

1 **Paleolimnological assessment of six lakes on the Kissimmee Chain,**
2 **with implications for restoration of the Kissimmee-Okeechobee-**
3 **Everglades System, Florida USA**

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16 Abbreviated title: Paleolimnology of six lakes on the Kissimmee Chain

17

18 **Abstract**

19 The Kissimmee Basin in south central Florida contains a large, freshwater network that includes
20 the Kissimmee River and nearly two dozen lakes that are headwaters of the Florida Everglades.
21 Management of these lakes is an important part of Everglades restoration. We report a
22 paleolimnological investigation of six lakes in the Upper Kissimmee Basin. Engineering
23 activities connected the lakes and permanently altered hydrology in the 19th and 20th centuries.
24 The lakes were naturally meso-eutrophic, but changes in lake levels and nutrient loading
25 contributed to different degrees of eutrophication. Cyanobacteria were present historically at low
26 levels in Lakes East Tohopekaliga, Cypress, and Tohopekaliga, but increased during the 20th
27 century. Lake Jackson lacked cyanobacteria until recently, but Lakes Kissimmee and Marian had
28 high levels of cyanobacteria since pre-disturbance times. Profound changes in the lakes occurred
29 after engineering activities eliminated natural large fluctuations in water levels that periodically
30 dried large portions of the basins. Salt-tolerant biological indicators previously alternated with
31 freshwater organisms. Large water-level fluctuations moderated aquatic-plant standing crops and
32 reduced organic-matter accumulation. Lakes Kissimmee and Marian showed greatest evidence of
33 former associated wetlands, but lacked large variation in water levels. We recommend
34 disconnecting these lakes from each other and from the Kissimmee River to reestablish large,
35 natural fluctuations in water levels that were part of healthy ecosystem function. Former
36 wetlands should be restored to slow the downstream cascade of nutrients to Lake Okeechobee
37 and the Everglades. This study demonstrates that paleolimnology is useful for assessing
38 hydrological changes that potentially affect lake-restoration efforts.
39

40 **Key words:** diatoms: Florida: Kissimmee Chain of Lakes: paleolimnology: aquatic plants:
41 paleohydrology: stable isotopes:
42

43 The Kissimmee Chain of Lakes is a series of shallow, connected warm-temperate lakes in central
44 Florida, USA. Lakes on the chain are headwaters of the Kissimmee-Okeechobee-Everglades
45 system, which extends from Orange County southward through Lake Okeechobee to the tip of
46 the Florida Everglades, where discharge from the Everglades affects nearshore coral reefs. The
47 lakes are situated in the ~6164-km² Kissimmee Basin, which contains the Kissimmee River, as

48 well as associated streams and wetlands. Historically, the lakes were surrounded by freshwater
49 marshes, pine flatwoods, and wet prairies that were connected by broad, shallow wetlands and
50 creeks (SFWMD: <https://www.sfwmd.gov/our-work/kissimmee-river>, accessed Sept. 2019).
51 Water levels fluctuated seasonally, which facilitated the connection of upper to lower lakes
52 through an extensive marsh complex (U.S. Army Corps of Engineers 1996). A major effort to
53 connect the lakes to the Kissimmee River and to Lake Okeechobee through canal construction
54 began by the early 1880s. Canals were constructed to lower water levels and drain the northern
55 Everglades region, to lessen flood impacts, to expand areas available for agriculture and
56 ranching, and to reduce water flow and flooding in the lower Everglades. Water levels dropped
57 by ~ 1.8 m in lakes throughout the Upper Kissimmee Basin (U.S. Army Corps of Engineers
58 1996), and connections between lakes and associated wetlands were severed (Atlantic and Gulf
59 Coast Canal and Okeechobee Land Company 1885). Throughout the 1900s, wetland areas were
60 drained for agriculture. Marshes adjacent to lakes were reduced to narrow littoral zones, which
61 affected plant and animal communities (U.S. Army Corps of Engineers 1996). Modern areas of
62 the lakes are substantially smaller than their historic sizes because of drainage activities (Osceola
63 County Community Development Department 2015). Upstream urbanization and agriculture led
64 to increases in nutrient loading in some lakes. Point-source inputs had pronounced effects on
65 Lake Tohopekaliga, which in turn affected Lake Cypress (Huber et al. 1982, Dierberg et al.
66 1988, James et al. 1994, Williams 2001). Subsequent channelization of the Kissimmee River by
67 the Army Corps of Engineers in the 1960s had adverse ecological and water-quality
68 consequences for Upper Basin lakes. Current management and nutrient mitigation of lakes on the
69 Kissimmee Chain are important parts of the restoration initiative for the Florida Everglades, the
70 largest Ramsar Convention wetland complex in the USA.

71 Paleolimnology has a well-established role in ecosystem management because it provides

72 long-term environmental information that is often undocumented (Smol 1992, Brenner et al.
73 1993, Battarbee and Bennion 2011, Bennion et al. 2011, Davidson and Jeppesen 2013, Larocque-
74 Tobler 2016). Pre-disturbance conditions in lakes of the Upper Kissimmee Basin are unknown,
75 which has posed a challenge for establishment of appropriate restoration targets for the lakes.

76 This study used paleolimnological methods to analyze a total of 18 sediment cores from
77 Lakes Kissimmee, Cypress, Marian, Jackson, Tohopekaliga, and East Lake Tohopekaliga on the
78 Kissimmee Chain (Fig. 1). The objective was to describe water-quality and ecological
79 conditions, including aquatic plants, algae, and cyanobacteria, during reference periods that
80 represented low human impact on the lakes during the early 1800s, and to document subsequent
81 changes. Additionally, the purpose was to assess changes in nutrient-deposition rates, and to
82 determine whether associated wetlands were present that might have contributed significant
83 amounts of colored dissolved organic carbon to the lakes and attenuated algal production. Our
84 intention was to assist Osceola County Public Works and the Florida Department of
85 Environmental Protection (Florida DEP) in defining appropriate restoration goals for the lakes.

86

87 **Study Sites**

88

89 Lakes on the Kissimmee Chain are managed by South Florida Water Management District, the
90 U.S. Army Corps of Engineers, Florida Fish and Wildlife Conservation Commission, Osceola
91 County Public Works, Florida Department of Environmental Protection, and the U.S. Fish and
92 Wildlife Service. Water quality is highly variable, but recently measured values are shown in
93 Table 1. All lakes have high dissolved color values, and therefore are subject to target
94 chlorophyll *a* values of 20 µg/L (Florida Dept. of Environmental Protection 2013). Lakes

95 Cypress, Jackson, Kissimmee, and Marian are considered impaired because limnetic chlorophyll
96 *a* values exceed this standard, whereas East Tohopekaliga and Tohopekaliga are not impaired
97 (Osceola County Community Development Department 2015). Because of their better water
98 quality, East Tohopekaliga and Tohopekaliga are designated Class III lakes that are protected for
99 fish consumption, recreation, and for wildlife. Tohopekaliga, however, demonstrated extreme
100 hypereutrophic conditions in recent decades (Huber et al. 1982). Lakes Tohopekaliga and
101 Cypress require management of invasive *Hydrilla*. Lake Cypress is impaired for total phosphorus
102 and total nitrogen concentrations as well as for chlorophyll *a*. East Lake Tohopekaliga does not
103 require management to control *Hydrilla*, but it has extensive vegetation that creates problematic
104 floating tussocks. Although Lake Jackson is impaired, it is nearly surrounded by the Three Lakes
105 Wildlife Management Area and by private agricultural lands. Lakes Marian and Kissimmee
106 sustain the highest limnetic total P and chlorophyll *a* concentrations (Table 1). Lake Kissimmee
107 was placed on the federal list of impaired waters in 2006, and it is subject to management for
108 invasive *Hydrilla*.

109

110 ***Historical influences on the lakes***

111 In 1884, Lake Topekaliga and other lakes along the Kissimmee River were described as having
112 "pure, clear water" (Atlantic and Gulf Coast Canal and Okeechobee Land Company 1885).
113 Prairie lands and hardwood forests were situated along the lake shores, with large tracts of
114 cypress (*Taxodium*) in intermittent swamps. Sawgrass (*Cladium jamaicense*), organic-rich
115 sediments, and aquatic plants were reported in wetlands near East Lake Tohopekaliga. A
116 continuous marsh extended from Lake Cypress to the north bay of Lake Kissimmee.

117 Cattle ranches were well established in the Kissimmee Basin by the 1860s (Otto 1985).

118 More extensive impacts began with settlement after the Civil War (c. 1865), when the region was
119 further developed for agriculture and cattle ranching. Kissimmee City was founded on the
120 northern shore of Lake Tohopekalgia in 1883, and the city of St. Cloud was founded in 1909 on
121 the southern shore of East Lake Tohopekaliga.

122 Canal construction to join Upper Basin lakes to the Kissimmee River began in the 1880s.
123 The St. Cloud Canal was dug through marshes to drain East Lake Tohopekaliga into Lake
124 Tohopekaliga. Prior to 1884, East Lake Tohopekaliga was surrounded by cypress swamps and
125 marshes that were left stranded above water levels when the lake was lowered, and logging took
126 place on the shores (Atlantic and Gulf Coast Canal and Okeechobee Land Company 1885). East
127 Lake Tohopekaliga fell 1.1 m in 30 days from the drainage. Sugar-cane agriculture was
128 established in drained areas of East Lake Tohopekaliga by 1883. On the western and southern
129 shores of Lake Tohopekaliga, dredging of wetlands and logging occurred in 1883 and 1884
130 (Atlantic and Gulf Coast Canal and Okeechobee Land Company 1885). Lake Tohopekaliga
131 dropped 0.8 m from drainage, and lakes south of it had lowered water levels. The water level of
132 Lake Okeechobee fell 0.45 m in one year.

