both much larger (19–1808 ha) and deeper (18–32 m) than Kelly Lake. Not only do our results extend the potential usefulness of single lake-transfer functions to the Mediterranean climate region of CA, but they also demonstrate its applicability to relatively small and shallow lakes. Our study adds to growing evidence that differences in diatom assemblages related to lake depth are preserved in the sediments of small lakes and have the potential for developing lake-specific diatom-depth-transfer functions. Some aspects of diatom ecology pertinent to the results, and the water-depth-inference models developed here are discussed below.

Diatom ecology

Although there are a variety of factors that affect diatom assemblages in the lacustrine environment, this study indicates that the diatom-assemblage compositions in Kelly Lake have a clear correlation with lake-water depths. There are three depth zones identified in Kelly Lake: shallow (0–1.25 m), mid-depth (1.25–3.75 m), and deep zones (3.75–5.2 m). These three distinct depth zones are similar to those discerned for a previous single lake conducted in Canada; although there are many co-occuring diatom species in the Canadian lakes and this study, there were few equivalent major diatom assemblages (Laird and

Cumming 2009; Laird et al. 2010). Recent work by Gushulak and Cumming (2020) indicates that light availability may be the most important factor controlling such depth-dependent diatom-assemblage distributions within individual lakes. It is notable that at Kelly Lake the deep zone identified by the constrained cluster analysis is largely within the aphotic zone that ranges in depth from 3.3 to 4.9 m.

Although details of the ecology of many diatom species remain uncertain, the statistical results from Kelly Lake regarding depth and diatom assemblages can be assessed in light of the known ecology for some individual diatom taxa that show strong depth preferences. Some individual diatom taxa show strong depth preferences. For example, *Fragilaria crotonensis* rarely appears at shallow depths, but it begins to appear at middle depths and becomes dominant in deep zones (Fig. 4). *Fragilaria crotonensis* is known as planktonic and non-motile (Morales et al. 2013). The species forms ribbon-like floating colonies and are associated with the pelagic zone. They prefer strong turbulence to stay afloat (Rioual 2000). *Staurosirella pinnata* is also one of the predominant species in the deep zone. Although some studies demonstrated *S. pinnata* as benthic or planktonic (Fluin et al. 2010; Laird et al. 2011; Hofmann et al. 2020; Park et al. 2017), it can be considered as tychoplankton because of its lifestyle (Hobbs et al. 2017). The species is also known as well adapting to low light-penetration conditions (Laird et al. 2010). These characteristics of *S. pinnata* explain why it appears dominantly at larger depths in Kelly Lake, even under some low photic or aphotic conditions (Fig. S1) because it could inhabit greater depths as tychoplankton, or as a benthic form tolerant to low light conditions.

There are also many distinguishing species for mid-depth zones in Kelly Lake. *Nitzschia semirobusta* is the predominant species for the mid-depth zone. This species is known as a motile benthic species and has a wide tolerance for trophic status even though it favors oligotrophic conditions (Bartozek et al. 2018). As the water-chemistry results from Kelly Lake indicate oligotrophic to mesotrophic conditions, it seems the water chemistry of the lake is favorable to *N. semirobusta*. Also, the environment with enough light penetration and the species' motility help this species to be dominant in mid-depth areas.

Pseudostaurosira parasitica is mainly found in shallow depth zones, and this is readily explainable because the species is benthic and must remain in the photic zone to survive (Morales 2010a). Abundant *Aulacoseira* spp. are indicative of the shallow zone. The genus is well-known for including a variety of planktonic species, especially meroplankton (having both benthic and planktonic characteristics depending on their life-cycle stages). There are possible reasons why *Aulacoseira* spp. appear more predominantly in the shallow than the deep in Kelly Lake. Some *Aulacoseira* spp. (e.g., *A. pusilla*) prefer shallow depths to take in more nutrients and light (Rioual 2000) or low lake level and enhanced convective mixing (Dean et al. 1984 as cited in Rioual 2000). These reasons might suggest why *Aulacoseira* spp. appears in shallow depth sediments in Kelly Lake.

In addition to the relationships between taxa and three depth zones, there are also a few species typically found in environments at the very margin/edge of the lake or near the shore (e.g., *Meridion constrictum* and *Odontidium mesodon*). These species inhabit very shallow or flowing water or live on emergent plants (Potapova 2009; Hoidal 2013; Leira et al. 2017).