133 Population increases occurred after World War II in the cities of Kissimmee and St.
134 Cloud. Point-source discharges into Lake Tohopekaliga began in the 1950s (Williams 2001). By
135 1969, four waste-water treatment plants discharged 82.5 metric tons of phosphorus and 140
136 metric tons of nitrogen per year into Lake Tohopekaliga and its tributaries. Water-quality
137 deterioration was evident by 1969. By 1982, limnetic total P averaged 322 $\mu\text{g/L}$ and chlorophyll
138 *a* averaged 71 $\mu\text{g/L}$ in Lake Tohopekalika (Huber et al. 1982), and nutrients affected lakes that
139 were downstream. In 1988, waste-water discharge into the lake was discontinued.

140 Massive flooding in 1947 after a hurricane prompted the Army Corps of Engineers to
141 deepen and straighten the Kissimmee River to implement flood-control measures (South Florida

142 Water Management District 2014). In the 1960s, the river was extensively channelized, which
143 had serious consequences in terms of shortened water-residence times, higher nutrient
144 concentrations, and ecological impacts on fish and wildlife in Upper Basin lakes and in Lake
145 Okeechobee. In 1999, South Florida Water Management District and the U.S. Army Corps of
146 Engineers began the Kissimmee River Restoration Project, which is scheduled to restore 71 km
147 of the natural meandering system by 2020.

148

149 ***Recent water-level manipulation for sediment removal***

150 Florida Fish and Wildlife Conservation Commission has lowered water levels and dewatered
151 sediments in several of our study lakes to remove invasive plants and sediment by burning and
152 scraping operations in recent years. Water levels in Lake Tohopekaliga were drawn down ~ 1.8
153 m in 1971, 1979, 1987, and 2004, and scraping occurred in 1987 and 2004. During the 2004
154 operation, approximately 1350 ha. of lake bottom were exposed, and 6.04 million cubic meters
155 of organic material were removed (K. Lawrence, pers. comm.). In 1995, Lake Kissimmee was
156 drained to half the size of its normal area for scraping and burning. Because Lake Cypress is
157 controlled by the structure in Lake Kissimmee, its water level also fell. In 2004, East Lake
158 Tohopekaliga was drawn down approximately 1.8 m, and 95% of the littoral zone was scraped.
159 Drawdowns and sediment removal continue as a management practice in lakes of the Kissimmee
160 Chain.

161

162 **Materials and Methods**

163

164 ***Field methods and core collection***

165 We conducted a systematic spatial survey of sediment distribution (Whitmore et al. 1996) in
166 Lakes Cypress, East Tohopekaliga, Kissimmee, Jackson, Marian, and Tohopekaliga to identify
167 optimal coring sites. Water depth at each site was measured by lowering a weighted, metered
168 steel cable to the sediment/water interface. Total depth to hard, sandy sediments was measured at
169 each site by inserting magnesium/zirconium rods into the sediment and subtracting the water
170 depth to estimate soft-sediment thickness. Sediment cores of ~ 1 m in length were recovered with
171 a 1.83-m-long, 7-cm diameter piston corer (Fisher et al. 1992), and backup cores for pollen and
172 macrofossil analyses were taken at the same stations using a 4-cm diameter, 1.83-m-long
173 cellulose acetate butyrate piston corer.

174 Cores were sectioned in the field at 5-cm intervals to 20 cm depth, then at 3-cm or 4-cm
175 intervals to the base of the cores. Samples were stored in Nalgene plastic cups in the dark on ice
176 until they were refrigerated in the laboratory. Diatom samples were collected in the field at the
177 top of each sectioned interval and were preserved with alcohol.

178

179 *Lead and cesium dating and core chronologies*

180 ^{210}Pb dating of all sediment cores was performed at University College London by gamma
181 spectrometry using an ORTEC HPGe GWL series well-type coaxial low background intrinsic
182 germanium detector (Appleby et al. 1986, Schelske et al. 1994). Unsupported ^{210}Pb activity was
183 calculated by subtracting ^{226}Ra , as estimated from ^{214}Pb , from the total ^{210}Pb activity. ^{210}Pb was
184 determined via its gamma emissions at 46.5 keV, and ^{226}Ra by the 295 keV and 352 keV gamma
185 rays emitted by its daughter isotope ^{214}Pb . ^{137}Cs and ^{241}Am , which are artificial radionuclides
186 from weapons testing, were measured by their emissions at 662 keV and 59.5 keV to provide
187 absolute time markers for c. 1963 (Appleby et al. 1986). Corrections were made for the effect of

188 self-absorption of low energy gamma rays within the sample (Appleby et al. 1992). For Lake
189 Marian core 31_III_2018_MAR_328, radioisotopic analyses stopped just short of ^{210}Pb
190 supported levels, so excess ^{210}Pb activity was extrapolated by linear regression for two samples.
191 Sediment age/depth relationships were calculated using the constant rate of supply model
192 (Appleby and Oldfield 1983), with occasional age adjustments based on location of ^{137}Cs peaks.
193

194 *Diatom analyses*

195 Diatom samples were digested in the laboratory with 35% H_2O_2 and $\text{K}_2\text{Cr}_2\text{O}_7$ according to Van
196 der Werff (1955), and slides were prepared with Naphrax mounting medium. Approximately 500
197 valves were counted and identified at each level at 1500x magnification using compound
198 microscopy. Diatoms were identified using standard floras (Patrick and Reimer 1966, 1975,
199 Krammer and Lange-Bertalot 1986-1991) and taxonomic websites (<https://diatoms.org/>).
200 Zonation of diatom assemblages in sediment cores was determined by constrained incremental
201 sum of squares (CONISS) hierarchical agglomerative cluster analysis using the statistical
202 program R and the rioja package (Juggins 2012). The number of significant zones in each cluster
203 analysis was determined with a broken-stick model (Bennett 1996) using the rioja package.

204 Historic water-quality inferences were obtained with two diatom-based inference models.
205 The models were constructed with a calibration set of 75 Florida lakes that we utilized in past
206 studies (Riedinger-Whitmore et al. 2005, Kenney et al. 2014, Whitmore et. al. 2015), but the
207 models were updated slightly in the present study. Limnetic total P concentrations were inferred
208 by weighted-averaging inverse tolerance regression using \log_{10} limnetic total P values and a
209 calibration of 71 P-limited or nutrient-balanced lakes ($r^2 = 0.880$, $\text{RMSE} = 0.186 \log_{10}$ total P).
210 In some lakes that have very high limnetic total P values, particularly those that have been N

211 limited, the limnetic total P model will not perform reliably. Consequently, N-limited lakes were
212 removed from the calibration set for that model. Limnetic chlorophyll *a* concentrations were
213 inferred by weighted averaging inverse tolerance regression using \log_{10} limnetic chlorophyll *a*
214 values for a calibration set of 73 lakes (r^2 adj. = 0.831, RMSE = 0.265 \log_{10} limnetic chlorophyll
215 *a*). Statistical analyses for all diatom-based inferences were performed using R Version 3.0.2
216 software (R Core Team 2014) and the package rioja (Juggins 2012). In the calibration set of
217 lakes, the correlation coefficient between log total P and log chlorophyll *a* (the inferred
218 variables) is approximately 0.86 ($p < 0.001$), so the models are interdependent and their
219 inferences are not reported simultaneously. Selection of the appropriate model and model
220 performance were evaluated by comparing water-quality inferences with measured water quality
221 during recent periods.

222 We used Analog Matching with dissimilarity cutoffs determined by Bray-Curtis (10%
223 cutoff) and Monte Carlo simulation methods (cutoff = 0.617) to assess whether there were
224 suitable analogs for the sediment-core samples among lakes in the calibration set. Sediment cores
225 that did not have sufficient analogs to interpret significant parts of their histories were interpreted
226 by qualitative methods only. Analog matching was performed using R Version 3.0.2 software (R
227 Core Team 2014) and the package rioja (Juggins 2012).

228 ***Sedimented algal and cyanobacterial pigment analyses***

230 Approximately 7-10 g of wet sediment were taken from archived sediment samples for pigment
231 analyses. Pigments were extracted using acetone, following Swain (1985), Riedinger-Whitmore
232 et al. (2005), and Whitmore et al. (2018). Acetone was added to sediment samples, and samples
233 were shaken on a Thermo Scientific MaxQ 2000 shaker table following each acetone addition for
234 approximately 30 minutes. Samples were centrifuged at low speed (2000-3000 RPM, IEC HN

235 SII centrifuge) for ~10 minutes, and the supernatant from each sample was removed using an
236 adjustable volume pipette.

237 We assayed percent organic matter content of samples from all cores by loss on ignition
238 at 550° C (Heiri et al. 2001). Loss on ignition data were used to estimate the organic matter
239 content per gram wet sediment for each sample, and to determine pigment concentrations.
240 Chlorophyll derivatives were estimated by measuring extracts at 665 nm (Swain 1985) using a
241 Hitachi U-2800A UV- VIS Spectrophotometer, and are reported as absorbance/g organic matter.
242 Percent native chlorophyll, an indicator of pigment degradation in samples, was determined by
243 measuring absorbance at 665 nm before and after acidification with HCl. Subsamples for total
244 carotenoids were saponified using a 20% KOH/methanol mixture, extracted into petroleum ether,
245 and measured at 448 nm. Total carotenoids were reported as absorbance/gram organic matter.

246 Subsamples for oscillaxanthin and myxoxanthophyll cyanobacterial pigments were
247 extracted into petroleum ether, air dried, and re-dissolved in ethanol. Absorbance was measured
248 at 412, 504, and 529 nm, and the trichromatic method was used to correct for phorbins
249 contamination, and to calculate oscillaxanthin and myxoxanthophyll at the major peaks of
250 absorbance for each pigment. Pigment concentrations were expressed as µg pigment/g organic
251 matter.

252

253 *Sediment chemistry analyses*

254 Total P was assessed by colorimetry following EPA Method 365.1 for 10 cores in the IFAS Soil
255 and Water Science Department Analytical Research Lab at the University of Florida,
256 Gainesville, Florida, and for 8 cores on a Spectro Acros 2 ICP by Waters Agricultural
257 Laboratory in Waycross, Georgia using AOAC Method 957.02. Total N, total C, and stable

258 isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analyses of organic matter were performed at the University of Florida
259 Department of Geological Sciences on freeze-dried sediment. A Thermo Electron DeltaV
260 Advantage isotope ratio mass spectrometer coupled with a ConFlo II interface linked to a Carlo
261 Erba NA 1500 CNHS Elemental Analyzer was used for these analyses. Sample gases were
262 measured relative to laboratory reference N_2 and CO_2 gases. CO_2 values were standardized to
263 CMUF REF (Carrara Marble-University of Florida Reference Gas), and N_2 values were
264 standardized to UF- N_2 REF, both of which are UF in-house reference standards. $\delta^{13}\text{C}$ was
265 expressed as per mil (‰) deviation from the Vienna PeeDee Belemnite (VPDB) limestone
266 standard, and $\delta^{15}\text{N}$ was expressed as per mil (‰) deviation from the atmosphere.

267

268 *Pollen, macrofossil, and ostracod analyses*

269 Pollen and macrofossil analyses were performed on a minimum of 5 samples from each sediment
270 core around the depths that corresponded to the pre-disturbance reference periods to determine
271 the nature of reference aquatic-plant communities, and to investigate the presence of associated
272 wetlands. The number of samples analyzed was limited by funding constraints, but analyses for
273 two entire cores were provided voluntarily by student investigators on our projects.

274 Preparation of pollen samples followed Faegri and Iversen (1989) and Bennett and Willis
275 (2001). Deflocculation of samples was done using a dilute detergent solution. A 10% HCl
276 solution was added to remove carbonates. Samples were boiled in a KOH (or NaOH) solution to
277 remove humic acids and unsaturated organic soil colloids. Samples were then washed through a
278 0.2-mm sieve with deionized water to remove coarse mineral particles and large organic matter.
279 The supernatant was decanted into distilled water, then a few drops of 10% HCl was added to
280 prevent the formation of the precipitant $\text{Zn}(\text{OH})_2$. Remaining cellulose and organics were

281 removed by acetolysis with anhydric acetic acid (nine parts) and H₂SO₄ concentrate (one part),
282 and samples were centrifuged at 1500 rpm for 20 minutes. Samples were washed with glacial
283 acetic acid and heated briefly in 10% KOH to halt acetolysis and to prepare them for staining.
284 Semi-permanent mounts with silicone oil were prepared for microscopic analysis at 400x. Pollen
285 was identified using standard references, including Willard et al. (2004).

286 Macrofossil analysis was performed following methods outlined by Birks (2017).
287 Approximately 20-50 cc of sediment were measured for each sample by water displacement in a
288 graduated cylinder, then the sample was soaked in 10% sodium hexametaphosphate [(NaPO₃)₆]
289 to disperse sediment particles from macrophyte remains. The sediment and deflocculant mixture
290 was rinsed through sieves with screen sizes of 1 mm, 500 μm, 250 μm, 125 μm using a shower-
291 head attachment that distributed the point of water impact to reduce damage to the macrofossils.
292 The 1-mm screen allowed for separation of larger seeds and macrophyte parts, and the 125-μm
293 screen was used for recovery of small material, including small seeds and characean oospores.
294 Screened material was suspended in water in a petri dish for examination under a dissecting
295 binocular microscope. Identification was performed with the use of a macrofossil reference
296 collection at the University of South Florida St. Petersburg.

297 Ostracods also were examined using stereo microscopy in samples that had been cleaned
298 and screened for macrofossil analysis and that disclosed the presence of ostracods. Ostracods
299 were identified using references that included Furtos (1936), Keyser (1977), Teeter (1980), and
300 Perez (2010).

301

302 ***Stable carbon isotopes versus C/N ratio plots***

303 We plotted δ¹³C values versus C/N ratios of organic matter in sediment cores to investigate

304 changes over time in the primary producer communities that contributed organic matter to the
305 sediments. We included in those plots some representative $\delta^{13}\text{C}$ and C/N values for aquatic
306 macrophytes, algae, and cyanobacteria. Our intention was not to determine which specific taxa
307 were present in the past, but rather we sought to assess general changes in past macrophyte
308 lifeform groups and algal/cyanobacterial populations. Funding did not permit analysis of $\delta^{13}\text{C}$
309 and C/N values of modern plants and algae in lakes of our study, so we used published $\delta^{13}\text{C}$
310 values for primary-producer taxa and functional groups collected from similar highly productive
311 Florida lakes. Floating-leaved and emergent plants, as well as surface bloom-forming algae and
312 cyanobacteria, use atmospheric CO_2 as a carbon substrate ($\delta^{13}\text{C}$ about -8‰; Gu and Alexander,
313 1986), so $\delta^{13}\text{C}$ values of organic matter derived from those groups should be similar across lakes.
314 In contrast, the $\delta^{13}\text{C}$ values of submerged primary producers can vary across lakes as a function
315 of the $\delta^{13}\text{C}$ of dissolved inorganic carbon in the water, which is influenced by carbonate
316 dissolution in the watershed, inputs of allochthonous carbon, and the in-lake rate of primary
317 production (Brenner et al., 1999). Most of the $\delta^{13}\text{C}$ and C/N data we used came from the Brenner
318 et al. (2006) study of Lake Panasoffkee, Sumter County, Florida, a shallow, eutrophic lake that
319 lies in karst bedrock, similar to the lakes of our study. Lake Panasoffkee receives substantial
320 amounts of bicarbonate-rich groundwater input. Thus, our plots of $\delta^{13}\text{C}$ versus C/N values
321 display relative positions for the modern taxa, and stratigraphic changes in the sedimented
322 organic-matter values in cores are interpreted in general terms with respect to those taxa.

323 Brenner et al. (2006) reported $\delta^{13}\text{C}$ and C/N values for *Typha*, *Sagittaria*, *Hydrocotyle*,
324 *Pontederia*, *Scirpus*, *Salix*, *Nymphaea*, *Ceratophyllum*, *Najas*, *Potamogeton*, *Vallisneria*, and
325 *Hydrilla*, and for periphyton and epiphytic algae. Stable isotope values for submerged aquatic
326 primary producers can vary seasonally, but that study reported averages from summer and winter

327 seasons, which displayed little difference. We used $\delta^{13}\text{C}$ values for *Pistia* from the Florida
328 Everglades (Wang et al. 2002), and assumed a C/N ratio similar to that for *Nymphaea*, because
329 both genera have similar structural tissue for the floating lifeform (much aerenchyma tissue). We
330 found few published $\delta^{13}\text{C}$ values for cyanobacteria in our region, and those displayed a wide
331 range depending on taxonomic affinity and location in the water column. Rosen et al. (2017)
332 reported that a 2016 cyanobacterial surface bloom on Lake Okeechobee was caused mostly by
333 *Microcystis aeruginosa*, so we used the reported $\delta^{13}\text{C}$ value for that species (Gu and Alexander
334 1996), which is distinctly negative compared with subsurface algae and cyanobacteria as a
335 consequence of atmospheric CO_2 fixation. We assumed a C/N ratio the same as that for algae (~
336 <10).

337

338 **Results**

339

340 ***Field survey and core collection***

341 Sediment distribution is highly variable in shallow Florida lakes because of resuspension and
342 transport. These processes can affect the completeness of sediment records (Whitmore et al.
343 1996). Sediment surveys and replicate cores were needed to ensure that one or more intact
344 historical records would be obtained from each lake. In addition, lake drawdowns and sediment-
345 removal operations in recent decades posed significant risks that portions of records would be
346 missing.

347 Sediments were probed at 62 stations in Lake Cypress, 59 stations in East Lake
348 Tohopekaliga, 34 stations in Lake Jackson, 50 stations in Lake Kissimmee, 26 stations in Lake
349 Marian, and 74 stations in Lake Tohopekaliga to find suitable coring sites. A total of 18 primary

350 cores were taken from the six lakes between November 2016 and March 2018. Three cores were
351 retrieved from Lake Cypress, three from East Tohopekaliga, three from Lake Kissimmee, two
352 from Lake Jackson, and two from Lake Marian. Five sediment cores were collected from Lake
353 Tohopekaliga: one from the northern basin, two from the central basin, and two from the
354 southern basin.