Conversely, some species are abundant at a wide range of depths, such as *Achnanthidium minutissimum* and *Pseudostaurosira brevistriata*. For example, *A. minutissimum* is ubiquitous in diatom-based, paleolimnological studies. Although they are normally classified as benthic, their habitat preferences are variable. Some studies have found that *A. minutissimum* occurs at ∼2 m or shallower depths (Yang and Duthie 1995; Moos et al. 2005), while another study found it occurs at a broad range of depths (Laird et al. 2010). One study concluded that the species is largely found on submerged *Isoetes* (Haberyan 2018). While *A. minutissimum* may not be a useful species for representing distinct depth zones, it may signify zones of overall ecotone changes within a lake (Moos et al. 2005). Similarly, *P. brevistriata* has a complex ecology, classified as tychoplanktonic and non-motile (Morales 2010b). As a result, it is not surprising that *P. brevistriata* is found at various depths at Kelly Lake.

By interpreting diatom assemblages according to each species' habitat preferences and the subsequent statistical results, we conclude that there are clear divisions based upon water-depth zones, and water depth is a crucial factor in the composition of diatom assemblages preserved in the Kelly Lake surface sediments.

Water-depth-inference models

A good transfer-function model should meet two conditions: (1) observations and estimates must be strongly positively correlated, (2) there should be no trends in the residuals (Yoon et al. 2017). There are many ways to develop a transfer function, and WA-PLS and MAT are the two of the most common techniques (Bloom et al. 2003; Cunningham et al. 2005; Laird et al. 2011; Park 2011; Faith and Lyman 2019). In this study, both MAT and WA-PLS perform well in terms of the requisite conditions. However, overall, the MAT transfer model showed better performance than the WA-PLS model with higher R^2 and lower RMSEP values. However, for both transfer functions, the R^2 values were higher than 0.95, and both models showed good representations of diatom-inferred water depths.

In this study, the dissimilarity measure for MAT was determined using a squared chord, which is a metric to assess the signal-to-noise relationship. This distance metric is considered the best for evaluating modern analogs (Jackson and Williams 2004 as cited in Kemp and Telford 2015). It is said that chord-squared distance is more acceptable for closed compositional assemblage data, such as relative abundances, because it highlights the major patterns, while it down-weights rare species (Kemp and Telford 2015). Both MAT and WA-PLS are vulnerable to uneven sampling of the elevation gradient (Kemp and Telford 2015), but most of the samples in this study have been collected evenly, so the weakness should not be influential here.

There are over- and under-estimations at deep and shallow depths in the WA-PLS model within the 95% confidence ellipse, and this could reflect the "edge effect" problem common for weighted average-based models, such as WA and WA-PLS (Birks 2010). This problem causes over- or under-estimations at the edges of the sample depths. However, Kemp and Telford (2015) argued that the influence of "edge effects" is lessened in WA-PLS. The results of our study show that WA-PLS does seem to present some "edge effect" as there are more variable residuals at deep and shallow depths (the edges; Fig. 8b). The

WA-PLS performs better for the middle depths. Conversely, there are over-estimations in the MAT model for the mid-depth ranges, especially in the range of 2 and 3 m. Both models have over- or under-estimations at different depth zones; therefore, inferences of past depths might best be made by using both models.

Conclusions

There are clear, statistically significant differences between diatom assemblages and lake depth in the surface sediments of Kelly Lake. The correlations are strong enough to develop single-lake diatom-inferred lake-depth-transfer models. Our findings indicate that a quantitative reconstruction of past lake depth using diatom assemblages is reasonable for Kelly Lake. As in many parts of the world, CA has few natural lakes outside of the formerly glaciated Sierra Nevada Mountains, yet regional information on long-term hydroclimatic variability throughout the state is very important in providing a context for twenty-first century climate change. Kelly Lake is in a different climatic zone and is also smaller in area and shallower in depth than the Canadian lakes previously examined to develop single lake-transfer functions for depth. This suggests a potentially wider applicability of this approach in terms of region being studied and lake characteristics. The ability to use surface samples from a single lake, coupled with a core from that lake to reconstruct past lake depths, is an important and still developing methodological advance for reconstructing past hydroclimatic variations.

Declarations

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