355 We selected one core to represent each study lake in this paper because including all
356 eighteen cores would have been too excessive for presentation, and would not have been more
357 informative. Many cores did not yield complete records. We used sediment dating results to
358 select cores that had more intact profiles, and evaluated that based on radioisotopic activities and
359 total ^{210}Pb inventories, among other evidence. Some cores contained more sand lenses than other
360 cores, and diatom breakage was occasionally too extensive for interpretation in portions of the
361 profiles. Sediment records showed good concurrence within lakes, but certain records were more
362 intact and informative. We chose the most intact record to represent each of the six lakes, but
363 occasionally explain that some evidence, such as *Ruppia* seeds or ostracods, were more abundant
364 in other cores that had less complete records. We also chose cores from the central portions of
365 basins for this presentation rather than cores from peripheral areas and embayments.

366

367

368 ***Lake Cypress***

369 Radioisotopic activities for Lake Cypress core 29_XII_2017_CYP_3 are shown in Fig. S1, and
370 dates are shown in Table S1. In the lower 60 cm of Lake Cypress core 29_XII_2017_CYP_3
371 (Fig. 2), prior to the 1880s, salt-tolerant diatom taxa such as *Mastogloia smithii*, *Campylodiscus*
372 *clypeus*, and *Anomoeoneis sphaerophora* var. *sculpta* indicated that extremely low water levels

373 occurred at times (Whitmore et al. 2018). These taxa co-occurred with *Cyclotella meneghiniana*,
374 a eutrophic species (optimum total P = 61 µg/L; Whitmore et al. 2018) that is less salt tolerant.
375 Mixed assemblages suggested extreme variations in water levels. Excessive diatom breakage,
376 which precluded quantitative assessment, occurred several times in pre-disturbance samples of
377 one core from Lake Cypress, and it was associated with brief periods of dry conditions prior to
378 the 1880s. Constrained incremental sum of squares hierarchical agglomerative cluster analysis
379 (CONISS) and the broken-stick model showed that a statistically significant change in diatom
380 assemblages occurred c. 1881 (Fig. 2). Salt-tolerant taxa disappeared in all three cores around the
381 time of engineered water-level changes, after which there was a transition to dominance by
382 *Aulacoseira granulata*, a eutrophic species (optimum total P = 45 µg/L; Whitmore et al. 2018)
383 that requires open waters for suspension in the water column. Another change occurred in the
384 early 1900s to dominance by hypereutrophic, tychoplanktonic *Pseudostaurosira brevistriata* and
385 *Staurosira construens* var. *venter* (optimum total P, respectively, = 127 µg/L and 89 µg/L),
386 which our studies have shown is often associated with cyanobacteria in the water column
387 (Whitmore et al. 2018). Tychoplanktonic taxa spend much of their life histories growing on
388 surfaces, but they are intermittently suspended in the water column by waves and currents.
389 Diatom-based water-quality inferences from Lake Cypress were not available because the mixed
390 salt-tolerant assemblages in the lower halves of the cores had no analogs among lakes in the
391 calibration set (Table S1).

392 Pigment concentrations in the sediments are shown for core 18_XI_2016_CYP_40 (Fig.
393 2). Chlorophyll and carotenoid pigment values were stable below 50 cm in the core, then
394 increased rapidly more than 3 fold after 1883 when Lake Cypress was connected to the
395 Kissimmee Chain by canals. The cyanobacterial pigments oscillaxanthin and myxoxanthophyll

396 were present occasionally prior to 1945, then increased more than 10 fold to the present time
397 (Fig. 2). Total P deposition rates increased 19 fold, and total N increased 3.5 fold since c. 1855.

398 The plot of $\delta^{13}\text{C}$ versus C/N ratios showed that sedimented carbon at the base of the core
399 was composed primarily of submerged aquatic plants and epiphytic algae (Fig. 3). Sediment
400 carbon sources initially were largely floating-leaved vegetation, then in the top 40-cm of the core
401 (since c. 1945), sources were cyanobacteria and/or algae that used atmospheric CO_2 for
402 photosynthesis. In pre-disturbance samples of core 18_XI_2016_CYP_40, *Taxodium* (cypress)
403 pollen represented about 5% of the assemblage, which was a low-level indication that there were
404 associated swamps in the area. *Taxodium* pollen was comparatively rare in the other two cores
405 (Table S7). Pollen from other wetland taxa *Morella* (bayberry), *Nyssa* (water tupelo), and *Salix*
406 (willow) also were present. Pollen data from the pre-disturbance period indicated the presence of
407 *Pontederia*, *Typha*, *Sagittaria*, *Nymphaea*, *Nuphar*, and *Myriophyllum*. Macrofossil analyses
408 showed abundant *Chara* in lowermost pre-disturbance samples, which was evidence of relatively
409 clear waters (Table S13). *Chara* declined rapidly prior to the 1880s and was replaced by
410 *Nymphaea*, a shift that often occurs with eutrophication and diminished light availability
411 (Blindow 1992, Sayer et al. 2010a, 2010b, Bennion et al. 2018). Plant macrofossils during the
412 pre-disturbance period also included remains of *Najas* and *Potamogeton*.

413

414

415 ***East Lake Tohopekaliga***

416 Radioisotopic activities for East Lake Tohopekaliga core 9_VIII_2017_ETOH_244 are shown in
417 Fig. S2, and dates are shown in Table S2. In profiles of two cores from East Lake Tohopekaliga,
418 diatoms were nearly absent from ~10-cm segments in each record because of substantial
419 breakage. This breakage occurred in core 9_VIII_2017_ETOH_244 around the 25-35-cm depth

420 (Fig. 4). Diatoms below that level, principally those towards the left in Fig. 4, were largely
421 benthic and epiphytic taxa. Several benthic taxa below the 30-cm level were noteworthy for high
422 salinity tolerances, and those included *Nitzschia scalaris*, *Mastogloia smithii*, *Anomoeoneis*
423 *sphaerophora* var. *sculpta*, and particularly *Campylodiscus clypeus*. Prior to 1879, salt-tolerant
424 diatoms co-occurred with *Cyclotella meneghiniana* and *Aulacoseira ambigua*, which are
425 eutrophic indicators (*A. ambigua* optimum total P = 49 µg/L; Whitmore et al., 2018) that
426 typically occur as plankton in the open-water limnetic zone of lakes. These mixed assemblages
427 suggested extreme fluctuations in water levels. An increase to a high percentage (72%) of *C.*
428 *clypeus* above the 40-cm level indicated that the large preservation hiatus in Fig. 4 was a
429 prolonged low-water-level event. CONISS showed statistically significant changes in diatom
430 assemblages after c. 1879 (Fig. 4). These changes occurred around the time (1883) that water
431 levels were changed permanently by canal construction. Dominance shifted to planktonic
432 *Aulacoseira granulata* until c. 1980, then to tychoplanktonic *Pseudostaurosira brevistriata* and
433 *Staurosira construens* var. *venter*, which indicated persistent cyanobacteria (Whitmore et al.
434 2018). Diatom-based water-quality inferences for the early history of East Lake Tohopekaliga
435 were not available because mixed salt-tolerant assemblages in the lower portions of the cores
436 resulted in those samples having no analogs in the calibration set (Table S2).

437 Percent native chlorophyll values for core 9_VIII_2017_ETOH_244 indicated fairly
438 consistent pigment preservation throughout the core. Chlorophyll derivatives and total carotenoid
439 values were low below the 45-cm level in the core (no date available), then increased from c.
440 1879 to the 1970s (Fig. 4). Myxoxanthophyll and oscillaxanthin cyanobacterial pigments
441 appeared only above the 10-cm level (c. 1973; Fig. 4), which was consistent with the timing of
442 diatom indication of cyanobacteria influence.

443 $\delta^{13}\text{C}$ and C/N ratios (Fig. 3) showed that carbon deposited in pre-disturbance basal
444 sediments was largely from submerged vegetation and epiphytic algal sources. Sedimented
445 carbon sources progressed to floating-leaved vegetation towards the core top, and a recent
446 decrease in C/N ratios possibly indicated cyanobacterial influence. Pollen grains in pre-
447 disturbance samples were generally sparse, and *Taxodium* (cypress) and *Morella* (bayberry)
448 pollen were low in abundance despite the reported presence of associated swamps before the
449 1880s. Pollen grains, however, did show evidence of emergent and floating-leaved *Pontederia*,
450 *Sagittaria*, *Nymphaea*, *Nuphar* and sedges, as well as submerged *Myriophyllum* and
451 *Potamogeton*. Macrofossil evidence from pre-disturbance samples showed abundant *Chara*,
452 which indicated clear or shallow waters. In the 41-44-cm sample from the core, seeds of *Ruppia*
453 *maritima* were observed, which indicated very high solute concentrations prior to c. 1865.

454

455 ***Lake Jackson***

456 Below the 70-cm level in core 16_III_2018_JAC_307 (Fig. 5), salt-tolerant diatoms were
457 present as in Lakes Cypress and East Tohopekaliga. These taxa included *Nitzschia scalaris*,
458 *Anomoeoneis sphaerophora* var. *sculpta*, *Campylodiscus clypeus*, and *Halamphora*
459 *coffaeiformis*. These species co-occurred with eutrophic taxa that included *Cyclotella*
460 *meneghiniana*, *Aulacoseira ambigua*, and *A. granulata*, the latter two being planktonic forms
461 that indicated deeper limnetic waters. Water-level fluctuations were suggested by these mixed
462 assemblages. Diatoms between the 70- and 40-cm levels showed extensive breakage that
463 suggested a long period of extremely low water levels, as in East Lake Tohopekaliga.
464 Radioisotopic activities for core 16_III_2018_JAC_307 are presented in Fig. S3. Unsupported
465 ^{210}Pb activity showed an abrupt decline at the 12.5-cm level (c. 1975), which suggested a

466 possible hiatus caused by sediment transport. As a result, we adopted a conservative approach
467 and rejected the calculated ^{210}Pb dates, and assigned a nominal reference date of "c. 1900" to the
468 depth at which unsupported ^{210}Pb activity reached zero. The error term for excess ^{210}Pb activity
469 in the 20-24-cm interval was greater than the excess ^{210}Pb activity value, so we set the date of "c.
470 1900" for 24 cm depth in the core. Diatom assemblages changed significantly above the section
471 of extensive diatom breakage. The planktonic, eutrophic taxa *Aulacoseira ambigua* and *A.*
472 *granulata* became dominant just before c. 1900, and salt-tolerant taxa no longer were present.
473 Diatom assemblages near the top of the core showed an increase in some periphytic taxa (e.g.,
474 *Karayevia clevei*) without prominent indication of change in water quality, and the
475 tychoplanktonic taxa that we associate with competitive exclusion by cyanobacteria were not
476 present. As in Lakes Cypress and East Tohopekaliga, quantitative water-quality inferences were
477 not available because salt-tolerant assemblages in the lower portions of the cores resulted in
478 samples having no analogs in the calibration set (Table S3). Equivocal dates did not permit
479 estimation of changing rates of nutrient deposition.

480 Chlorophyll derivative values were low (< 1.0 abs/g org matter) in sediments deposited
481 prior to c. 1900 (~30 cm) in core 16_III_2018_JAC_307, which indicated low historical algal
482 productivity (Fig. 5). Chlorophyll derivatives and total carotenoid concentrations increased to ~
483 2-3 abs/g above the 20-cm level. Percent native chlorophyll, the indicator of pigment
484 preservation quality, declined in the upper 28 cm of the core, which showed that pigment
485 concentration increases were not an artifact of preservation. Myxoxanthophyll and oscillaxanthin
486 cyanobacterial pigments were present occasionally at low concentrations below the 15-cm level
487 in the core, but they increased to 7.3 and 3.8 $\mu\text{g/g}$ organic matter, respectively, in the top 10 cm.

488 $\delta^{13}\text{C}$ versus C/N ratios (Fig. 3) indicated that carbon deposited in sediments at the bottom

489 of the core was largely from submerged aquatic vegetation that might have included *Vallisneria*,
490 *Ceratophyllum*, and *Najas*, as well as carbon from algae or periphyton. Sedimented carbon
491 signatures changed to sources that probably included floating-leaved vegetation and
492 algae/cyanobacteria towards the core top. Pollen analysis of pre-disturbance samples at 70-100
493 cm deep in the core showed very low numbers of grains of the wetland *Taxodium* (cypress),
494 *Nyssa* (water tupelo), *Salix* (willow), and *Morella* (bayberry), but pollen was present from
495 grasses and asters, such as are found in natural grasslands and dry prairies in the vicinity of the
496 lake today (Table S9). Pollen analysis revealed *Myriophyllum* in pre-disturbance samples, and
497 plant macrofossils included *Chara*, *Najas*, and some seeds of *Nymphaea*. Macrofossil remains
498 showed that *Chara* was abundant in the 80-85 cm sample, but disappeared above that level in the
499 core (Table S15).

500

501 ***Lake Tohopekaliga***

502 Lake Tohopekaliga core 19_I_2017_TOH_202 was retrieved in the central basin of this 3-lobed
503 lake. Radioisotopic activities for core 19_I_2017_TOH_202 are shown in Fig. S6, and dates are
504 shown in Table S6. Diatom assemblages below the 60-cm level contained a large number of
505 planktonic taxa that included *Cyclotella meneghiniana*, *Synedra radians*, and *Cyclotella*
506 *distinguenda*. In addition, these samples included *Anomoeoneis sphaerophora* var. *sculpta*,
507 *Mastogloia smithii*, *M. braunii*, and *M. smithii* var. *lacustris*, which indicated high solute
508 concentrations that resulted from low water-level conditions (Fig. 6). We interpreted these mixed
509 assemblages as being caused by large fluctuations in water level prior to the 1890s. CONISS and
510 the broken-stick model showed a statistically significant change in diatom assemblages above the
511 60-cm level (c. 1890), and taxa indicative of high-salinity conditions were no longer present.

512 Eutrophic and planktonic species of *Aulacoseira* spp. became dominant around the 50-cm level
513 in the core (c. 1916). After c. 1931, diatom dominance shifted to more highly eutrophic benthic
514 taxa that included *Pseudostaurosira brevistriata*, *Staurosirella berolinensis*, and *Staurosira*
515 *construens*. This transition suggested increased influence of cyanobacteria on planktonic diatom
516 assemblages (Whitmore et al. 2018). Salt-tolerant diatoms below the 50-cm level resulted in
517 samples that had no analogs in the calibration set (Table S6), so quantitative water-quality
518 inferences were not available.

519 Chlorophyll derivative concentrations were <0.3 abs/g organic matter below the 65-cm
520 level (prior to 1897), and they increased steadily to about 4.0 abs/g organic matter at the top of
521 the core (Fig. 6). Total carotenoid concentrations varied around 0.5 abs/g organic matter below
522 the 40-cm level in the core (c. 1950), then increased to 1-2 abs/g organic matter in the topmost
523 samples. Oscillaxanthin and myxoxanthophyll cyanobacterial pigments were present and
524 variable around 0.1-1 µg pigment/g organic matter below the 40-cm level, then increased to ~ 2
525 µg pigment/g organic matter of oscillaxanthin and 5 µg pigment/g organic matter of
526 myxoxanthophyll in the topmost samples. Although $\delta^{15}\text{N}$ values of sedimented organic matter
527 tended to be unchanged in all other lakes of this study, $\delta^{15}\text{N}$ values in Tohopekaliga core
528 19_I_2017_TOH_202 showed a decline (Fig. 6) that is a typical response to nitrogen-fixing
529 cyanobacteria (Brenner et al. 1999; Riedinger-Whitmore et al. 2005). The decline in $\delta^{15}\text{N}$ values
530 was consistent with diatom evidence of increased cyanobacteria presence (Whitmore et al. 2018).

531 $\delta^{13}\text{C}$ versus C/N ratios indicated that submerged aquatic vegetation, periphyton, and algae
532 were important sources of sedimented carbon prior to 1897, but signatures changed rapidly
533 thereafter to reflect sources that included cyanobacteria, algae, and possibly floating-leaved-
534 vegetation (Fig. 3).

535 Pollen from grasses, sedges, and asters in pre-disturbance samples (~100-60 cm depth)
536 indicated that marshes or open grasslands were present in the vicinity (Table S12). Pollen from
537 wetland taxa, which included *Taxodium*, *Salix*, and *Morella*, were present only in very low
538 numbers. Pollen from *Pontederia*, *Myriophyllum* and *Typha domingensis* were present. Plant
539 macrofossils in pre-disturbance samples (~113-60 cm depth) showed abundant *Chara*, which
540 indicated clear or shallow waters. *Nymphaea* appeared around 65-cm depth in the core as *Chara*
541 declined (Table S18). Macrofossil analyses also showed *Ruppia maritima* seeds in pre-
542 disturbance sediments of three cores from Lake Tohopekaliga, which indicated periods of very
543 high solute concentrations during pre-disturbance times. *Ruppia* appeared in two cores from the
544 southern basin and in one core from the central basin. In one core from the southern basin, up to
545 111 *Ruppia* seeds were found in analyzed samples.

546 Ostracods showed evidence of very high solute concentrations as a result of extreme
547 water-level fluctuations during pre-disturbance times. In the 113-89-cm levels of core
548 19_I_2017_TOH_202, freshwater to oligohaline ostracods included *Darwinula stevensoni*,
549 *Cyprideis salebrosa*, *Physocypria krapelini*, *Limnocythere floridensis*, *Limnocythere inopinata*,
550 and *Cypridopsis vidua*. Several of these taxa plus *Cypretta brevisaepta* and *Cypridopsis*
551 *okeechobei* were present in pre-disturbance samples from a core in the southern basin. Ostracods
552 were not observed again after the 1890s in any sediment samples. Their disappearance likely
553 resulted from stabilized water levels that precluded high dissolved solute concentrations, but
554 reduction of macrophytes and increased sediment deposition also might have contributed to their
555 decline (Keyser 1977, Holmes 1992, Ruiz et al. 2013). Total P accumulation rates increased 4-12
556 fold in the central basin, and total N accumulation rates increased 4-23 fold.

557

558 **Lake Kissimmee**

559 Lake Kissimmee core 27_XII_2017_KIS_2 was retrieved from the main basin of the lake.
560 Radioisotopic activities for core 27_XII_2017_KIS_2 are shown in Fig. S4, and dates are
561 presented in Table S4. The diatom assemblage profile (Fig. 7) shows that *Aulacoseira* spp. were
562 present at ~10% of assemblages or greater throughout the entire core. *Pseudostaurosira*
563 *brevistriata* and *Staurosira construens* var. *venter*, which are most abundant during advanced
564 eutrophication with cyanobacteria (Whitmore et al. 2018), were present consistently at
565 percentages similar to *Aulacoseira* spp. These diatoms indicated that Lake Kissimmee was
566 eutrophic and has sustained high productivity since well prior to 1826. Salt-tolerant diatoms were
567 not present in the Lake Kissimmee cores, and analog matching results showed that diatom
568 assemblages throughout the core had many analogs (5-13, generally > 10) among lakes in the
569 calibration set (Table S4). Diatom-based limnetic total P inferences obtained by weighted
570 averaging for the pre-disturbance period were approximately 61 µg/L at the base of the core
571 during the early 1800s, and they generally increased to the present time (Fig. 7, Table S4).
572 Florida Department of Environmental Protection (Florida DEP) provided a modern limnetic total
573 P average of 64.1 µg/L for 2000-2006 (Table 1) for comparison, and our diatom-based limnetic
574 total P inference for that time period was ~76.6 µg/L. We note that the lake has highly variable
575 water quality, with a limnetic total P range of 9-700 µg/L during 2000-2006 (Polk County Water
576 Atlas <https://polk.wateratlas.usf.edu/>), so although our inference is somewhat high, there might
577 be a question about representativity of the modern reported mean. Total P accumulation rates in
578 core 27_XII_2017_KIS_2 increased approximately 74 fold from 1886 to the present time, and
579 total N accumulation rates increased approximately 12 fold.

580 Chlorophyll derivative values were < 1 abs/g organic matter below ~50 cm (prior to

581 1880s) in core 27_XII_2017_KIS_2, then increased gradually above the 50-cm level to 4.4 abs/g
582 organic matter at the top of the core (Fig. 7). Total carotenoid values were < 1 abs/g organic
583 matter below the 20-cm level (c. 1990), but increased to 2 abs/g organic matter. Most notably,
584 the cyanobacterial pigments myxoxanthophyll and oscillaxanthin were found throughout the
585 Lake Kissimmee cores at values ranging from 1-6 µg pigment/g organic matter, which indicated
586 that cyanobacteria populations were continuously present since prior to the 1880s.

587 $\delta^{13}\text{C}$ versus C/N ratios (Fig. 8) were essentially unchanged throughout the length of the
588 sediment core (since prior to 1826), and they suggested that carbon deposited in sediments was
589 consistently influenced by cyanobacteria and algae, and possibly to some extent by floating-
590 leaved vegetation as well.

591 Pollen from pre-disturbance samples showed high amounts of *Taxodium* grains (~17% of
592 assemblages), which indicated that swamps were associated with Lake Kissimmee prior to 1826.
593 Pollen from the wetland taxa *Nyssa*, *Salix*, and *Morella* supported that conclusion (Table S10).
594 Plant macrofossils showed virtually no evidence of submerged aquatic vegetation, but seeds
595 from floating-leaved nymphaeids were present (Table S16), which indicated turbid waters from
596 algae/cyanobacteria, or high dissolved organic carbon concentrations (color) from associated
597 swamps.

598

599 ***Lake Marian***

600 Radioisotopic activities for Lake Marian core 31_III_2018_MAR_328 are shown in Fig. S5, and
601 dates are shown in Table S5. In Lake Marian, as in Lake Kissimmee, diatoms showed highly
602 productive conditions throughout the entire 1.5-m profile, with no evidence of salt-tolerant
603 diatoms that would suggest water-level fluctuations (Fig. 9). The eutrophic, planktonic diatom

604 *Aulacoseira ambigua* represented 50-60% of diatoms in the assemblages from 150-100-cm depth
605 in the core. *A. ambigua* progressively declined above the 100-cm level (c. 1898) to 10% of the
606 assemblage at the top of the core, while *Pseudostaurosira brevistriata*, *Staurosira construens*
607 and *Staurosirella berolinensis* increased and represented 10-20% of the assemblage at the core
608 top. This shift is consistent with increased competitive exclusion of planktonic diatom taxa by
609 cyanobacteria (Whitmore et al. 2018). Diatom samples in the core had 7-9 analogs in the
610 calibration set before c. 1837, and 12-15 analogs at all depths higher than that in the core (Table
611 S5).

612 Florida DEP provided a mean of measured limnetic total P for 2000-2006 of 155 $\mu\text{g/L}$,
613 and our diatom-inferred value for that period was 82.1 $\mu\text{g/L}$, which substantially underestimated
614 the reported value. The modern measured value is beyond the reliable range of our total P
615 inference model, and we suspect at least intermittent nitrogen limitation in Lake Marian. As a
616 result, we rejected use of the limnetic total P inference model for Lake Marian. Instead, we
617 applied the weighted-averaging model that is used to infer chlorophyll *a* from diatom
618 assemblages in sediments. Florida DEP reported a measured mean chlorophyll *a* value of 54.5
619 $\mu\text{g/L}$ for 2000-2006, and our inferred value was 53.6 $\mu\text{g/L}$ for that period, which indicated
620 reliable performance. Limnetic chlorophyll *a* inferences for Lake Marian are shown in Fig. 9 and
621 Table S5. Inferred limnetic chlorophyll *a* at the base of the core, which was deposited well
622 before c. 1837, was 28.3 $\mu\text{g/L}$. Limnetic chlorophyll *a*, therefore, increased significantly in Lake
623 Marian from the early 1800s to the present time.

624 Chlorophyll derivatives and total carotenoid concentrations were less than 1.0 abs/g
625 organic matter c. 1837 (Fig. 9). Chlorophyll derivatives increased progressively after c. 1898 to ~
626 5 abs/g organic matter at the top of the core. Total carotenoids increased rapidly after c. 1960-
627 1973 to ~ 2 abs/g organic matter at the top of the core (Fig. 9). Myxoxanthophyll and

628 oscillaxanthin cyanobacterial pigment concentrations showed considerable variation over time,
629 but prior to c. 1837, they were nearly as high as during recent decades. Myxoxanthopyll
630 increased rapidly after c. 1999.

631 As in Lake Kissimmee, stable isotopes and C/N ratios of organic matter in sediments
632 showed that algae and cyanobacteria, and possibly some floating-leaved macrophytes, were the
633 primary sources of sediment organic matter from prior to 1837 up to the present time (Fig. 8).
634 Macrofossil remains were very sparse, with no indication of submerged aquatic vegetation, and
635 only a few sclereids of nymphaeids were found in one core in deposits that dated to the early
636 1900s (Table S17). Pollen grains of *Taxodium* (~13-17% of assemblages) as well as *Morella*
637 (bayberry) were abundant in samples prior to 1837 (Table S11), which indicated that swamps
638 were well established in the vicinity of Lake Marian. Pollen and macrofossil evidence, therefore,
639 supported an interpretation of waters that were high in algae/cyanobacteria concentrations, as
640 well as possible high color from dissolved organic carbon from associated swamps.

641

642 **Discussion**

643 ***Pre-disturbance water quality and eutrophication***

644 Eutrophication occurred in all of the study lakes to varying degrees. This was evidenced
645 by increased deposition rates of phosphorus and nitrogen, by increased sedimented
646 pigment concentrations of algae and cyanobacteria, and by diatom autecology and
647 statistical inferences of water quality. $\delta^{13}\text{C}$ versus C/N plots and plant macrofossils in
648 Lakes Cypress, East Tohopeliga, Jackson, and Tohopekaliga showed a shift from
649 submerged plant communities to floating-leaved taxa, then to algae/cyanobacteria, a
650 progression that is typical of light limitation caused by eutrophication (Sayer et al.

651 2010a, b, Bennion et al. 2018). Multiple lines of evidence showed that all lakes in this
652 study were meso-eutrophic to eutrophic during pre-disturbance times. None of the lakes
653 in this study held oligotrophic waters during their reference periods in the early 1800s.
654 Qualitative diatom evidence based on well-documented autecological preferences in the
655 literature, as well as the limnetic total P optima reported for dominant taxa (Whitmore et
656 al. 2018), showed that Lakes Cypress, East Tohopekaliga, Jackson, and Tohopekaliga
657 had high productivity during their pre-disturbance periods in the early 1800s. Pre-
658 disturbance inferences for limnetic total P in Lake Kissimmee (61 $\mu\text{g/L}$) and for limnetic
659 chlorophyll *a* in Lake Marian (28.3 $\mu\text{g/L}$) were within the eutrophic range for lakes.

660 High productivity in these lakes during their pre-disturbance periods is consistent with
661 their geological setting. Paleolimnological studies have shown that a significant number of
662 Florida lakes, particularly alkaline lakes with color, were productive during pre-disturbance
663 periods because of naturally high edaphic nutrient supply (e.g., Brenner et al. 1993, Riedinger-
664 Whitmore et al. 2005, Kenney et al. 2014). For such lakes, nutrient criteria standards less than
665 40-45 $\mu\text{g/L}$ total P would not be appropriate. Naturally high productivity in lakes on the
666 Kissimmee Chain suggests that relatively small amounts of nutrient additions could occur before
667 modern nutrient-criteria standards would be exceeded. Paleolimnological studies have
668 demonstrated naturally high productivity and sustained cyanobacterial populations in other
669 regions as well (McGowan et al. 1999, Brooks et al. 2001, Simmatis et al. 2020).

670 In Lakes Cypress, East Tohopekaliga, Tohopekaliga, and Marian, diatom communities
671 changed in response to increased cyanobacteria presence. Tycho planktonic taxa increased as
672 cyanobacteria became well established and planktonic taxa, including *Aulacoseira* spp., were
673 subject to competitive exclusion (Whitmore et al. 2018). Although this shift might seem

674 paradoxical in hypereutrophic conditions because of potential light limitation of algae that grow
675 on surfaces, frequent mixing in Florida's shallow, wind-stressed lakes affords tychoplanktonic
676 taxa the opportunity to meet minimum light requirements. Recognition of this community shift
677 might serve as an early warning indicator of pending system changes in modern Florida lakes,
678 and it might be used to better inform decisions about lake management (Reavie 2019). This
679 diatom community change was not evident in Lake Jackson, however, and sedimented pigments
680 showed that cyanobacteria increased in that lake only recently. Lakes Kissimmee and Marian
681 sustained substantial cyanobacteria populations throughout their entire records since the early
682 1800s.

683

684 *Associated wetlands and their possible influence on lake color*

685 Carpenter et al. (1998) showed strong effects of dissolved organic color on chlorophyll
686 concentrations and primary production in lakes because of light attenuation in the water column.
687 Persistent and highly colored humic and fulvic acids that contribute to colored dissolved organic
688 carbon (C-DOC) in lakes often have allochthonous sources from nearby wetlands, although pine
689 flatwoods in Florida often contribute C-DOC because shallow, impervious clay layers direct
690 tannins laterally to nearby waterbodies. In contrast, autochthonous DOC from the breakdown of
691 phytoplankton and macrophyte biomass is less highly colored and is easily degraded. Because of
692 its potential for moderating primary production, Williamson et al. (1999) maintained that there is
693 a clear need to incorporate C-DOC into lake-management approaches. However, C-DOC is not
694 equally effective in controlling algal production in lakes across a wide range of trophic state.
695 Carpenter et al. (1998) stated that eutrophication is responsible for a broad range of P inputs to
696 lakes, and this strong environmental gradient tends to mask the effects of C-DOC in multi-lake

697 comparisons. Karlsson et al. (2009) concluded that light availability, as influenced by C-DOC,
698 controls productivity most effectively in low-productivity lakes, whereas nutrient availability
699 controls productivity in lakes that are eutrophic and dominated by pelagic production. Based on
700 these studies, it seems appropriate to conclude that the potential moderating effect of C-DOC on
701 primary productivity is likely to be more effective during periods of low disturbance than it is
702 when lakes have undergone advanced eutrophication. This suggests the importance of protecting
703 associated wetlands for lakes that have not been subject to high nutrient loading, and for
704 implementing wetland restoration after high nutrient concentrations have been reduced.

705 At the beginning of the 1800s, wetlands covered nearly 50% of the surface area of
706 Florida (Fernald and Purdum 1998). Subsequent logging and alteration of lake levels caused
707 substantial loss of wetlands associated with Florida's 8000 lakes. When the present study was
708 initiated, Osceola County Public Works conducted a statistical evaluation of water-quality
709 measures for a large set of lakes to determine whether C-DOC has a moderating influence on
710 phytoplankton concentrations in this region. Limnetic concentrations of total nitrogen, total
711 phosphorus, and chlorophyll *a* were compared for two categories: lakes with low color
712 concentrations (i.e., < 75 platinum cobalt units; PCU) and lakes with high color concentration (>
713 75 PCU). Results showed that nutrient concentrations were likely to be higher under high-color
714 conditions, but concentrations of chlorophyll *a* were likely to be lower under high-color
715 conditions. Osceola County and Florida DEP concluded that C-DOC has the potential to alter
716 relationships between watershed loadings and in-lake concentrations of chlorophyll *a* in
717 Kissimmee Basin lakes.

718 Lakes Kissimmee and Marian showed high pollen concentrations of *Taxodium* (cypress)
719 *Nyssa* (water tupelo), *Salix* (willow), and *Morella* in bottommost core samples, which indicated
720 clear association of swamps with the lakes. Macrofossil evidence was scarce, except for floating-

721 leaved nymphaeids that can grow in waters with high color or turbidity. There was little evidence
722 for submerged aquatic plant communities. Our conclusion is that during pre-disturbance times in
723 Lakes Kissimmee and Marian, waters were high in C-DOC that probably moderated algal
724 productivity.

725 In contrast, pollen in reference samples from Lakes East Tohopekaliga and Tohopekaliga
726 showed relatively little evidence of swamp taxa, and macrofossils showed substantial amounts of
727 *Chara* and *Ruppia* that indicated clear waters (Dressler et al. 1987, Bennion et al. 2018). This
728 also was the case with Lakes Cypress and Jackson, but they lacked *Ruppia* in early deposits.
729 Because historical drainage reports indicated that some swamps were present near Cypress, East
730 Tohopekaliga, and Tohopekaliga (Atlantic and Gulf Coast Canal and Okeechobee Land
731 Company 1885), it might be appropriate to consider restoration efforts to support associated
732 wetlands near those lakes. We concluded from pollen evidence, however, that Lake Jackson had
733 fairly clear waters and apparently lacked associated swamps that might have contributed
734 significant amounts of C-DOC.

735 Regarding the question about whether restoring more natural water levels and
736 colored dissolved organic carbon concentrations might mitigate algal productivity and
737 alter restoration strategies in lakes on the Kissimmee Chain, we recommend that this
738 approach should first be implemented for Lakes Kissimmee and Marian, because
739 paleolimnological evidence showed greater original wetland presence for those lakes.

740

741 ***Historical changes in lake water levels***

742 Modern water levels in lakes of the Kissimmee Chain are substantially lower than they were
743 prior to engineered drainage activities that began in the 1880s. Decreases in water levels during

744 the 19th and 20th centuries contributed to management challenges, such as a greater potential for
745 internal nutrient loading from sediment resuspension over a larger portion of the lake areas (e.g.,
746 Nagid et al. 2001), a reduced volume of water that would make the lakes more susceptible to
747 eutrophication for a given increase in nutrient loading, and a potential loss of allochthonous C-
748 DOC from associated wetlands that might have helped to moderate algal production by light
749 limitation.

750 A potentially greater disturbance resulted from reducing the large natural variations in
751 water levels that prevailed prior to engineered changes. It was speculated that water levels in
752 Kissimmee Chain lakes fluctuated during pre-disturbance times up to 3 m (Army Corps of
753 Engineers 1996), and that was confirmed by the present study. Salinity preferences of diatoms,
754 microfossils, and ostracods showed that these fluctuations greatly exceeded seasonal water-level
755 variations, and that they occasionally led to total drying in portions of the lakes. Large water-
756 level fluctuations would have increased habitat diversity and helped to maintain the integrity of
757 the lake ecosystems, and natural fires during low water levels would have burned organic matter
758 in exposed littoral areas (Army Corps of Engineers 1996). Early natural fires were evident from
759 charcoal that appeared periodically in diatom samples of the present study, although charcoal
760 was not analyzed in detail. Multiple indicators in all sediment cores showed that Lakes Cypress,
761 East Tohopekaliga, Jackson, and Tohopekaliga changed significantly after the 1880s because
762 they failed to undergo very low water-level events that concentrated solutes on a periodic basis.
763 Modern water levels are held relatively constant (within 0.6-0.9 m) by South Florida Water
764 Management District (Osceola County Community Development Department 2015). This has
765 promoted organic-matter accumulation, and favored proliferation of certain nuisance plants such
766 as *Hydrilla* over native plants that depend on seasonal water-level variations for propagation.

767 Results of the present study show that the cessation of natural water-level fluctuations had
768 greater impact on lake processes, water quality, and community compositions than generally has
769 been recognized. Changes in water-level fluctuations were shown to affect the structure and
770 function of shallow lakes in other paleolimnological studies as well (e.g., Levi et al. 2016).

771 The most prominent diatom indicator of high-solute conditions during extreme low
772 water-level events in Lakes Cypress, East Tohopekaliga, Jackson, and Tohopekaliga was
773 *Campylodiscus clypeus*. Pouličková and Jahn (2007) described this species as widespread mostly
774 in hypersaline waters, but at specific conductance values beginning as low as 2000-3000 $\mu\text{S}/\text{cm}$,
775 and where dominant anions tend to be carbonate or sulphate rather than chloride. Carvalho et al.
776 (1995) reported that *Campylodiscus clypeus* occurred most often in hypersaline sites with
777 *Anomoeoneis sphaerophora* var. *costata*. In the present study we observed *Anomoeoneis*
778 *sphaerophora* var. *costata* as well as two of its salt-tolerant varieties.

779 *Ruppia maritima* seeds were abundant in cores from Lakes Tohopekaliga and East
780 Tohopekaliga prior to 1880. Although *Ruppia* is often described as an estuarine plant in areas of
781 lower salinity, it is actually a freshwater plant that has pronounced salinity tolerance, and it
782 occurs in clear waters <2.0 m deep (Zieman 1982, Kantrud 1991). We have collected *Ruppia*, for
783 example, in the littoral zone of a freshwater Florida lake that has a specific conductance of about
784 1500 $\mu\text{S}/\text{cm}$. *Ruppia* seeds are ingested by waterfowl and can be transported 280 km
785 (Charalambidou et al. 2003), so it could have been distributed from coastal areas to these lakes
786 during low water-level stands. Its presence in the sediment record of inland lakes provides clear
787 indication of former elevated concentrations of dissolved solutes.

788 Ostracods provided additional evidence of elevated dissolved solute concentrations at the
789 base of several Lake Tohopekaliga cores. *Darwinula stevensoni*, *Limnocythere inopinata*, and

790 *Cypridopsis vidua* occur in fresh to oligohaline waters (Keyser 1977, Holmes 1992, Ruiz 2013).
791 *Cypridopsis okeechobei* has an optimum range of 0.3-0.5 ppt salinity (Keyser 1977, Holmes
792 1992). *Cypretta brevisaepta* is an oligohaline indicator that occurs below 0.5 ppt, but it has an
793 optimum range of 0.5-1 ppt (Keyser 1977). *Limnocythere inopinata* and *Cypridopsis vidua* prefer
794 organic substrates with vegetative cover and are often associated with *Chara* (Matsuda et al.
795 2015), as they were in core samples prior to c. 1890. Ostracods were absent in Lake
796 Tohopekaliga after c. 1890, which signaled the disappearance of naturally low water levels. It
797 appears evident that the hydrological alterations that began in 1883 prevented extremely low
798 water levels after that time.

799 Many shallow Florida lakes are subject to very large fluctuations in water level, in part
800 because of elution, or downward leakage in karst bedrock (Deevey 1988), which contributes to
801 falling levels during drier periods. Natural fluctuations up to 3.5 m have been demonstrated in
802 multi-year studies of Florida lakes (Hoyer et al. 2005), and up to 10 m in lakes that are astatic
803 (Deevey 1988). Large water-level fluctuations are not caused so much by precipitation in a given
804 year, but by cumulative inter-annual precipitation patterns that affect groundwater levels on the
805 order of decades (Deevey 1988).

806 Because most Florida lakes are shallow (< 5m), water-level fluctuations can greatly affect
807 lake area and volume. We calculated the percent volume curve for modern Lake Tohopekaliga
808 using contour areas and depths indicated in a contemporary morphometric map
809 (<http://plants.ifas.ufl.edu/manage/overview-of-florida-waters/public-waters/bathymetric-maps/>).
810 A drop of 2 m in current water level would reduce the lake to 23% of its volume, and would
811 expose ~ 37% of the lake area to drying. A drop of 3 m in Tohopekaliga would reduce the
812 current volume to 4%, and would expose 70% of the lake bed to drying, which could easily

813 increase total dissolved solids sufficiently to support salt-tolerant taxa. Although downward
814 elution likely would have removed some solutes as well as water during drier periods (Deevey
815 1988), the lakes in this study achieved impressively high salinities as indicated by diverse
816 biological indicators, so evaporation had to exceed leakage by a substantial amount.

817 Lakes Kissimmee and Marian did not show evidence of extreme water-level fluctuations
818 like the other lakes, and they demonstrated the clearest evidence of associated wetlands. We note
819 that pre-disturbance water levels in East Tohopekaliga (70.3 ft, 21.4 m) and Tohopekaliga (64.6
820 ft., 19.7 m) stood at higher elevations than in Kissimmee (59.1 ft, 18.0 m) (surveyed prior to the
821 NGVD elevation standard: Atlantic and Gulf Coast Canal and Okeechobee Land Company
822 1885). Although the pre-disturbance water-level of Lake Cypress was not reported, it would have
823 been between 60 and 64 ft (18.3-19.5 m). It appears that local hydrological factors made
824 Kissimmee and Marian less subject to drying than East Tohopekaliga, Tohopekaliga, and
825 Cypress, which stood at higher elevations. Lake Jackson is situated between Kissimmee and
826 Marian, but it showed evidence of high solutes and dry periods that Kissimmee and Marian did
827 not. Jackson has been bordered by dry prairies historically, so it has a different edaphic setting.
828 Jackson and Cypress are the smallest and volumetrically shallowest lakes in this study: a 2-m
829 water-level drop would currently reduce both lakes to <1 % of their volume, and a 3-m drop
830 would cause the lakes to go dry.

831

832 **Conclusions**

833

834 Two major types of changes occurred in these lakes during the late 19th and 20th centuries. All
835 lakes in this study were meso-eutrophic prior to the mid 1800s, but eutrophication was observed

836 in five of the six lakes, as shown by multiple lines of evidence. East Lake Tohopekaliga showed
837 the least evidence of nutrient changes, and eutrophication was most pronounced in Lake Marian.
838 Onset of eutrophication began in the late 1800s immediately after engineered hydrological
839 changes, and it increased distinctly during the 20th century because of nutrient loading that likely
840 arose from urbanization, land-use change, agriculture, and cattle ranching. Engineered
841 connection of the lakes facilitated a downstream cascade of nutrients, and the loss of former
842 connecting wetlands reduced the biological filtering of nutrients that occurred prior to
843 disturbance.

844 The second and possibly more prominent change in four of the six lakes was that
845 hydrology was altered dramatically, both by lowering water levels with respect to former
846 associated wetlands, and importantly, by permanently preventing the lakes from undergoing
847 natural large fluctuations in water levels. This was evident in Lakes Cypress, East Tohopekaliga,
848 Jackson, and Tohopekaliga, but was not the case in Lakes Kissimmee and Marian. Large natural
849 fluctuations shaped the types of native plant communities that were present, whereas more static
850 water levels in recent times have contributed to organic matter accumulation and high standing
851 crops of aquatic plants. Although lake levels have been lowered occasionally in recent decades
852 so littoral sediments can be scraped and burned, this is mechanically doing the work that natural
853 processes did before engineered activities prevented large natural fluctuations in water levels.

854 Current management approaches often emphasize in-lake nutrient concentrations and
855 mitigation without adequately considering other significant changes in ecology or ecosystem
856 function, but restoration can not be effective when it regards system changes as univariate
857 (Davidson et al. 2018). Contemporary challenges for management of these lakes include
858 satisfying stakeholder needs related to the sport-fishing economy, recreational uses, water
859 supply, and flood prevention. The lakes, however, are distinctly out of balance with respect to

860 nutrient content and recycling, standing crops of native and invasive plants, and the
861 accumulation of nutrient-rich organic sediments. Considerable energy and costs are required for
862 periodic drawdowns, scraping of sediments, and management of aquatic plants. The sustained
863 connection of the lakes, which originated as a 19th-century paradigm, also facilitates transport of
864 nutrients through the Kissimmee-Okeechobee-Everglades system, and it contributes to
865 downstream restoration challenges.

866 Based on the findings of this study, we recommend disconnecting the lakes from each
867 other and from the Kissimmee River to reestablish large, natural fluctuations in water levels that
868 were part of healthy ecosystem function. Some structures might need to be retained but modified
869 to prevent flooding in developed areas. The current downstream nutrient cascade challenges
870 local management agencies to deal with nutrient loads that partly arise outside of their
871 jurisdictions. Hydrological restoration would return nutrient loading to more local issues. Former
872 wetlands between the lakes should be restored because this would reestablish biological
873 communities that sequester nutrients that currently enter the lakes and river system, and that
874 subsequently reach Lake Okeechobee, the Everglades, and offshore coral reef systems.

875 The focus of the 19th and early 20th centuries was on engineering changes in
876 natural systems for perceived human benefit, but that led to many unanticipated
877 problems in lakes on the Kissimmee Chain. We advocate for a management paradigm in
878 the 21st century that places greater emphasis on sustainability, reduced energy
879 expenditure, and restoring the benefits that were provided by natural ecosystem
880 functions.

881

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890
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1162 **Figure legends**

1163 Figure 1. Location of the six study lakes in the Upper Kissimmee Basin. Modified from
1164 a map prepared by Kissimmee Division, Ecosystem Restoration Department, South
1165 Florida Water Management District. May 2005. \\ha1-
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1167
1168 Figure 2. Diatom profile with CONISS zonation for core 29_XII_2017_CYP_3 from Lake
1169 Cypress. Lower panels show sedimented algal and cyanobacterial pigment profiles from Lake
1170 Cypress core 18_XI_2016_CYP_40.

1171
1172 Figure 3. Plots of $\delta^{13}\text{C}$ versus C/N ratios in sedimented organic matter for cores from Lakes
1173 Cypress, East Tohopekaliga, Jackson, and Tohopekaliga, the four lakes that showed prominent
1174 changes in primary producer communities over time. Specific taxa are placed in relative
1175 positions based on $\delta^{13}\text{C}$ and C/N values reported for studies of other Florida lakes, and are used
1176 here to provide general indication of trends in community change.

1177
1178 Figure 4. Diatom profile with CONISS zonation for core 9_VIII_2017_ETOH_244 from East
1179 Lake Tohopekaliga. Lower panels show sedimented algal and cyanobacterial pigment profiles.

1180
1181 Figure 5. Diatom profile with CONISS zonation for core 16_III_2018_JAC_307 from Lake
1182 Jackson. Lower panels show sedimented algal and cyanobacterial pigment profiles. CONISS was
1183 not performed because of the broad gaps in diatom presence.

1184

1185 Figure 6. Diatom profile with CONISS zonation for core 19_I_2017_TOH_202 from Lake
1186 Tohopekaliga. Lower panels show sedimented algal and cyanobacterial pigment profiles.

1187

1188 Figure 7. Diatom profile with CONISS zonation for core 27_XII_2017_KIS_2 from Lake
1189 Kissimmee. Lower panels show sedimented algal and cyanobacterial pigment profiles. Lower
1190 right panel presents diatom-based limnetic total P inferences.

1191

1192 Figure 8. Plots of $\delta^{13}\text{C}$ versus C/N ratios in sedimented organic matter for cores from Lakes
1193 Kissimmee and Marian from the early 1800s until 2017. Both lakes lacked macrofossil evidence
1194 and were consistently dominated by algae and cyanobacteria over time. Specific taxa are placed
1195 in relative positions based on $\delta^{13}\text{C}$ and C/N values reported for studies of other Florida lakes, and
1196 are used here to provide general indication of trends in community change.

1197

1198 Figure 9. Diatom profile with CONISS zonation for core 31_III_2018_MAR_328 from
1199 Lake Marian. Lower panels show sedimented algal and cyanobacterial pigment profiles.
1200 Lower right panel presents diatom-based limnetic chlorophyll *a* inferences.